

UNIVERSITE DE LILLE 1 – SCIENCES ET TECHNOLOGIES

Ecole doctorale 104

Sciences de la Matière, du Rayonnement et de l'Environnement

Dossier de candidature à l'habilitation à diriger des recherches

# Evolutionary ecology of fluxes

**François Massol**

Soutenu le 27 Mai 2015

## JURY

Dries BONTE	Associate Professor, University of Ghent, Belgium	Rapporteur
Joël CUGUEN	Professeur, Université Lille 1	Examineur
Annick LESNE	Directrice de Recherche CNRS, Paris	Examinatrice
Hélène MORLON	Chargée de Recherche CNRS, Paris	Rapporteur
Nathalie NIQUIL	Directrice de Recherche CNRS, Caen	Rapporteur
Jean-Christophe POGGIALE	Professeur, Université Aix-Marseille	Examineur



A life spent making mistakes is not only more honourable, but more useful than a life spent doing nothing.

George Bernard Shaw





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## PREFACE

Before starting to inspire readers with serious boredom or frenetic enthusiasm, I think I owe them some explanations. The present document is an attempt at synthesising my academic life and work so far, at a moment when I am applying for the highest diploma in the French system, *i.e.* the “habilitation à diriger des recherches” (HDR for connoisseurs). Seven years ago, I defended my PhD in Montpellier, already knowing that, if I were to continue upon the academic path, I would have to “do it again” one day in order to convert the try. And now it’s time.

Although this document does not weigh as much as a PhD thesis (at least mine), there are some important hurdles to cross to complete it, which have few things in common with the ones posed by completing a PhD dissertation. First, and this is really crucial, HDR means solitude; contrary to PhD students, who do form some kinds of cohorts by the year they began their PhD in, HDR candidates are on their own – well, at least to write the first draft. There is no real fixed calendar stating “this is the season when candidates will defend their HDR”. Thus, emulation is absent from the HDR candidate’s mind and this can be both a boon and a curse.

Second, because there is no “life-or-death” imperative to actually write one’s HDR “on time” (*i.e.* it is always possible to procrastinate and obtain delays), the HDR candidate needs to personally settle the issue of internal discipline. In my case, I decided to apply in September 2014, well knowing that I could not start writing before February 2015 and with the aim of defending before the end of June 2015. Thus, my time window was slightly ajar, but not that much. I could make it, provided I slowed down on everything else I would be doing in March 2015.

Third, having an already replete schedule means the writing period will not be devoid of other academic chores, however fiercely one tries to avoid them. Declining to review papers and proposals is a good first move, but it’s never sufficient. This means that writing is interspersed with many other fancy activities. My strategy was to maintain a flurry of text files with strange quick notes as to what I should not forget to write about.

Fourth, because a researcher’s achievements are more numerous at the time of their HDR than at the time of their PhD defence, the temptation is great to transform this document into some kind of legacy, a jewel that would perfectly represent the essence of one’s scientific goals. This looks insane. Given time and energy, this would probably turn me into some kind of Gollum-like creature, never ready to release his “precious” to the jury. A good way to deal with this from the very start is, in my opinion, to allow oneself very little time to actually complete the deed. This is what I did – I don’t know whether this was a good move yet...

Before I finish this initial rambling, I’d add a word on the subject of this document, *i.e.* the evolutionary ecology of fluxes. As I have worked on quite distinct subjects over the years, I have encountered the same issue that I already met at the end of my PhD when I needed to find a common theme on studies that never dealt twice with the same model or study system. The problem has not really worsened because I have become a repeated offender on certain questions, such as the evolution of dispersal or spatial food web models. However, there might have been other ways to connect most of these studies together and still make it appear as a whole. In the end, I think fluxes and dispersal are quite the leading theme linking what I am doing most of the time, not only in my academic life, but also in life generally. From my master internship to my current situation, I have been in five different labs, occupied eight different offices and made quite a lot of trips between all these labs. Being able to drive from Montpellier and Aix-en-Provence blindfolded probably does not qualify me as being a migratory mammal, nor does the fact that I switched labs twice in two years between 2012 and 2013 make me a specialist of dispersal. The irony of life made it so that I study fluxes while moving between labs. I owe it to the ones that have stood ground in the face of my incessant flitting around to write it on fluxes.



## CURRICULUM VITÆ

### In real life

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Born September 17<sup>th</sup>, 1979

Civil union (PACS)

Two children, one cat and likely many other minute life forms around

### On the web

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francois.massol@m4x.org

<https://sites.google.com/a/polytechnique.org/francoismassol/home>

[https://www.researchgate.net/profile/Francois\\_Massol](https://www.researchgate.net/profile/Francois_Massol)

### Recent professional positions

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2002 – 2008	Ingénieur des Ponts, Eaux et Forêts (IPEF) at l'Ecole Nationale du Génie Rural, des Eaux et des Forêts (ENGREF)
2002 – 2003	Paris / Dijon / Montpellier / Nancy
2003 – 2004	Montpellier / Thonon-les-Bains / Inari (Finland)
2004 – 2008	Montpellier
2008 – 2012	IPEF at l'Institut national de Recherche en Sciences et Technologies pour l'Environnement et l'Agriculture (IRSTEA)
2008 – 2009	Aix-en-Provence
2009 – 2010	Austin, TX (USA) – post-doctoral stay at M. Leibold's lab
2010 – 2012	Aix-en-Provence
2012 –	Chargé de Recherche at the Centre National de la Recherche Scientifique (CNRS)
2012 – 2014	Montpellier
2013 –	Lille

### Education

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1997 – 1999	Preparatory classes MPSI / MP* to nationwide competitive exams, Paris
1999 – 2002	Engineer-student at Ecole Polytechnique, Palaiseau. MSc in 2003
2002 – 2004	Engineer-student at ENGREF, Paris. MSc in 2004
2003 – 2004	MSc in Evolutionary Biology & Ecology at the University of Montpellier 2
2004 – 2008	PhD in Population Biology & Ecology at the University of Montpellier 2

### Grants & awards

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#### As principal investigator (PI)

2009 – 2011	Post-doctoral fellowship (EU Marie Curie programme) on “dispersal effects on food web functioning: theory and experimental research based on freshwater plankton systems” [DEFTER] (going to M. Leibold's laboratory in Austin, TX)
2010 – 2012	Working group at the National Institute for Mathematical and Biological Synthesis (NIMBioS) on “food web dynamics and stoichiometric constraints in metaecosystems” (PIs: C. Klausmeier, M. Leibold, F. Massol & R. Sterner)
2013 – 2014	Working group funded by the Réseau National Systèmes Complexes (RNSC) on “interdisciplinary methods for the study of seed exchange networks” [MIREs] (PIs: P. Barbillon, S. Caillon & F. Massol)
2013 – 2014	Working group funded by the RNSC on “biodiversity dynamics in spatial ecological networks” [DyBRES] (PIs: S. Manel, F. Massol & F. Munoz)
2014 – 2017	Working group at the Centre de Synthèse et d'Analyse de la Biodiversité (CESAB) on “Predicting community resilience to invasions from diversity and network structure” [COREIDS] (PIs: P. David & F. Massol)

2014	Bilateral cooperation (funded by the University of Lille 1) with the University of Exeter on “selection regimes, dispersal and local adaptation” [RESEDA] (PIs: F. Débarre & F. Massol)
2014 – 2019	Project funded by the Agence Nationale de la Recherche (ANR) on “adaptation and resilience of spatial ecological networks to human-induced changes” [ARSENIC] (PIs: N. Loeuille & F. Massol)
2015	Working group funded by the Institut National de la Recherche Agronomique (INRA) applied mathematics and informatics department on “interdisciplinary methods for the study of seed exchange networks” [MIREs] (PIs: P. Barbillon, S. Caillon, F. Massol, M. Thomas & N. Verzelen)

### Others

2011 – 2014	Working group at the CESAB on “seed exchange networks” [NETSEED] (PI: D. McKey)
2012 – 2016	Project funded by the ANR BIOADAPT programme on “adaptation of fragmented freshwater assemblages in rapidly-changing environments” [AFFAIRS] (PI: P. David)
2015 – 2019	Project funded by the Région Nord Pas-de-Calais / FRB programme on “adaptation, regression and expansion at species range margins” [AREOLAIRE] (PI: A. Duputié)
2015	Project funded by the CNRS interdisciplinary mission MoMIS programme on “modelling and analysis of the dynamics of seed exchange networks” [MADRES] (PI: S. Martin)

## Advising & student supervision

Bachelor level	Involvement
▪ M. Dubart (2014; supervision: F. Massol)	100%
▪ T. L'Honoré (2014; supervision: F. Massol)	100%
<b>Master 1 level</b>	
▪ T. Perrot (2013; supervision: F. Massol et F. Laroche)	50%
▪ R. Cuveliez (2014; supervision: F. Massol)	100%
▪ J. Denton (2014; supervision: F. Débarre & F. Massol)	40%
▪ M. Dubart (2015; supervision: F. Massol)	100%
<b>Master 2 level</b>	
▪ E. Canard (2008; supervision: P. David & P. Jarne)	10%
▪ F. Laroche (2010 – 2011; supervision: P. Jarne & F. Massol)	50%
▪ F. Laso (2012 – 2013; supervision: D. McKey & F. Massol)	80%
▪ T. Koffel (2014; supervision: T. Daufresne, C. Klausmeier & F. Massol)	30%
<b>PhD level</b>	
▪ C. Dehais (2007 – abandon; supervision: C. Argillier & D. Pont)	10%
▪ F. Laroche (2011 – 2014; supervision: P. Jarne & F. Massol)	50%
<b>Post-doctoral fellows</b>	
▪ D. Schleuter (2008 – 2010; hired by C. Argillier [ANR funding])	
▪ M. Pautasso (2011 – 2013; hired as part of the CESAB NETSEED working group)	
▪ J. Astegiano (2012 – 2013; FAPESP fellow between São Paulo & Montpellier)	
▪ M. Thomas (2013 – 2014; hired as part of the CESAB NETSEED working group)	
▪ G. Mollot (2014 – 2017; hired as part of the CESAB COREIDS working group)	
▪ J. Pantel (2015 – 2016; hired by P. David [ANR funding])	

### Thesis committees

- J. Radoszycki (INRA, Toulouse)
- M. Jacquot (Cirad, La Réunion)
- A. Sagouis (IRSTEA, Aix-en-Provence)
- N. Joffard (CNRS, Montpellier)

### Teaching

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2005	Introduction to applied ecological modelling (ENGREF, 60h)
2013	Introduction to metacommunity theory (ETH/Uni. Zürich winter school, Ascona, CH)
2013	Dynamical systems & networks in ecology (M2R, Université Lille 1, 3h)
2013 –	Evolution of dispersal (M2R, Université Lille 1, 2h)
2014	Evolutionary dynamics (invited courses at the South American Institute for Fundamental Research summer school, São Paulo, Brazil, 4h + advice)
2014	Introduction to MATHEMATICA for adaptive dynamics (open course, 6h)
2014 –	Ecological modelling (M2R, Université Lille 1, 6h)

### Juries

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#### Examiner at PhD juries

- E. Georgelin (10/2014; supervision: N. Loeuille; Paris UPMC)
- G. Huth (11/2014; supervision: F. Munoz & E. Pitard; Montpellier)

#### Referee at HDR juries

- V. Ravigné (04/2015; Montpellier)

### Other scientific activities

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#### Editing papers

*Oikos* (2014 –)

#### Reviewing papers

*Acta Oecologica, Advances in Ecological Research, American Naturalist, Ecography, Ecological Modelling, Ecology, Ecology Letters, Ecosphere, Evolution, Functional Ecology, Integrative and Comparative Biology, Journal of Evolutionary Biology, Journal of Theoretical Biology, Journal of Vegetation Science, Oecologia, Oikos, PLoS ONE, Proc. Royal Society Series B, Theoretical Population Biology*

Also reviewing for *Axios Review*

#### Reviewing proposals

*Israel Science Foundation* (2011)  
*Agence Nationale pour la Recherche* (2013)  
*Austrian Science Fund – FWF* (2013)

#### Learned society affiliations

*American Society of Naturalists, British Ecological Society, Ecological Society of America, European Society for Evolutionary Biology, European Society for Mathematical and Theoretical Biology, Société Française d'Ecologie, Society for the Study of Evolution*

## Scientific animation & responsibilities

2005 – 2007	Delegate of temporary personnel at the Centre d'Ecologie Fonctionnelle et Evolutive (CEFE)'s council
2007	Organisation of the first CEFE's "student day" (presentations by students for students)
2007 – 2008	Coordination of the journal club "evolutionary ecology" at the CEFE
2008 – 2009	Organisation of a weekly seminar (IRSTEA, Aix-en-Provence)
2011	Principal organiser of a special session at the annual meeting of the Ecological Society of America (ESA): <i>Trait Evolution and the Dynamics of Food Webs</i>
2012	Board member of the CNRS pluridisciplinary thematic network "mathematics & biodiversity"
2012	Co-organiser of the symposium "Web of Life" (Montpellier), in charge of the poster session
2013	Coordination of the journal club "networks" at the CEFE
2014	Co-organiser of a symposium at the annual meeting of the British Ecological Society (BES): <i>Eco-evolutionary feedbacks: theoretical and empirical perspectives</i>
2015 –	Member of the administrative board of the Société Française d'Ecologie (SFE)
2015	Member of the electoral committee for the election of the EEP laboratory council

## Bibliometry

**Citations:** 596 [Google scholar]; 374 [ISI]

**H index:** 13 [Google scholar]; 11 [ISI]

In 26 published papers + 1 book chapter:

87 different co-authors, among whom 39 international collaborators,

12 co-authors with whom I wrote more than one paper,

From 1 to 28 authors per paper (median: 4; average: 5.4)

Journal	Number	IF ISI 2013	First author	Last author
<i>Advances in Ecological Research</i>	2	6.250	1	
<i>Agronomy for Sustainable Development</i>	1	2.841		
<i>American Naturalist</i>	2	4.454		2
<i>Biogeosciences</i>	1	3.753		
<i>Biological Reviews</i>	1	9.790		
<i>Ecological Complexity</i>	1	2.000	1	
<i>Ecological Monographs</i>	1	7.107		
<i>Ecology Letters</i>	4	13.042	1	
<i>Evolution</i>	3	4.659	3	
<i>Interface Focus</i>	1	3.124		1
<i>Journal of Animal Ecology</i>	1	4.726	1	
<i>Journal of Evolutionary Biology</i>	1	3.483		
<i>Methods in Ecology and Evolution</i>	1	5.322		
<i>Nature</i>	1	42.351	1	
<i>Oikos</i>	1	3.559		
<i>PLoS ONE</i>	1	3.534		
<i>Proceedings of the Royal Society series B Biological Sciences</i>	1	5.292	1	
<i>Theoretical Population Biology</i>	1	1.531	1	

In the following, speakers are in CAPITALS and students are underlined.



### Articles published in peer-reviewed journals

- (1) **Massol, F.**, David, P., Gerdeaux, D., & Jarne, P. (2007) The influence of trophic status and large-scale climatic change on the structure of fish communities in Perialpine lakes. *Journal of Animal Ecology*, **76**, 538-551.
- (2) **Massol, F.** & Crochet, P.-A. (2008) Do animal personalities emerge? *Nature*, **451**, E8.
- (3) **Massol, F.**, Calcagno, V., & Massol, J. (2009) The metapopulation fitness criterion: proof and perspectives. *Theoretical Population Biology*, **75**, 183-200.
- (4) Duputié, A., **Massol, F.**, David, P., Haxaire, C. & McKey D. (2009) Traditional Amerindian cultivators combine directional and ideotypic selection for sustainable management of cassava genetic diversity. *Journal of Evolutionary Biology*, **22**, 1317-1325.
- (5) Cheptou, P.-O. & **Massol, F.** (2009) Pollination fluctuations drive evolutionary syndromes linking dispersal and mating system. *American Naturalist*, **174**, 46-55.
- (6) Lavoie, A.-V., Staudt, M., Schnitzler, J. P., Landais, D., **Massol, F.**, Rocheteau, A., Rodriguez, R., Zimmer, I., & Rambal, S. (2009) Drought reduced monoterpene emissions from the evergreen Mediterranean oak *Quercus ilex*: results from a throughfall displacement experiment. *Biogeosciences*, **6**, 1167-1180.
- (7) Schleuter, D., Daufresne, M., **Massol, F.**, & Argillier, C. (2010) A user's guide to functional diversity indices. *Ecological Monographs*, **80**, 469-484.
- (8) **Massol, F.**, Duputié, A., David, P., & Jarne, P. (2011) Asymmetric patch size distribution leads to disruptive selection on dispersal. *Evolution*, **65**, 490-500.
- (9) **Massol, F.** & Cheptou, P.-O. (2011) Evolutionary syndromes linking dispersal and mating system: the effect of autocorrelation in pollination conditions. *Evolution*, **65**, 591-598.
- (10) **Massol, F.** & Cheptou, P.-O. (2011) When should we expect the evolutionary association of self-fertilization and dispersal? *Evolution*, **65**, 1217-1220.
- (11) **Massol, F.**, Gravel, D., Mouquet, N., Cadotte, M. W., Fukami, T., & Leibold, M. A. (2011) Linking ecosystem and community dynamics through spatial ecology. *Ecology Letters*, **14**, 313-323.
- (12) Calcagno, V., **Massol, F.**, Mouquet, N., Jarne, P., & David, P. (2011) Constraints on food chain length arising from regional metacommunity dynamics. *Proceedings of the Royal Society Biological Sciences Series B*, **278**, 3042-3049.
- (13) Gravel, D., **Massol, F.**, Canard, E., Mouillot, D., & Mouquet, N. (2011) Trophic theory of island biogeography. *Ecology Letters*, **14**, 1010-1016.
- (14) Duputié, A., **Massol, F.**, Chuine, I., Kirkpatrick, M., & Ronce, O. (2012) How do genetic correlations affect species range shifts in a changing climate? *Ecology Letters*, **15**, 251-259.
- (15) Pautasso, M., Aistara, G., Barnaud, A., Caillon, S., Clouvel, P., Coffey, K., Coomes, O., Delêtre, M., Demeulenaere, E., De Santis, P., Doering, T., Eloy, L., Emperaire, L., Garine, E., Goldringer, I., Jarvis, D., Joly, H., Leclerc, C., Louafi, S., Martin, P., **Massol, F.**, McGuire, S., McKey, D., Padoch, C., Rerkasem, B., Soler, C., Thomas, M., & Tramontini, S. (2013) Seed exchange networks for agrobiodiversity conservation. A review. *Agronomy for Sustainable Development*, **33**, 151-175.
- (16) Mouquet, N., Gravel, D., **Massol, F.**, & Calcagno, V. (2013) Extending the concept of keystone species to communities and ecosystems. *Ecology Letters*, **16**, 1-8.
- (17) Loreau, M., Daufresne, T., Gonzalez, A., Gravel, D., Guichard, F., Leroux, S., Loeuille, N., **Massol, F.** & Mouquet, N. (2013) Unifying sources and sinks in ecology and Earth sciences. *Biological Reviews*, **888**, 365-379.
- (18) Gritti, E., Duputié, A., **Massol, F.**, & Chuine, I. (2013) Achieving consensus among inherently different species distribution models. *Methods in Ecology and Evolution*, **4**, 442-452.

- (19) **Massol, F.** (2013) A framework to compare theoretical predictions on trait evolution in temporally varying environments under different life cycles. *Ecological Complexity*, **16**, 9-19.
- (20) Duputié, A. & **Massol, F.** (2013) An empiricist's guide to theoretical predictions on the evolution of dispersal. *Interface Focus*, **3**
- (21) **Massol, F.** & Petit, S. (2013) Interaction networks in agricultural landscape mosaics. *Advances in Ecological Research*, **49**, 291-338.
- (22) Bohan, D.A., Raybould, A., Mulder, C., Woodward, G., Tamaddon-Nezhad, A., Blüthgen, N., Pocock, M.J.O., Muggleton, S., Evans, D.M., Astegiano, J., **Massol, F.**, Loeuille, N., Petit, S., & Macfadyen, S. (2013) Networking agroecology: integrating the diversity of agroecosystem interactions. *Advances in Ecological Research*, **49**, 1-67.
- (23) Schmidt, K., Johansson, J., Kristensen, N., **Massol, F.**, & Jonzén, N. (2015) Consequences of information use in breeding habitat selection on the evolution of settlement time. *Oikos*, **124**, 69-80.
- (24) Laroche, F., Jarne, P., Lamy, T., David, P., & **Massol, F.** (2015) A neutral theory for interpreting correlations between species and genetic diversity in communities. *American Naturalist*, **185**, 59-69.
- (25) Astegiano, J., **Massol, F.**, Vidal-Morais, M. M., Cheptou, P.-O., & Guimarães, P. R. Jr. (2015) The robustness of plant-pollinator communities: linking plant centrality and sensitivity to pollinator loss. *PLoS ONE*, **10**, e0117243.

#### Other articles

- (1) Lavoit, A.-V., Staudt, M., Schnitzler, J. P., Landais, D., **Massol, F.**, Rocheteau, A., Rodriguez-Cortina, R., Zimmer, I., & Rambal, S. (2009) Drought reduced monoterpene emissions from *Quercus ilex* trees: results from a throughfall displacement experiment within a forest ecosystem. *Biogeosciences Discussions*, **6**, 863-893.

#### Book chapters

- (1) **Massol, F.**, Jabot, F., Manel, S., & Munoz, F. (in press) Etude des réseaux en écologie. In: *Les Réseaux dans les Sociétés Animales* (ed.: Sueur, C.) Editions Matériologiques.

#### Papers at various stages along the publication process

- (1) Jacquet, C., Moritz, C., Morissette, L., Legagneux, P., **Massol, F.**, Archambault, P., & Gravel, D. (in revision) The complexity-stability relationship in empirical ecosystems
- (2) Poisot, T., Baiser, B., Dunne, J., Kéfi, S., **Massol, F.**, Wood, S., & D. Gravel (in revision) MANGAL – making complex ecological network analysis simpler
- (3) Gravel, D., **Massol, F.**, & Leibold, M. (in revision) Stability and complexity in model metaecosystems
- (4) **Massol, F.** & Débarre, F. (in revision) Evolution of dispersal in temporally variable environments: the importance of life cycles
- (5) Coomes, O. T., McGuire, S., Garine, E., Caillon, S., McKey, D., Demeulenaere, E., Jarvis, D., Aistara, G., Barnaud, A., Clouvel, P., Empereire, L., Louafi, S., **Massol, F.**, Martin, P., Pautasso, M., Thomas, M., Violon, C., & Wencelius, J. (in revision) Farmer seed networks make a limited contribution to agriculture? Four common misconceptions
- (6) Tasiemski, A., **Massol, F.**, Cu villier-Hot, V., Boidin-Wichlacz, C., Roger, E., Rodet, F., Fournier, I., Thomas, F., & Salzert, M. (in revision) Reciprocal immune benefits based on the complementary production of antibiotics by the leech *Hirudo verbana* and its gut symbiont *Aeromonas veronii*
- (7) Laroche, F., Jarne, P., Perrot, T., & **Massol, F.** (in preparation) The effects of dispersal polymorphism on  $\alpha$  and  $\beta$  diversity patterns in a heterogeneous metacommunity

- (8) Lamy, T., Laroche, F., Jarne, P., David, P., & **Massol, F.** (in preparation) Decomposing species-genetic diversity correlation on neutral markers: a novel approach to unravel the rules of community assembly
- (9) **Massol, F.** & Duputié, A. (in preparation) The evolution of dispersal with different types of cost
- (10) Dubart, M., Cheptou, P.-O., & **Massol, F.** (in preparation) Evolutionary syndromes linking dispersal and mating system: kin competition under uncertain pollination

## Other scientific communications (non exhaustive list)

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### Invited oral communications

- (1) CHEPTOU, P.-O. & **Massol, F.** (08/2007) The evolution of dispersal/outcrossing syndrome in spatially heterogeneous pollination environment (why are there so many dioecious plants on islands?) *ESEB meeting*, Uppsala, Sweden
- (2) **MASSOL, F.**, Gravel, D., Mouquet, N., Cadotte, M. W., Fukami, T., & Leibold, M. A. (08/2010) Recasting spatial food web ecology as an ecosystem science. *ESA meeting*, Pittsburgh, USA
- (3) GRAVEL, D., **Massol, F.**, Canard, E., Mouillot, D., & Mouquet, N. (08/2010) Trophic theory of island biogeography. *ESA meeting*, Pittsburgh, USA
- (4) Gravel, D., **MASSOL, F.**, Canard, E., Mouillot, D., & Mouquet, N. (11/2010) Prise en compte de l'information trophique en biogéographie insulaire. *Journée d'Ecologie Numérique*, Montpellier
- (5) Gravel, D., **MASSOL, F.**, Canard, E., Mouillot, D., & Mouquet, N. (06/2011) Prise en compte de l'information trophique en biogéographie insulaire. *Journée biodiversité & bioinformatique*, Grenoble
- (6) GRAVEL, D., Loreau, M., **Massol, F.** & Mouquet, N. (06/2012) Toward a spatial theory of interaction networks. *Web of Life in a changing world conference*, Montpellier
- (7) **MASSOL, F.** (09/2012) Metapopulation-based approaches to spatial food webs. *Networks and interactions in agriculture workshop*, Dijon
- (8) **MASSOL, F.** (06/2014) Community dynamics and the evolution of dispersal. *ECMTB meeting*, Göteborg, Sweden
- (9) **MASSOL, F.** (08/2014) Rescuing metacommunity ecology using random matrix theory. *Journées Modélisation Aléatoire et Statistique*, Toulouse
- (10) **MASSOL, F.** (09/2014) Communities and the evolution of dispersal: some ideas. *Dispersal evolution in a community context workshop*, Fabrikschleichach, University of Würzburg, Germany
- (11) **MASSOL, F.** (10/2014) Ecology of interaction networks & the evolution of dispersal: some new and ongoing projects. *Biodiversity Theory and Modelling workshop*, Moulis
- (12) **MASSOL, F.** (11/2014) Individual dispersal, fluxes of nutrients and the stability of ecosystems. *SysBio conference*, Lyon

### Contributed oral communications

- (1) **MASSOL, F.** & Couvet, D. (11/2006) Conséquences évolutives de l'ingénierie d'écosystème sur la dissimilarité au sein des communautés. *GDR ComEvol*, Montpellier
- (2) DUPUTIÉ, A., **Massol, F.**, David, P., Haxaire, C. & McKey D. (07/2007) Selection of sexually produced seedlings of a clonally propagated crop in a traditional Amerindian agroecosystem. *ATBC meeting*, Morelia, Mexique
- (3) Schleuter, D., Daufresne, M., **MASSOL, F.** & Argillier, C. (01/2009) A user's guide to functional indices: Are functional diversity indices consistent and complementary? *ASLO meeting*, Nice

- (4) **MASSOL, F.**, Calcagno, V., & Rousset, F.. (09/2010) Comment calcule-t-on une valeur sélective dans un cadre spatialisé ? *Ecologie 2010*, Montpellier
- (5) DUPUTÉ, A., **Massol, F.**, Chuine, I., Ronce, O., & Kirkpatrick, M. (09/2010) Influence des interactions entre traits soumis à sélection sur l'aire de répartition d'une espèce. *Ecologie 2010*, Montpellier
- (6) DUPUTÉ, A., **Massol, F.**, Chuine, I., Kirkpatrick, M., & Ronce, O. (08/2011) Multivariate adaptation in a changing environment: a theoretical model. *ESA meeting*, Austin, USA
- (7) **MASSOL, F.** & Débarre, F. (09/2011) Evolution in temporally variable environments: the importance of life cycles. *Mathematical & Theoretical Ecology conference*, Colchester, UK
- (8) DUPUTÉ, A., **Massol, F.**, Chuine, I., Kirkpatrick, M., & Ronce, O. (09/2011) « Responding to rapid environmental change » - How fast exactly? A theoretical model in a multivariate environment. *EEF meeting*, Avila, Spain
- (9) Gravel, D., Leibold, M., & **MASSOL, F.** (03/2013) Solving the complexity-stability paradox with spatial structure. *Thematic workshop "complex network dynamics"*, GDR PHENIX, Montpellier
- (10) Lamy, T., LAROCHE, F., Jarne, P., David, P., & **Massol, F.** (11/2013) Species diversity-gene diversity correlations in meta-communities: insights from neutral theories. *Symposium of the International Biogeography Society*, Montréal, Québec
- (11) **Massol, F.** & DÉBARRE, F. (12/2014) Evolution of dispersal in spatially and temporally variable environments: the importance of life cycles. *British Ecological Society meeting*, Lille
- (12) LAROCHE, F., Perrot, T., Jarne, P., & **Massol, F.** (12/2014) From neutral theory to competition-dispersal trade-off: a theoretical study of species diversity patterns in patchy habitats. *British Ecological Society meeting*, Lille

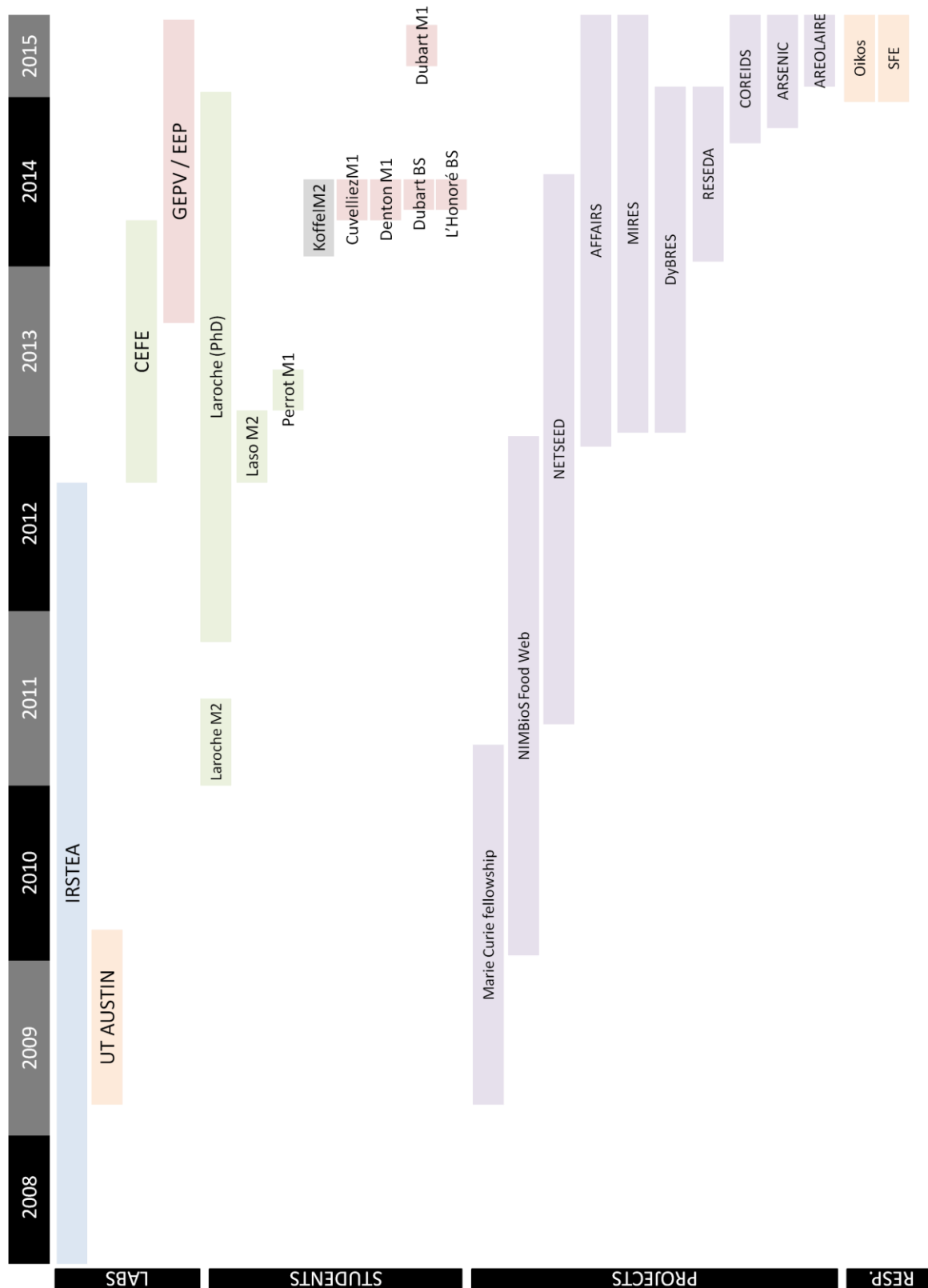
## Seminars

- (1) **MASSOL, F.**, Calcagno, V., Mouquet, N., Jarne, P. & David, P. (11/2009) How metacommunity dynamics limit food chain length: the patchy prey hypothesis *University of Texas, Austin, US*
- (2) **MASSOL, F.** & Cheptou, P.-O. (01/2010) Reciprocal selection pressures and evolutionary syndromes: to self-fertilize or to disperse? *University of Texas, Austin, US*
- (3) **MASSOL, F.** (03/2012) The evolution of dispersal: old questions, new answers. *Ecology & Evolution laboratory, Paris*
- (4) **MASSOL, F.** (02/2013) Adaptive dynamics in a heterogeneous and uncertain world. *DGSE department at the CEFÉ, Montpellier*
- (5) **MASSOL, F.** (05/2013) Evolution of dispersal in heterogeneous and uncertain environments. *Models in Evolutionary Ecology special seminars, Montpellier*
- (6) **MASSOL, F.** (06/2013) Evolution of dispersal in heterogeneous and uncertain environments. *GEPV laboratory, Lille*
- (7) **MASSOL, F.** (06/2014) A model for the evolution of dispersal in heterogeneous environments. *Terrestrial Ecology laboratory, Ghent, Belgium*
- (8) **MASSOL, F.** (02/2015) The evolution of dispersal in heterogeneous environments: a model with applications. *EDB laboratory, Toulouse*

## Posters

- (1) **MASSOL, F.** & Sherbakov, D. Y. (09/2002) On a phylogenetic tree comparison-based criterion for diagnosis of past dispersion and speciation patterns of endemic species flocks in great lakes. *SIAL meeting*, Irkutsk, Russia
- (2) DUPUTÉ, A., **Massol, F.**, David, P., Haxaire, C. & McKey D. (08/2007) Management of genetic diversity of a clonally propagated crop in a traditional Amerindian farming system. *ESEB meeting*, Uppsala, Sweden

- (3) CANARD, E., David, P., **Massol, F.**, & Jarne, P. (08/2008) Y-a-t-il un rôle du système de reproduction dans la coexistence d'espèces au sein des communautés ? *Petit Pois Dérivé*, Rennes
- (4) DUPUTIÉ, A., **Massol, F.**, David, P., Haxaire, C. & McKey, D. (03/2009) Création et maintien de la diversité génétique d'une plante cultivée dans un agroécosystème traditionnel. *Le Réveil du Dodo*, Montpellier
- (5) **MASSOL, F.**, Duputié, A., David, P., & Jarne, P. (08/2009) Asymmetric patch size distribution leads to disruptive selection on dispersal. *ESEB meeting*, Turin, Italy
- (6) LAROCHE, F., Jarne, P., & **Massol, F.** (06/2012) Selection leads to dispersal niches in networks of quasi-neutral communities. *Web of Life in a changing world conference*, Montpellier
- (7) LAROCHE, F., Jarne, P., Lamy, T., David, P., & **Massol, F.** (08/2013) Impacts of non-selective processes on species-genetic diversity correlations: a neutral approach. *ESEB meeting*, Lisbon, Portugal
- (8) LASO, F., **Massol, F.**, & McKey, D. (10/2013) Seed exchange network properties and agroecosystem resilience. *Student Conference on Conservation Science*, New York, USA



My academic life since my PhD defence...

## SYNTHESIS: THE EVOLUTIONARY ECOLOGY OF FLUXES

As I began working in the mysterious world of academics, more than ten years ago, I had a personal bias when tackling ecological questions. This bias remains the same to this day: my education being first and foremost in the “hard sciences” (maths and physics) and only secondary in biology and ecology, I tend to approach every problem theory first, empirics second (if ever). I have tried hard to tame this bias over the years, especially thanks to extraordinary colleagues who have a knack for making empirical studies appealing to theoreticians. However, this is a *caveat* to the unprepared reader: there is going to be some (a lot of...) theoretical stuff therein.

A second point I wanted to explain before I begin this hopefully concise odyssey into the evolutionary ecology of fluxes: the exercise asked of the HDR applicant, being formal and aimed at putting a symbolic hurdle between being a PhD candidate and leading the work of PhD candidates, can be seen as rather dull. There is nothing really fancy, for the author of such a synthesis, in re-reviewing for the umpteenth time a scientific literature already well known, dissected and peppered by one’s own contributions. In other words, it is the duty of the applicant to run through their publication’s hall of fame and explain every paper’s merits like those of memorable soldiers dead at war. I have very little appetite for explaining “dead science” only and, given the opportunity, I’d rather explain the live ramifications of such papers. Hence, I have made the decision to discuss not only my published papers, but also some of the unpublished ones. However, contrary to a PhD dissertation, in which unpublished manuscripts are the norm in order to judge the value of a candidate, it is probably not so fashionable to act likewise when writing one’s HDR memoir. Thus, I have opted for very short presentations of ongoing work in one-page boxes. I hope the inclusion of such boxes, although based on work not yet acquainted with the cogs and springs of the academia publication machine, will provide more inspiration and ideas than the sole presentation of my papers’ hall of fame.

A few practical points to ease the reading of this synthesis: all acronyms and all terms followed by an asterisk the first time they appear in the text are defined in a glossary at the end of the document. My own papers are cited as P1, P2, etc., and personal and general bibliographies are separated at the end of the synthesis.

### 1. Introduction

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Basic research is like shooting an arrow into the air and, where it lands, painting a target.

Homer Adkins, quoted by Gratzer, W. (1984) The bomb and the bumble-bees. *Nature*, **312**, 211

Ecology, being a still moderately young science, might look like a teenager hybrid between a “pure biology” parent, who would have given it the habit of looking closely at everything it sees and of basing its judgment on replicating nature in the lab, and a hard science parent with an obvious tendency towards formalising laws and principles, with the secret hope that, at some point, things might become easier to understand. But ecology is not their only child – at least it has an older, split-personality sibling that goes by the names of population genetics / evolutionary biology – with whom ecology shares a lot of issues. For ecology to succeed in its quest for adulthood, it needs to acknowledge what it owes to both of its parents, to take whatever inspiration comes its way from its older sibling, but mainly to define its own research questions, its “programme” and its core methods.

Amidst this programme for scientific ecology, there is the recurrent notion of fluxes. Ecology, “the science of the house” in its Greek etymology, is “*about the distribution and abundance of different types of organism, and about the physical, chemical but especially the biological features and interactions that determine these distributions and abundances*” (Begon et al., 2006). This updated definition of ecology emphasizes “features and interactions” which determine the distributions and abundances of living organisms – but what are these “biological features and interactions” if not fluxes? Under this broad term, I would likely put all biotic and abiotic processes driving the

movement of matter, energy and information within and among ecosystems. As such, ecological fluxes encompass a variety of processes: a deer or a wolf moving from one place to another would contribute to ecological fluxes, as well as a wolf eating a deer at one place and defecating at another, or a deer carcass being decomposed by arthropods, worms, mushrooms and bacteria at a given location. In all of these cases, “something moves”, not necessarily far, nor in large quantities.

What ecological fluxes really comprise is a topic onto itself (DeAngelis, 1992, Holt, 2002, Rip and McCann, 2011; P11). Various ecological processes indeed produce fluxes between locations, trophic levels, organisms, etc. Categorising all of these processes is beyond the scope of this synthesis and would probably not lead to a greater understanding of ecological fluxes. A more interesting prospect is the potential consequences of such fluxes and how these relate to laws at different levels of organisation (Loreau et al., 2003, Loreau and Holt, 2004; P11). For instance, consider the movement of matter within and among ecosystems around the world. Whatever the scale of observations, once input and output are accounted for, the sum of all the fluxes of a given chemical element must abide by the law of conservation of mass. In ecological terms, this means that if caricatured ecosystems only consist of two mobile compartments, say predators and herbivores, then a long-term excess of predators going from location A to location B will inevitably lead either to drastic mass imbalance between the two locations or to the logically reverse excess of herbivores going from B to A (Loreau et al., 2003). This view of ecological fluxes, which I would deem “ecosystemic”, stems largely from the appropriation of the notions of “sources” and “sinks” – as defined by environmental scientists (*e.g.* Pressman and Warneck, 1970) – by ecologists (Pulliam, 1988, Runge et al., 2006, Vandermeer et al., 2010; P17).

At the other end of the spectrum, one correlate of long-range fluxes that is obvious to population biologists is the dispersal\* of organisms throughout the environment (Clobert et al., 2001, Clobert et al., 2012). Because all living things disperse in some way, as diffused gametes in the wind or the ocean, as seeds attached to fleshy fruits or as long-lived vertebrates changing their breeding site from one year to the next, they tend to reproduce in a setting that is slightly different from the one experienced by their biological parents. Dispersal is the expression of a peculiar flux: the flux of genes. Indeed, the expression “gene flow” has percolated throughout the evolutionary biology literature rather successfully (*e.g.* McNeilly and Antonovics, 1968, Slatkin, 1985, Rousset, 1997, Whitlock and McCauley, 1999, Lenormand, 2002, Nuismer and Kirkpatrick, 2003), even to the point that the current operational definition of dispersal equates with movements creating gene flow (Ronce, 2007; P20). Because dispersal propensity is a trait of living organisms, it must obey the same principle as other traits, *i.e.* those of natural selection. Thus, from a population biology standpoint, ecological fluxes are, at least partly, manifestations of natural selection at play (P11). Even for shorter-range movements that cannot be considered under the umbrella of dispersal because they do not cause gene flow *per se* (*e.g.* animals foraging for food), natural selection shapes the rates, directions, etc. of these movements, through the selection of movement strategies. Whatever the type of flux considered, be it dispersal across space, trophic interactions, decomposition of dead organic matter or photosynthesis, it must conform to the laws of biological evolution, *i.e.* be subject to evolutionary dynamics due to mutation, heritability and selection.

Because ecological fluxes deal with chemical elements getting in and out of place partly through living organisms, they display an ambivalent nature that a physicist, accustomed to the wave/particle conundrum, would regard as epistemologically intriguing. At the same time, these fluxes are governed by physical and biological laws, which make them all the more difficult to understand. One of the best examples illustrating how the two facets of ecological fluxes might drive important effects among ecosystems around the world has been provided over the years by James Estes and his colleagues. A relevant example is that of the observation that sea otter (*Enhydra lutris*) populations have declined at some point in the Aleutian archipelago and in South Alaska. This decline can be understood as the result of a logical cascade in four points (Estes et al., 1998; excerpt from P11): “(i) the decline of forage fish stocks in the North Pacific due to overfishing (or other causes), which provoked (ii) the decline of large



*pinniped populations in the Pacific, which in turn caused (iii) transient (i.e. highly mobile) killer whale populations to settle near the shores of Aleutian archipelago and South Alaska and, then, (iv) to prey more heavily on local sea otter populations.*” In other words, the demographic bad fortune of a given organism at a location A stems from the ecosystemic disruption of fluxes at a location B through the movement of large predators. Recently, the same team of researchers has even gone a step further. They proposed that this decline in sea otter populations, due to indirect causes mentioned above, might also affect fluxes of carbon between the ocean and the atmosphere through releasing urchins from otter predation, leading to higher grazing pressure on kelp by the urchins and thus driving a strong top-down control on kelp populations (Estes and Duggins, 1995, Wilmers et al., 2012). Whether this story is now complete or is only a part of the truth does not really matter yet; what is at stake is understanding that ecological fluxes are a subject worthy of investigation by interdisciplinary consortia comprising, at the very least, researchers able to understand both the demographic and ecosystemic consequences of organism movements.

Ecological fluxes, being a complex phenomenon, with a variety of drivers and at least two very different categories of correlates, require interdisciplinary breadth (P15, P21, P22). On top of appealing to the biological and physical notions enounced above, modelling ecological fluxes, *e.g.* among species within a food web, draws heavily upon the notions of graphs and networks, which have been a study subject in the hard sciences for quite a while (P26). As humans are part of most studied ecosystems, social sciences and humanities also provide needed pieces of the puzzle when trying to figure out the reasons for a given flux to exist, *e.g.* in agroecosystems (P15). For a variety of reasons, ecological fluxes, despite their name, are not a purely ecological subject, but rather an interdisciplinary one that borrows concepts and methods from across the board of both soft and hard sciences. As a “maths-and-physics-person-become-an-ecologist” fond of interdisciplinary dialogues, I find this state of affairs rather appealing as it provides a playground that is ecologically meaningful, mathematically challenging and prone to exchanges with researchers from other scientific worlds.

The rest of this synthesis is organized as a series of “big ecological questions” to which approaches based on fluxes have provided (or will hopefully provide) fruitful methods and answers. The delineation of these four “big questions” is becoming a kind of mantra in my recent papers (P11, P21, P26) – although the number of questions can vary –, but I think these are distinct, important objectives that ecological studies should consider worth studying:

- a. The evolutionary emergence and ecological coexistence of diverse life forms: how diversity can emerge and be maintained, and under which conditions coexistence mechanisms actually work;
- b. The complexity and functioning of ecological systems: how ecosystems are indeed tangled banks of intertwined species, how elements and energy flow through ecological compartments, and how ecological complexity and functioning are affected by spatial scale and exchanges among habitat patches;
- c. The dynamical nature of ecological systems: what could make ecosystems more or less stable and how ecological and evolutionary dynamics affect one another;
- d. The geographical distributions of species: how the combination of limited dispersal, maladaptation, species interactions and the distribution of environmental conditions in space affect geographical patterns of species distributions and the extent of their spatial ranges.

For each of the corresponding sections (2 to 5), the main text will be used to replace my work and the work of the students and post-docs I have supervised in current literature, with a brief overview of the questions and methods and a synthesis of obtained results, while the boxes will describe, as succinctly as possible, subjects that are “alive” and which have recently proved fruitful, without getting into a detailed presentation of such studies to prevent boredom and to keep this document at a convenient length.

## 2. Polymorphism and coexistence

---

Le monde avance à grands coups de préfixes. La modernité s'est pris un coup de post, elle a maintenant l'hyper aux fesses. Certains ont eu le trip méta comme on a sa période punk. D'autres se la jouent métro, néo, rétro, para, poly ou restent confinés dans l'anti.

Mara Goyet, *Formules enrichies*

As a science of biodiversity, one of the first objectives of ecology is to understand why there are so many different life forms and how these life forms coexist. This question can be sub-categorized in two sides of the same coin:

- a. Under which conditions do different life forms emerge from a common ancestor?
- b. Under which conditions do existing distinct life forms coexist on appropriately long time scales?

Depending on whether these are approached with a “selectionist” or a “neutralist” programme in mind, there are many ways to tackle these questions, and whether they are tackled by population geneticists or ecologists does not really affect the core concepts at work in the models (Vellend, 2010). The question of the emergence of differences is semantically related to the question of speciation (Orr and Smith, 1998) – be it allopatric or sympatric –, but also to the question of the emergence of polymorphism of traits or alleles. Likewise, conditions of coexistence can be explored from a perspective in which all species must be different in some way (Hutchinson, 1959) – the niche perspective if you will – or from the neutral community model perspective (Hubbell, 2001) in which all species are doomed eventually, but the distribution of their abundances by rank is a steady state output of the immigration/speciation vs. ecological drift balance.

Diversity pattern studies assess the degree to which species (or genotypes within a species) can coexist at a given spatial scale, over long time scales (typically, ecological time scales, *i.e.* for several hundreds or thousands of generations). By reference to Whittaker's early works (Whittaker, 1972), local diversity is often referred to as  $\alpha$  diversity, while the immediately larger spatial scale conditions  $\gamma$  diversity. The difference in diversity between the average of two local patches and their union is referred to as pairwise  $\beta$  diversity, while the difference in diversity between the union of all patches and the average  $\alpha$  diversity is called  $\beta$  diversity. There are many indices for the quantification of diversity (Magurran, 2004, Jost, 2007), and although they all describe the same concept, certain indices are more useful than others, mainly because of statistical properties (*i.e.* the absence of bias when estimating the index from data), concavity (Lande, 1996) which conditions the fact that  $\beta$  diversity is always nonnegative, and their sensitivity to rare/dominant species (Jost, 2007).

In the case of spatially structured systems, such as metapopulations\*, metacommunities\* and metaecosystems\*, questions pertaining to the emergence and the maintenance of diversity go back to a long tradition, with perhaps the most iconic landmarks being the book of MacArthur and Wilson (1967), “*The Theory of Island Biogeography*”, on the ecological side and the book of Levins (1968), “*Evolution in Changing Environments*”, on the evolutionary side. Spatially structured systems display four specificities that cast the problem of diversity in a different light. These specificities, although not strictly recognized as stemming from the spatial structure of ecological systems, have been listed early on in community ecology as “*biological determinants of diversity*” (Shmida and Wilson, 1985):

- a. Spatial structure can be synonymous with spatial heterogeneity of environmental conditions, *i.e.* individuals living in different locations might experience different conditions that affect their fecundity, survival, resource acquisition, etc. In population genetics and evolutionary ecology, this heterogeneity of environmental conditions has spurred the building of series of models on the emergence and maintenance of polymorphism of local adaptation alleles (Levene, 1953, Dempster, 1955, Wallace, 1975). In metacommunity parlance, this relates to the “species sorting” paradigm of metacommunity ecology (Leibold et al., 2004).
- b. Spatial structure can mean that biological entities may go extinct at a small scale yet persist at a larger spatial scale. This is at the core of the well-known Levins (1969) metapopulation model,

which has inspired many other models since (*e.g.* P12). Or, speaking as a metacommunity ecologist, this is the “patch dynamics” paradigm (Leibold et al., 2004). In evolutionary terms, such random perturbations can act as a selective pressure, *e.g.* on the evolution of dispersal (van Valen, 1971, Comins et al., 1980; P5, P9).

- c. Spatial structure is related to the concepts of gene flow and dispersal – if populations are subdivided in space, it is because they reproduce locally but still exchange genes through migration. In addition to the above-mentioned spatial heterogeneity, the existence of dispersal among patches is at the heart of source-sink dynamics (Pulliam, 1988, Kawecki, 2004, Runge et al., 2006; P17), *i.e.* the fact that certain patches may act as net exporters or importers of migrants (because individuals fare better or worse there than elsewhere at steady state) or, metacommunity-wise, the existence of a “mass effect”, *i.e.* coexistence of locally adapted and maladapted species through immigration of the latter from other locations (Leibold et al., 2004).
- d. Spatial structure implies the fragmentation of a big population into several smaller-sized populations. Demographically, this means that stochasticity in reproduction, recruitment and mortality have a different impact in spatially structured systems than in spatially unstructured ones, or, in more technical jargon, the structure of the coalescent differs between a single unstructured population and several populations connected by dispersal (Wakeley, 2008). This aspect of spatial structure means that, all else being equal, spatial structure tends to make ecological communities different “by chance” (the “neutral model” of metacommunity ecology, Leibold et al., 2004). It is also the basis of Hubbell’s (2001) neutral theory of biodiversity.

Over the years, I have tried to address these four determinants of diversity, both from an “emergence” and a “coexistence” viewpoint. Fabien Laroche, during his PhD (2011-2014), explored all these points with quasi-neutral ecological models in mind, inspired both from my own work (P8) and the interesting developments of Jabot (2010) around the concept of environmental filtering in neutral ecology models. Recent first-year MSc students (Thomas Perrot, Rémi Cuvellez and Joseph Denton) have also worked with me on the question of the evolution of dispersal, with Thomas extending Fabien Laroche’s second-year MSc work to the characterization of evolutionary branching in simulations, Rémi developing a model for the evolution of dispersal and local adaptation when one of two patch types is more productive but more disturbed than the other (based on P19), and Joseph splicing Day’s (2001) model of local adaptation into a discrete-time version of a model of the evolution of dispersal when carrying capacity differs among patches (P8). During his third year BSc internship, Maxime Dubart, now doing his first-year MSc internship on directed network metapopulation models, helped advance the development of a model (Box 2) to understand the joint evolution of selfing and dispersal under conditions of uncertain pollination (in line with P5, P9, P10).

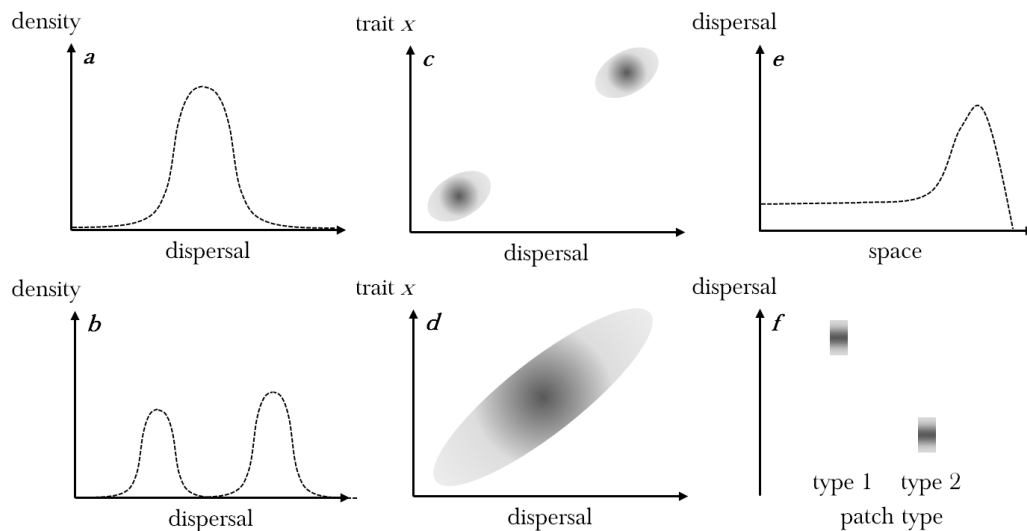
The following subsections focus on two aspects of my work pertaining to the question of diversity: (i) the evolution of dispersal in metapopulations and (ii) the maintenance of diversity in metacommunities. In Conclusions & Perspectives, I briefly present other evolutionary works that do not deal with the evolution of dispersal, as well as the perspectives emerging from Fabien Laroche’s PhD thesis and my recent, ongoing collaboration with empiricists interested in the evolution of dispersal in annelids living in archetypal metapopulations.

## 2.1. The evolution of dispersal

Understanding why organisms from all species have a tendency to disperse away from their parents is a key question in evolutionary ecology (Skellam, 1951, Levin et al., 1984, Levin et al., 2003, Ronce, 2007, Clobert et al., 2012). It is now well accepted that traits determining dispersal ability display some variability within and among species *in natura*. Within-species polymorphism in dispersal traits has been reported *e.g.* in plants (heterocarpy, *e.g.* Imbert et al., 1997, Hall et al., 2011) or insects (winged vs. wingless morphs; Roff, 1986, *Pgi* polymorphism in certain lepidoptera, Hanski and Saccheri, 2006). Dispersal traits have been reported as heritable (Saastamoinen, 2008, Charmantier et al., 2011). In

theory, five main factors determine selective pressures on dispersal rates (Dieckmann et al., 1999, Clobert et al., 2001, Bowler and Benton, 2005, Ronce, 2007; P20):

- a. The temporal variability of the environment, and especially the extinction risk linked to perturbations (Comins et al., 1980, Parvinen et al., 2003), can affect the evolution of dispersal. The basic prediction is that regular temporal variability tends to select for higher dispersal in order to “hedge one’s bets” (Travis, 2001, Kisdi, 2002, Blanquart and Gandon, 2011, Blanquart and Gandon, 2014; P5, P9).
- b. Spatial habitat heterogeneity, on the other hand, tends to select for decreased dispersal because, on average, dispersers tend to leave “good patches” for “bad ones” (Balkau and Feldman, 1973, Hastings, 1983, Holt, 1985).
- c. Kin competition\*, due to intra-deme relatedness, selects for higher dispersal: when patch sizes are finite, a proportion of offspring are expected to disperse, even when dispersal costs are high, to avoid competing with local relatives (Hamilton and May, 1977, Frank, 1986; P8).
- d. Avoiding inbreeding depression puts a positive pressure on dispersal rates (Bengtsson, 1978, Perrin and Mazalov, 1999, Perrin and Goudet, 2001) because it then pays off to disperse when staying home means having to reproduce with related individuals.
- e. Finally, direct dispersal costs (Bonte et al., 2012) select for less dispersal as dispersal becomes less profitable (Hamilton and May, 1977).



**Fig. 1** (excerpt from P20) – Classes of predictions about the evolution of dispersal. **(a)** The density of dispersal trait values within a metapopulation following an evolutionarily stable strategy (ESS), with residual variance corresponding to the result of mutation and local genetic drift (*i.e.* stochastic effects). **(b)** The density of dispersal trait values in a polymorphic population (here, with two modes). **(c)** Prediction of a positive association syndrome between dispersal and trait  $x$ . **(d)** Prediction of a genetic covariance between dispersal and trait  $x$  within a given population or metapopulation. **(e)** Spatial structure of average dispersal value along a one-dimensional space – here, dispersal is higher on the right, possibly because of an invasion wave into a new environment. **(f)** Structuring of dispersal trait values among two types of patches – here, dispersal is selected for in patches of type 1 and disfavoured in patches of type 2.

Combining these different ingredients allows for the development of quite different models of dispersal evolution, depending on whether dispersal is assumed to occur as “seeds” or “gametes”, whether dispersal representation is spatially explicit or implicit, whether dispersal is assumed to be unconditional or conditional on certain local characteristics, etc. (P20). In turn, these different models can generate different classes of predictions (Fig. 1), *i.e.* whether dispersal strategies converge towards an Evolutionarily Stable Strategy (ESS) or undergo evolutionary branching, whether there exists a

dispersal syndrome\* or dispersal becomes statistically associated with another trait value through genetic covariance, and whether dispersal ESS varies in space or among different habitats.

When investigating the evolution of dispersal, my work (in collaboration with others) has mainly focused on two different modelling contexts: (i) models of dispersal evolution in which the spatio-temporal variability of the environment and the cost of dispersal are the predominant selective pressures (P5, P9, Box 1, Box 2); (ii) models of dispersal evolution in which the environment is assumed temporally constant, but carrying capacities vary spatially, so that kin competition is spatially variable (P8, Box 3, Box 5). In both cases, the idea behind developed models was to look for the different types of singular strategies for dispersal predicted under the framework of adaptive dynamics\*, *i.e.* whether evolutionary dynamics eventually settle onto an ESS or pass through an evolutionary branching point before displaying a diversification of dispersal values (Geritz et al., 1998). In the case of dispersal evolution in uncertain environments, our studies also tackled the existence of syndromes linking dispersal and self-fertilization through their joint evolution under shared selective pressures.

### ***2.1.1. Evolution of dispersal in uncertain environments***

Temporal variability in environmental characteristics is predicted to select for dispersal. In particular, catastrophic perturbations select for dispersal as a means to evade large-scale extinction (van Valen, 1971, Comins et al., 1980). The frequency (Blanquart and Gandon, 2011), magnitude (P5, P9), variability in magnitude (Mathias et al., 2001), spatial correlation (Cohen and Levin, 1991), and predictability (Travis, 2001, McNamara and Dall, 2011; P9) of environmental changes all influence the strength of this selective pressure. By contrast, perturbations aimed at habitats (*i.e.* patch destruction), rather than at populations (*i.e.* local extinction), are expected to select against dispersal (Heino and Hanski, 2001, North et al., 2011). Spatial heterogeneity of the environment selects for less dispersal (Balkau and Feldman, 1973, Hastings, 1983, Holt, 1985).

In a series of theoretical studies on the joint evolution of self-fertilization and dispersal (P5, P9, P10, Box 2), Pierre-Olivier Cheptou and I have developed a model for the evolution of plant dispersal when outcrossed fertility depends on an extrinsic factor, *i.e.* the presence of a pollinator species, which is assumed to vary stochastically in space and time. The existence of a syndrome linking the dispersal rate and the mating system has long been debated in evolutionary ecology, especially in plants. Some verbal models hypothesise that the ability to self-fertilise may be associated to high dispersal, since a single individual from a completely outcrossing species cannot reproduce when it disperses to an empty destination site (Baker, 1955, 1967, Pannell and Barrett, 1998). However, empirical observations fail to support such a prediction (Price and Jain, 1981, Sutherland, 2004). Moreover, such theories predict a lower incidence of dioecy on islands, contrary to empirical observations (Bawa, 1980, Renner and Ricklefs, 1995).

We developed a model of the effects of pollination uncertainty on the joint evolution of dispersal and self-fertilisation. The model we built is based on a “Ravigné life cycle” (Ravigné et al., 2004, Débarre and Gandon, 2011; P19, Box 1), *i.e.* regulation is local and occurs right after immigration. The framework used to build the model (P19) allows controlling for the level of environmental autocorrelation in patch state, *i.e.* here, the probability that a given patch would be pollinated during the next time step depended on the overall frequency of non-pollinated patches and the autocorrelation of pollination state. Overall, evolutionary dynamics could only lead to two different syndromes: dispersing outcrossers or non-dispersing (partial) selfers. Depending on model parameters, evolutionary outcomes could be either convergence towards a single syndrome or bistability of the two syndromes. Because the zone of parameter values inducing bistability corresponds to intermediate parameter values, this model entails an evolutionary hysteresis phenomenon whereby changes in an environmental parameter (*e.g.* the cost of dispersal or the proportion of pollinated patches) might cause a switch from the currently selected strategy to the other one (*e.g.* from outcrosser to partial selfer), with a reverse switch occurring at a different value of the same environmental parameter (P5). When accounting for temporal autocorrelation in pollination conditions (P9), we also found that the disperser/outcrossing syndrome is favoured (resp. disfavoured) by negative (resp. positive) autocorrelation in pollination conditions.

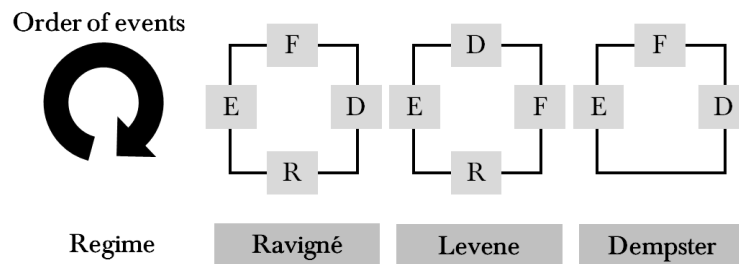
## Box 1: Life cycles and the evolution of dispersal

in collaboration with **Florence Débarre**

An important question is to understand how spatio-temporal variability in patch quality affects the evolution of dispersal. Specifically, this question entails two more or less intuitive answers (Gadgil, 1971, Levin et al., 1984, Travis, 2001): (i) spatial variability on its own does not select for dispersal (Balkau and Feldman, 1973, Hastings, 1983, Holt, 1985, Greenwood-Lee and Taylor, 2001) because, on average, emigrating individuals are going to leave good patches for bad ones; (ii) spatial and temporal variability together, however, select for higher dispersal (McPeck and Holt, 1992, Travis, 2001) because dispersal then acts as a bet-hedging strategy (*i.e.* not putting all eggs in one basket).

The specific issue that Florence Débarre and I wanted to address was the following: in some theoretical studies dealing with the evolution of dispersal under spatio-temporal variability (*e.g.* P5), evolutionarily stable strategies (ESS) for dispersal vary gradually with change in parameters; in other models (*e.g.* McNamara and Dall, 2011), this response looks like a step function, going from 0% dispersal to 100% dispersal as parameters change. Inspired by the works of Virginie Ravigné (Ravigné et al., 2004, Ravigné et al., 2009) and by the simulation results of Johst and Brandl (1997), we decided that a good way to proceed was to compare the predictions of simple, discrete-generation models of the evolution of dispersal when the possible order of events could vary within the life cycle, in ways that could mimic soft or hard selection models (Levene, 1953, Dempster, 1955, Christiansen, 1975, Karlin and Campbell, 1981, Ravigné et al., 2004).

A careful enumeration (based on commutability of certain events, see P19; Fig. 2) of possible life cycles incorporating reproduction (event F), change in the environment (event E), local or global regulation (event R, non-existent from an evolutionary viewpoint when regulation is global) and dispersal (event D) events leads to three different life cycles (E,D,F,R; E,F,D,R; E,F,D) when dispersal is unconditional, *i.e.* not allowed to vary depending on perceived patch quality.



**Fig. 2** – Possible life cycles for models of the evolution of unconditional dispersal.

The model Florence and I developed to deal with different life cycles was designed based on “event matrices”. Basically, each event affected the density of dispersal mutants through a matrix, and the fitness of such mutants could be accessed through the computation of the dominant eigenvalue of the resulting matrix product. As matrices do not commute in general, the different life cycles lead to different fitness functions.

To summarise the results of our investigations, we found that:

- The “Levene cycle” (*i.e.* when regulation immediately follows reproduction, thus leading to no variance of offspring output among patches) inevitably led to zero dispersal.
- Under the “Ravigné cycle” (local regulation follows dispersal), evolutionary branching could occur when environmental change was negatively autocorrelated in time. The dispersal ESS, when it existed, decreased gradually with this autocorrelation (up to 0 dispersal at autocorrelation of 1, *i.e.* when variability is spatial only).
- Under the “Dempster cycle” (global regulation), dispersal was either total or inexistent. Negative autocorrelation of the environment led to 100% dispersal; positive autocorrelation, to 0% dispersal. With non-zero cost of dispersal, bistability arose (*i.e.* two possible evolutionary outcomes existed under the same parameter values).

Overall, our results highlight the fact that different predictions are expected under different life cycles. When trying to connect theoretical models with empirical results, our results might help make a clearer connection by emphasising the need to ascertain (i) whether regulation is local (Levene or Ravigné) or global (Dempster) and (ii) whether dispersing individuals are adults (Levene or Dempster) or juveniles (Ravigné or Dempster), following the analogy made by Débarre and Gandon (2011).

At the moment, our study on the evolution of unconditional dispersal is under revision following a first round of referees’ comments. We plan to submit at least one other paper on the evolution of conditional dispersal, with the same systematic approach to life cycles (thus complementing the works of Johst and Brandl, 1997, McNamara and Dall, 2011, Aguilée et al., 2015 on certain life cycles).

In another, yet unpublished, series of models (Box 1, based on P19), Florence Débarre and I have developed a general approach to compare the evolution of dispersal in spatio-temporally variable environmental conditions under different life cycles. Here, the concept of life cycle refers to the ordering of basic events affecting fitness, such as dispersal, reproduction or population regulation. Following the forerunners on the subject (Ravigné et al., 2004, Ravigné et al., 2009, Débarre and Gandon, 2011), we have explored life cycles in which “juveniles disperse” (*i.e.* dispersal happens before population regulation) or “adults disperse” (*i.e.* dispersal happens after population regulation), and life cycles in which regulation is local (think of limiting space for marine larvae looking for a place to settle) or global (think of salmon populations regulated at sea, when juveniles born in different rivers congregate together in search of food).

As stated in Box 1, we have found that, in line with similar investigations on the effect of life cycles on the evolution of local adaptation (Ravigné et al., 2004, Ravigné et al., 2009, Débarre and Gandon, 2011; P19), predictions on the evolution of dispersal differ drastically from one life cycle to the next. Depending on the precise life cycle and model parameters, evolutionary bistability, evolutionary branching, intermediate dispersal strategies, total dispersal or total philopatry could be selected for. In retrospect, our findings highlight the need to (i) have precise enough method sections in theoretical papers envisaging a model for the evolution of dispersal (or other traits) in a spatially structured context and/or (ii) compare results obtained under a given life cycle with what would have been obtained under a different life cycle.

### ***2.1.2. Evolution of dispersal under spatially heterogeneous carrying capacity***

When carrying capacities differ among patches, mean-field theory, *i.e.* models stemming from neglecting stochasticity in mutant population dynamics, predicts that dispersal is disfavoured, because migrants will on average go from large patches with high associated fitness to smaller patches with lower fitness (Hastings, 1983, Holt, 1985). However, such mean-field models explicitly assume the absence of stochasticity in the reproduction, recruitment and mortality of individuals, hence, the absence of genetic drift. In the absence of such stochasticity, relatedness becomes a void notion, which, in turn, makes these models incapable of modelling the effect of kin competition. Worded differently, mean-field population dynamics implies that the coefficient of variation of abundance is very low and so can only be realised when mean abundance is sufficiently high. Hence, mean-field models implicitly have zero intra-population relatedness and, thus, do not take kin competition into account when modelling the evolution of dispersal (P20).

To remedy the inability of classic demographic models to account for the effect of kin competition, a powerful tool is to make models based on a fitness criterion more refined than the simple population growth rate. In the case of spatially implicit metapopulations, such a criterion exists and is nowadays noted  $R_m$  (Chesson, 1984, Gyllenberg and Metz, 2001, Metz and Gyllenberg, 2001, Ajar, 2003; P3). The  $R_m$  criterion quantifies the “lifetime dispersal success” of a newly colonised patch in a metapopulation that is sparsely occupied by the focal type. When  $R_m > 1$ , each newly founded population produces, on average, more than one effective future population founder, so that the focal type can persist. The  $R_m$  criterion has been described for discrete-time (Chesson, 1984, Ajar, 2003) and continuous-time models (Gyllenberg and Metz, 2001, Metz and Gyllenberg, 2001).

During my PhD, I developed a model of the evolution of dispersal under a variable distribution of carrying capacity based on the  $R_m$  criterion (P8). Since then, this model has been the basis for Fabien Laroche’s second-year MSc internship and PhD thesis, Thomas Perrot’s first-year MSc internship and has partly inspired Joseph Denton’s first-year MSc internship. Hence, I think I owe the reader a short explanation of this model.

## Box 2: Kin competition, selfing and the evolution of dispersal

in collaboration with **Maxime Dubart** and **Pierre-Olivier Cheptou**

The evolution of dispersal and selfing have often been considered separately in theoretical models; however, when considered jointly (P5, P9), their selective pressures interfere and feed back onto one another. For instance, pollination uncertainty acts both on the evolution of selfing through reproductive assurance phenomena and on the evolution of dispersal in outcrossing plants since the absence of pollination means perturbation to such organisms (P5). While pollination uncertainty is undoubtedly a shared selective pressure for the evolution of dispersal and selfing, there is also the possibility that selfing and dispersal might affect one another not through common selective pressures but also directly through a relatedness-mediated effect: because self-fertilised broods are twice as related as outcrossed ones, this might heighten the need for high dispersal in self-fertilising organisms due to kin competition (following the argument of Hamilton and May, 1977). However, since selfing already entails a high cost through inbreeding depression, the multiplication of costs – dispersal cost and inbreeding depression – might also make it very profitable to both lower the selfing rate and the dispersal rate.

A key practical issue in investigating such a phenomenon resides in changing from haploid-like adaptive dynamics to diploid ones. In a simple model of dispersal evolution, it has been shown that accounting for diploid genetics does not change predictions from an adaptive dynamics model in a drastic way (Parvinen and Metz, 2008). However, when dealing with a trait that interacts with the underlying genetic structure (*e.g.* selfing rate), we expect model predictions to be different between haploid and diploid cases. The haploid-like adaptive dynamics model for the joint evolution of dispersal and mating system (P5, P9) is based on the fitness formula given by Lande and Schemske (1985). This expression for fitness is intended to account for inbreeding depression and the twofold advantage of selfers over outcrossers in transmitting their genes. This formula accounts for one consequence of diploidy in studied organisms (the twofold transmission advantage), but does not accurately describe the feedback between selfing rate and the selective pressure on dispersal – most notably, it obliterates the effect of selfing on relatedness among progeny. As relatedness among patch mates selects for higher dispersal (Hamilton and May, 1977, Frank, 1986), the expression for dispersal- and mating system-dependent fitness is bound to be more complicated than previously thought (P5, P9), but possibly computable through the metapopulation fitness criterion (Chesson, 1984, Metz and Gyllenberg, 2001, Ajar, 2003, Parvinen and Metz, 2008; P3).

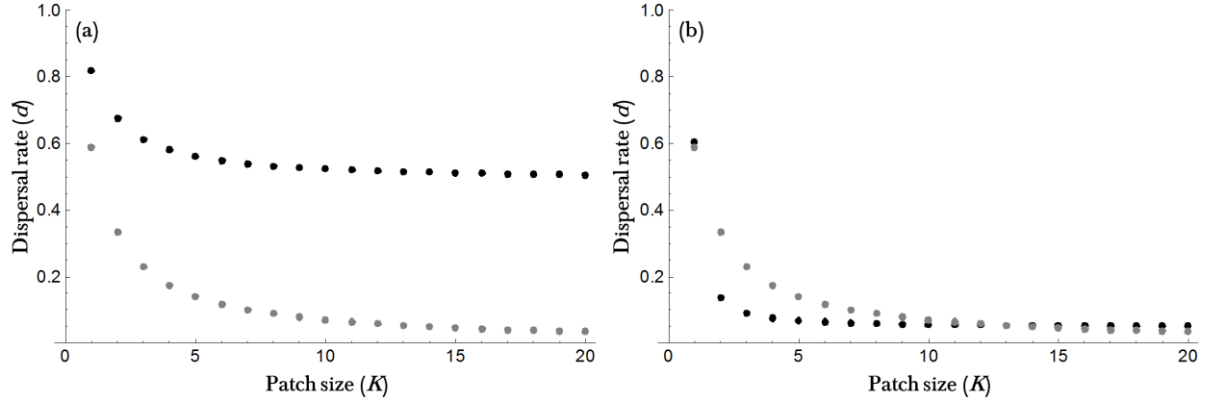
In a paper in preparation, we extend an earlier model (P5, P9) on the joint evolution of selfing and dispersal, by recasting the model in an explicit diploid genetics context and considering local competition and global pollination. In (P5, P9), there is no kin competition because every patch contains an infinite number of individuals. In the present study, we were able to compute all analytical predictions for the model with one individual per patch ( $K = 1$ ), and the dispersal ESS for total outcrossers and total selfers for any size of local populations (any  $K$ ). During Maxime Dubart's BSc internship, he simulated the model for small population sizes ( $K$ ) and looked at how these simulations differed from both the one-individual and infinite-individual patch size assumptions.

To summarise, our results were the following:

- when  $K = 1$ , partial selfing is never selected for. As in (P5, P9), evolutionary bistability is induced by the fact that both dispersing and selfing entail costs. Contrary to (P5, P9), however, selfers do not always disperse less than outcrossers. More specifically, selfers disperse more than outcrossers when temporal autocorrelation of pollination is high and the cost of dispersal is low.
- When comparing our results with  $K = 1$  and (P5, P9), we find that kin competition generally disfavors the evolution of selfing at moderate values of inbreeding depression, and only favors selfing at high inbreeding depression and high frequency of pollinated patches, a situation in which outcrossers are selected to disperse less, thus allowing outcrossing or selfing to alternatively evolve as both types are rarely in local competition for a site.
- For any  $K$ , when the selfing strategy is initially (at  $K = 1$ ) associated with a higher dispersal rate than the outcrossing one, this difference tends to disappear and becomes inverted as  $K$  increases (Fig. 3). When the selfing strategy initially disperses less, the difference in dispersal rates tends to increase with large  $K$  values.
- Interestingly and contrary to both extreme cases ( $K = 1$  and  $K = \infty$ ), simulations suggest that evolutionary branching can occur for small population sizes, with population branching into two morphs (total outcrossers and total selfers).

The manuscript relating the results of this study is currently being written. A natural extension of this study is to splice the question of selfing/dispersal joint evolution with the context of variable carrying capacity in models of the evolution of dispersal (P8) to account for selfing/dispersal joint evolution not imputable to an external pollination agent, but rather to mate availability (*e.g.* in organisms such as *Physa acuta* snails capable of controlling their selfing rate in response to the quantity of encountered conspecifics, Tsitrone et al., 2003).





**Fig. 3** – Sensitivity of singular dispersal strategies to patch size ( $K$ ) in the model presented in Box 2. Dispersal rates ( $d$ , ordinates) are presented as functions of  $K$  (abscissas) following analytical computations. Black dots represent singular dispersal strategy for total outcrossers,  $d_0(K)$ , whereas gray dots correspond to singular dispersal strategy for total selfers,  $d_1(K)$ . Parameter values:  $\bar{c}$ nbreeding depression = 0.9, dispersal cost = 0.7, proportion of non-pollinated patches = 0.4, (a) temporal autocorrelation in pollination state = 0 or (b) = 0.9.

The model deals with a metapopulation consisting of an infinite number of patches, with a specified distribution of carrying capacities. Patches are assumed to have fixed population sizes (“carrying capacities”,  $K$ ), *i.e.* resources freed by an individual’s death are immediately allocated to a newly settled individual, and there is no catastrophe wiping out a whole population. The general functioning of the model can be summarised by the following rules (Fig. 4):

- All individuals have the same mortality rate;
- A dead individual is immediately replaced by either a resident or immigrant (dispersed) offspring;
- All individuals have the same birth rate;
- Generations are overlapping and replacements of dead individuals occur one at a time. The odds of a given patch to be the location in which the next death occurs are proportional to its carrying capacity;
- Individuals displaying dispersal strategy  $d$  send a proportion  $d$  of their offspring to the propagule pool (and a proportion  $1 - d$  remains in their natal patch);
- A proportion  $c$  of propagules (the dispersal cost) dies before reaching a randomly chosen destination patch.

Following these rules, the probability that the next death (in a patch with carrying capacity  $K$ ) affects a type  $s$  individual (local abundance  $k_s$ ) is  $k_s/K$ , and the ensuing probability that a dead individual is replaced by a type  $s$  individual (dispersal  $d_s$  and average abundance over all patches  $\bar{k}_s$ ) is proportional to  $(1 - d_s)(k_s - 1) + (1 - c)d_s\bar{k}_s$ .

The main results of this model are the following:

- Spatial heterogeneity of carrying capacity effectively acts as a cost of dispersal when computing the singular strategy of dispersal. Indeed, we find that the singular dispersal strategy is generally given by:

$$d^* = \text{Min} \left[ \frac{1}{(c + \gamma_2) \bar{K}}, 1 \right] \quad (2.1)$$

where  $\bar{K}$  is the average carrying capacity and  $\gamma_2$  is the squared coefficient of variation of the carrying capacity distribution.

- When the distribution of carrying capacity is positively skewed (*i.e.* there are many patches with small carrying capacity and a few patches with large carrying capacity), evolutionary branching

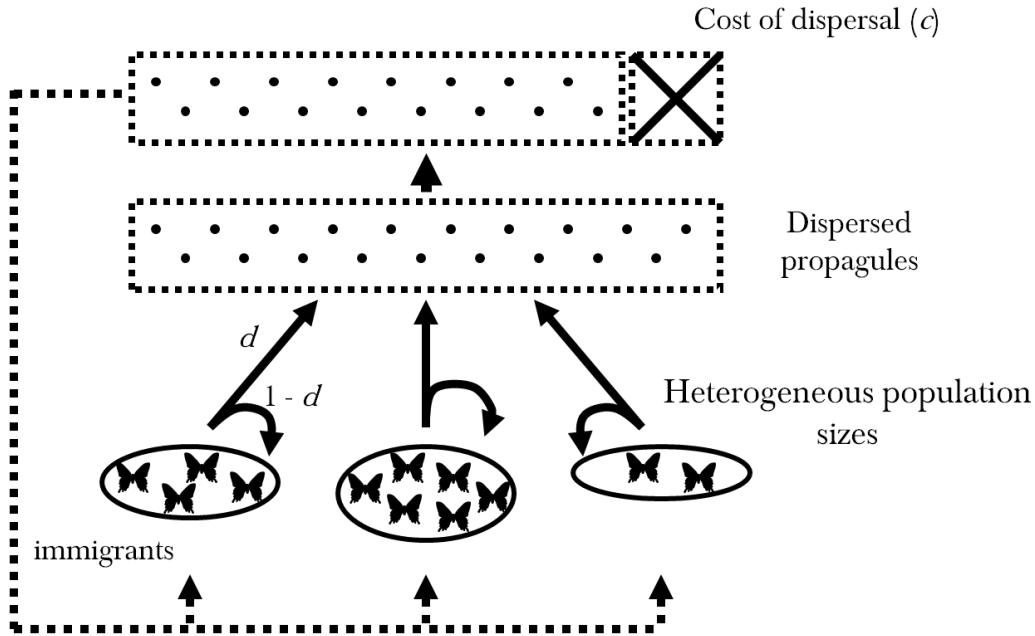
of dispersal rates occur. More explicitly, evolutionary branching only occurs when both of the two following conditions are verified:

$$(c + \gamma_2)\bar{K} > 1 \quad (2.2)$$

$$\gamma_3 > 2\gamma_2^{1/2} + \frac{(c\bar{K} - 1)}{\bar{K}}\gamma_2^{-1/2} + \frac{c(\bar{K} - 1)}{\bar{K}}\gamma_2^{-3/2} \quad (2.3)$$

where  $\gamma_3$  is the standardised skewness of the carrying capacity distribution.

- c. Considering the distribution of carrying capacity, not as perceived by an external observer weighting all patches in the same way, but rather as an individual from the metapopulation, *i.e.* weighting carrying capacity by carrying capacity, in a manner slightly reminiscent of the trick used in percolation theory on graphs to compute the size of “infected clusters” (Newman et al., 2001, Newman, 2002), one can re-interpret inequality (2.3) as a lower bound on the variance of the selective gradient on dispersal experienced by individual members of the metapopulation (P8).



**Fig. 4** (excerpt from P8) – Structure of the metapopulation model used to study the evolution of dispersal under a variable distribution of carrying capacity. Ovals indicate patches, with variable carrying capacity, butterflies are individuals. The dotted box represents the propagule pool, before and after applying the cost of dispersal, which removes a fraction  $c$  of propagules. Solid arrows represent the flows of offspring (a proportion  $d$  is dispersed, and  $1 - d$  remains in the natal patch); dotted arrows, the flows of propagules (dispersed offspring).

During his PhD, Fabien Laroche extended this model in different ways. One very important contribution was to recast the model in a metacommunity context by adding a speciation probability on top of the evolutionary dynamics of dispersal, *i.e.* adding a rate at which newborn individuals “found their own species” (paper in preparation). Using two “archipelagos” (*i.e.* carrying capacity distributions) consisting of only two patch sizes, but arranged in different proportions, Fabien performed simulations of evolutionary dynamics together with speciation process in an otherwise “neutral” context (*i.e.* no difference in fecundity, mortality or competitiveness was assumed among different species). Based on the results of these simulations, the main question was then to check whether  $\alpha$  and  $\beta$  diversity statistics, *i.e.* statistics of diversity within a patch ( $\alpha$ ) and among patches ( $\beta$ ), could help infer the underlying variance of dispersal rates within and among species, by comparing results in a purely neutral context (one dispersal rate for all species), with the possibility of dispersal

evolution in an archipelago selecting for a single dispersal ESS (dispersal rates centred around the ESS, with variance generated by “deleterious” mutations) and with the possibility of dispersal evolution in an archipelago inducing an evolutionary branching point (with eventually two clusters of dispersal rates).

Fabien Laroche indeed found that  $\beta$  diversity statistics could evince the existence of variability in dispersal rates among species. The evidence provided by the comparison of  $\beta$  diversity between the two archipelagos stemmed from the following points:

- a. As already alluded to in (P8) and explicitly shown in Fabien Laroche’s work, types with different dispersal rates tend to be associated with patches of different carrying capacity: individuals displaying high dispersal rates tend to occur mostly in patches with small carrying capacity, while individuals with low dispersal capacity occupy mostly patches with large carrying capacity. The rationale behind this association is that low dispersal types do not pay the cost of dispersal, and thus have a competitive advantage over high dispersal types on their own turf, but draw less benefit from occupying patches with low carrying capacity because of kin competition. Due to heterogeneity in carrying capacity, this means that high dispersal types are expected to occur in small patches, where they experience a less severe competitive disadvantage and where kin competition strikes at full force. This statistical association is especially clear under evolutionary branching scenarios, but is also true under ESS scenarios provided there exists at least a little bit of mutational variance in dispersal.
- b. Provided speciation is a sufficiently slow process, after an initial branching of dispersal rates in the “ancestor” species at the basis of the phylogeny, species occurring in the high- and low-dispersal branches tend to be more related within each branch than among branches. In other words, after some point in the simulations, no species can be found simultaneously in the two dispersal branches.
- c. Because of points (a) and (b), communities of species found in patches of small and large carrying capacities tend to differ phylogenetically (and, hence, differ in species names). This phenomenon leaves a signature in terms of  $\beta$  diversity:  $\beta$  diversity between large and small carrying capacity patches is larger in archipelagos inducing evolutionary branching than in archipelagos inducing a single dispersal ESS.
- d. Moreover, because patches with large carrying capacities tend to be inhabited by species that are not really mobile,  $\beta$  diversity is larger when comparing species composition between two large patches than when comparing species composition between two small patches.

Fabien Laroche’s work is an interesting first step towards building informative quasi-neutral metacommunity models, *i.e.* models that are “almost” like the neutral community model of Hubbell (2001), except for the addition of one (or a few) niche axes along which species can differentiate. The novelty of Fabien Laroche’s approach, when compared to existing ones (*e.g.* Jabot, 2010), is that the amount of inter-species variability in traits allowed to vary among species will be based on evolutionary outcomes, not on modeller’s whim. Based on the same general framework, Fabien has envisaged other applications of the model, *e.g.* to assess the effect of habitat fragmentation in terms of species persistence based on selected dispersal strategies, which I will not present in these pages for the sake of conciseness. In section 3, Box 5 (p. 46) proposes a model that Fabien and I have been discussing which would link the evolution of dispersal under variable carrying capacities with the notion of modularity<sup>\*</sup> in spatial networks of habitat patches.

### Box 3: Offspring vs. maternal costs and the evolution of dispersal

in collaboration with Anne Duputié

While the existence of different direct costs of dispersal has been acknowledged in the literature (Bonte et al., 2012), there are actually few studies investigating the precise effects of different types of cost on the evolution of dispersal (Fronhofer et al., 2015, Weigang and Kisdi, 2015). Whether dispersal is controlled by the mother's phenotype or by the offspring's, however, is known to affect *e.g.* selected dispersal distance (Starrfelt and Kokko, 2010), thus demonstrating that evolutionary selected dispersal kernels differ when the cost of dispersal is on the offspring or on the mother, which comes as no big surprise – although the result is actually quite neat (Fronhofer et al., 2015).

In this context, Anne Duputié and I endeavour to assess what changes would be wrought to the model of the evolution of dispersal under heterogeneous carrying capacities, described in 2.1.2 and (P8), if the cost of dispersal were allowed to be supported differently. Specifically, we envisage three different types of costs of dispersal, on top of the “survival to dispersal stage” cost already present in the initial model (P8):

- First, part of the cost of dispersal could be supported through a decrease in the mother's fecundity;
- Second, another option would be for the mother to support some of the cost of dispersal through an increase in mortality;
- Third, an indirect cost of dispersal might exist due to the fact that different patches might harbour different “fecundities”, *i.e.* some patches might increase the birth rate of their inhabitants while other patches might instead decrease birth rate.

The analysis of the modified model proceeds in the same way as (P8), *i.e.* computing the  $R_m$  criterion, computing the selection gradient, finding singular dispersal strategies, and checking for convergence and evolutionary stability (following Hofbauer and Sigmund, 1990, Geritz, 1998). First, dealing with the value of the singular dispersal strategy, we are able to obtain analogues to equation (2.1) when the average carrying capacity ( $\bar{K}$ ) is assumed very large. In the case of a maternal cost to fecundity, we find that the singular dispersal strategy is given by:

$$d^* = \text{Min} \left[ \frac{1}{(c_O + \alpha_M + \gamma_2 + \alpha_M \gamma_2) \bar{K} - \alpha_M}, 1 \right] \quad (\text{B3.1})$$

where  $c_O$  is the cost of dispersal to offspring,  $\alpha_M$  is the relative increase in the cost of producing dispersing offspring rather than philopatric ones and  $\gamma_2$  is the squared coefficient of variation in carrying capacity. When compared with equation (2.1), this suggests that maternal costs, contrary to costs to offspring, can “interact” with the heterogeneity of the landscape (term  $\alpha_M \gamma_2$ ). Without spatial heterogeneity ( $\gamma_2 = 0$ ), equation (B3.1) also shows that maternal costs only might lead to dispersal rates slightly larger than under offspring costs only.

In the case of a maternal cost through increased mortality, we find an expression similar to (B3.1):

$$d^* \approx \text{Min} \left[ \frac{1}{(c_O + \beta_M + \gamma_2 + \beta_M \gamma_2) \bar{K}}, 1 \right] \quad (\text{B3.2})$$

where  $\beta_M$  stands for the relative increase in the mother's mortality due to producing dispersing offspring. Finally, in the case of indirect costs due to heterogeneity in fecundity among patches, the singular dispersal rate is:

$$d^* \approx \text{Min} \left[ \frac{1}{(c_O + \gamma_2) \bar{K}} - \frac{2(1 - c_O)^2 \varphi_2 - [(\gamma_2 - 3)\bar{K} - 1][(2 + \gamma_2 - c_O) \bar{K} - 1] \kappa_2 / \bar{K}^2}{(c_O + \gamma_2)^2 [(1 + \gamma_2) \bar{K} - 1]}, 1 \right] \quad (\text{B3.3})$$

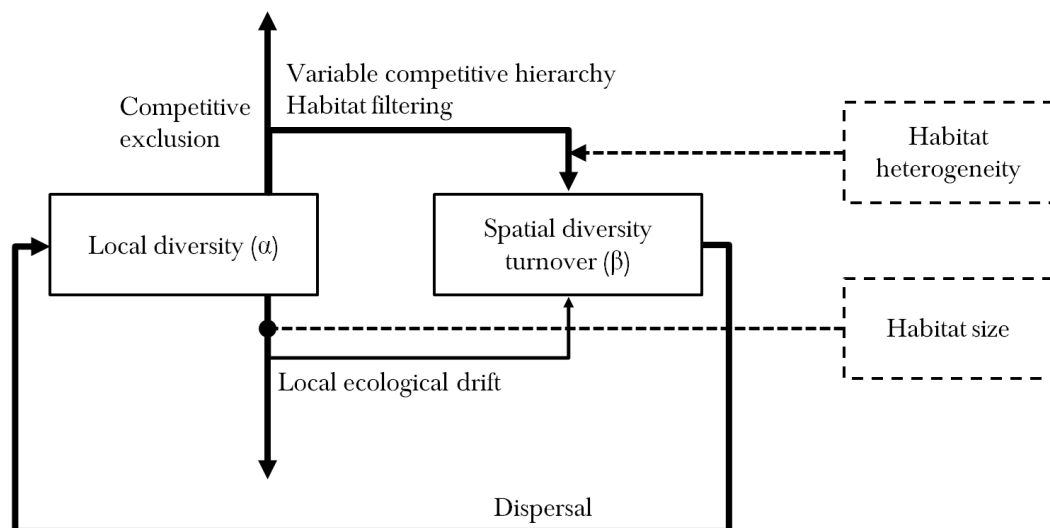
where  $\varphi_2$  is the squared coefficient of variation of fecundity (among patches) and  $\kappa_2$  is the correlation coefficient between patch carrying capacity and fecundity. As it can be seen from equation (B3.3), variability in patch fecundity ( $\varphi_2$ ) occurring independently of variability in patch carrying capacity ( $\gamma_2$ ) is always a cost of dispersal. However, when both quantities are allowed to co-vary, this co-variation ( $\kappa_2$ ) can be a cost or a benefit of dispersal, depending on whether carrying capacities are sufficiently variable ( $\gamma_2 > 3 - 1/\bar{K}$ ) and whether the correlation is positive or negative.

While the consequences of these different costs of dispersal on the occurrence of ESS or evolutionary branching is still under investigation, this model seems to be promising in the sense that it might effectively capture the interaction between different costs of dispersal and the heterogeneity of the landscape inhabited by the focal species. There are at least two other ways to model costs that we have not yet addressed (cost to offspring through increased mortality rate of migrants once settled and indirect cost of dispersal due to heterogeneity in mortality rates among patches), mostly because these models would pose serious analytical challenges...

## 2.2. Diversity in metacommunities

In the case of metacommunities, *i.e.* spatially structured communities linked by dispersal, the question of diversity boils down to understanding which ingredients favour the existence of more diverse communities at a local or regional scale. Diversity at the landscape scale depends on a few processes which, in turn, depend on the relative extents of the different habitat types (Fig. 5):

- Ecological drift (stochasticity in mortality and recruitment) tends to decrease the number of species that can neutrally coexist when the underlying hospitable area decreases (Hubbell, 2001, Etienne and Alonso, 2005). Because species persisting in different sites can be different, ecological drift also contributes positively to  $\beta$  diversity (Economo and Keitt, 2008);
- Local adaptation / habitat filtering tends to select different species in patches of different habitat types, and hence increases diversity with the number of habitat types (a phenomenon also described as species sorting, Leibold et al., 2004). Having too little habitat heterogeneity means having very few different habitats to live in and, thus, tends to display only species adapted to the dominant habitat types;
- Competitive exclusion due to differential adaptation of species to their environments and/or to differences in life-history traits (fecundity, survival, age at maturity, etc.) tends to bias species persistence more than expected under neutral dynamics (*i.e.* when species traits differ so that their competitive abilities are different, species persistence becomes less stochastic and more deterministic), hence reducing  $\alpha$  diversity. However, varying competitive hierarchies and/or the strength of competitive exclusions among habitat types contributes to a higher diversity of persisting species (Mouquet and Loreau, 2002; P16);
- Dispersal limitation (and limited dispersal scale) tends to limit the possibility for regionally competitive species to dominate the landscape (Mouquet and Loreau, 2002).



**Fig. 5** (slightly modified from P21) – Drivers of diversity patterns in metacommunities. Solid arrows represent increases (where the arrow is pointing) and decreases (the origin of the arrow) in diversity at both the local scale ( $\alpha$  diversity) and as turnover in diversity among sites ( $\beta$  diversity). Arrows pointing outwards are simple loss of diversity. The thickness of arrows represents the typical strength of the process, but this may vary depending on context (*e.g.* dispersal may be more or less intense depending on patch connectivity, or ecological drift may increase in small populations). Habitat characteristics are depicted in dashed boxes on the right. Dashed lines indicate the sign of the effect of these two characteristics on the aforementioned processes, with habitat size negatively affecting ecological drift (hence, the line ending with a disk) while habitat heterogeneity increases the effect of both variable competitive hierarchies and habitat filtering (hence, the line ending with arrow).

In the following, I present two studies pertaining to the question of diversity patterns in metacommunities. The first study, conducted by Fabien Laroche as part of his PhD (P24) deals with the joint assessment of genetic and species diversity in a neutral community context. The second one, in collaboration with Nicolas Mouquet, Vincent Calcagno and Dominique Gravel, tackles the conceptual foundation of keystone communities, *i.e.* the fact that, under some conditions, some communities might disproportionately contribute to diversity (or other metrics of interests).

### ***2.2.1. Species – genetic diversity correlations in a neutral context***

Despite close parallels between the processes governing variation in genetic diversity within species and in species diversity within communities (Vellend, 2003, 2005), these two fundamental levels of biodiversity have been mainly studied separately. It has been proposed that parallel processes, including neutral processes (*e.g.* drift and migration), could generate positive species-genetic diversity correlations (SGDCs; Vellend, 2005), *i.e.* correlations between species diversity in communities and the genetic diversity measured in a focal species within these communities. However, up to now, SGDCs have only been formalised verbally, or through a few simulations (Vellend, 2005, Vellend and Geber, 2005). With the emergence of analytically tractable community models based on Hubbell’s (2001) “*unified neutral theory of biodiversity and biogeography*”, the construction of such an integrative framework has become possible and desirable.

In a recently published paper stemming from Fabien Laroche’s PhD work (P24), we propose a framework to understand SGDCs based on a unified, neutral framework at both biodiversity levels – integrated through a coalescent approach (Etienne and Olf, 2004, Wakeley, 2008). We consider a mainland-island model to explore how variation in connectivity and carrying capacity among sites, local competition and genetic mutation shape SGDCs. We then introduce the formerly ignored mutation process, which affects genetic but not species diversity. When mutation rate is low, our model confirms that variation in the number of migrants among sites creates positive SGDCs. This work provides a theoretical basis to the verbal hypothesis that variation in carrying capacity and connectivity should generate a positive SGDC. In particular, this study indicates that, even under neutral assumptions, both positive and negative correlations between diversity levels can be obtained.

To briefly summarise the results of this study, we found that:

- a. The covariance between species and genetic diversities can be decomposed in two parts: (i) a “within” component of covariance due to local competition, *i.e.* which corresponds to the statistical association of both diversity measures if the same ecological systems were to be virtually replicated; (ii) an “among” component of covariance which arises from the variation in carrying capacity ( $K$ ) and migration ( $m$ ) among sites.
- b. Under a weak mutation regime, the “within” component vanishes because the species and genetic samples become statistically independent when controlling for sample size. The covariance between species and genetic diversity thus boils down to the “among” component which, in this case, is solely driven by variation in the effective number of immigrants per site. This leads to a positive “among” component and, thus, to the expectation that SGDCs must be positive.
- c. Under a strong mutation regime, however, the “within” component of covariance can be negative or null, while the “among” component of covariance is now driven by both the variation in the effective number of immigrants per site,  $I$ , and the variation in the migration rate among sites,  $m$ . In particular, a positive correlation between  $I$  and  $m$  among sites can generate a negative “among” component of covariance and, thus, an overall negative SGDC.

Overall, these results open the way to building null models and new empirical tests that will provide a decisive improvement when interpreting SGDC patterns. They also pinpoint a logical fallacy which consists in assuming that parallel processes should always create positive SGDCs, and thus question the usefulness of the current bandwagon of empirical studies on SGDCs (*e.g.* Cleary et al.,

2006, Derry et al., 2009, Adams et al., 2011, Blum et al., 2012, Taberlet et al., 2012, Avolio and Smith, 2013) and their recent ecological interpretations (Kahilainen et al., 2014, Vellend et al., 2014, Whitlock, 2014).

### 2.2.2. *Keystone communities*

Keystone species are defined in the ecological literature as species having disproportionate importance in their community (Mills et al., 1993, Menge et al., 1994, Leibold, 1996, Power et al., 1996). Historically, this idea arose from marine ecology with the famous case study published by Paine in the late sixties on rocky intertidal communities, in which predation by *Pisaster* starfish conditioned the coexistence of several species of bivalves, limpets, barnacles, etc. (Paine, 1966, 1969, 1974). This concept has proved useful and is now often used in conservation ecology. The recognition that landscapes are more than simple collections of communities naturally paves the way for an extension of the keystone concept to metacommunities. For instance, Amarasekare (2008) recently emphasised that spatial dynamics may switch keystone status within food webs, *i.e.* the identity of the species crucial for the coexistence of the other species, from the top predator to the predator-resistant inferior competitor, depending on the level of dispersal between distant patches. The keystone concept can also be applied to biological levels above species. For instance, some habitat patches might be critically important for the long-term persistence of metapopulations (Hanski, 1994). Keystone ecological structures have been defined as “*distinct spatial structures providing resources, shelter or ‘goods and services’ crucial for other species*” (Tews et al., 2004) and, at an even larger scale, keystone habitats, as sources maintaining biodiversity (Davidar et al., 2001).

In a recent study (P16), Nicolas Mouquet, Dominique Gravel, Vincent Calcagno and I introduce the concept of keystone communities (and ecosystems) within metacommunities (and metaecosystems). We define keystone and burden communities as communities with disproportionately large impacts (positive or negative outliers, respectively) on a given metric (diversity, productivity, etc.) relative to their weight in the metacommunity. Our study shows how a simple metric, based on the effects of single-community removals, can characterise communities along a ‘keystoneness’ axis. The usefulness of this approach is illustrated with two different theoretical examples:

- a. We first studied the existence of keystone communities with respect to regional diversity in a patch-occupancy model in which each patch could only be occupied by a single species and replacement probability was governed by a competition-colonisation trade-off (Hastings, 1980, Tilman, 1994, Calcagno et al., 2006). The shape of the competition-colonisation trade-off, which links a difference in colonisation rates between two species with the probability that one species can replace the other, was parameterised by two values (Calcagno et al., 2006): its slope at the origin and the pre-emption index (*i.e.* the maximal value of the replacement probability). Each patch could belong to one of  $n$  habitat types and each habitat type had its own set of trade-off parameters. Thus, keystone communities could be traced back as communities having peculiar values of these trade-off parameters (slope and maximum of the trade-off function).
- b. In a second example, we considered a metaecosystem model based on a recently published model (Gravel et al., 2010a) that introduced the possibility that certain patches could be sources of detritus and sinks of inorganic nutrients or *vice versa*. This model described the dynamics of nutrient cycling and primary production in a heterogeneous landscape in which soil fertility, *i.e.* the amount of extrinsic input of inorganic nutrients, varied from one patch to another, as well as the competitive hierarchy among the species exploiting this pool of nutrients (in a fashion comparable with Mouquet and Loreau, 2002). In this example, the property at stake was not diversity but rather total ecosystem productivity.

The two worked examples helped distinguish environmental heterogeneity from species trait heterogeneity as determinants of keystoneness. Not surprisingly, we found that both models could

generate keystone communities; in the second case, it was even possible for “burden” communities to exist, *i.e.* communities that had particular combinations of fertilities and competitive hierarchies which tended to diminish productivity at the metaecosystem level. In the first example, keystone communities corresponded either to communities that served as refuges for poorly competitive species, *i.e.* communities with low preemptive index and shallow trade-off slope, or to communities that favoured highly competitive species, *i.e.* communities with high preemptive index and a steep trade-off slope. In the second example, keystone communities seemed to be much more simply related to the fertility of the patch (the more fertile, the more keystone), but the removal of a patch dominated by a species very efficient at nutrient uptake had thus much more impact than the removal of a patch dominated by an inefficient species, *i.e.* keystone communities also increased with a decrease in the minimal resource requirement of the dominant species within the patch.

The concept of keystone communities/ecosystems will probably be useful, not only as a fundamental step towards understanding species interactions in a spatial context, but also as a tool for the management of disturbed landscapes. In the future, such an approach can be extended to metacommunities and metaecosystems structured as a spatial network, *e.g.* splicing the work presented in (P16) with network metacommunity models (Economo, 2011).

### 2.3. Conclusions & perspectives

The question of the emergence and maintenance of diversity has been the focus of much of my work during and after my PhD defence. As such, this section might seem a little too rich for one in the four sections devoted to the four “big questions” enounced in the introduction of this synthesis. The work I can now present under the label “diversity” has been particularly enhanced by Fabien Laroche’s PhD work, which dealt with “*the study of diversity patterns, from genes to species, in metacommunities, with a focus on quasi-neutral models*” (approximate translation of the thesis’ title). Thanks to Fabien’s work, the model of the evolution of dispersal under variable kin competition (P8) has been extended to encompass communities. Based on his work, it is now conceivable to extend this model further by *e.g.* generating the same kind of diversity statistics when dispersal evolves jointly with traits such as local adaptation (P19, MSc.1 internship of Joseph Denton), settling rate (Box 2, BSc internship of Maxime Dubart) or an allocation to two concurrent types of costs of dispersal (Box 3).

In the few pages devoted to the models on the evolution of dispersal, I didn’t find the courage to pollute a quite pristine picture of a research programme focused on the evolution of a single trait with other works I have been associated with which, unfortunately, do not deal at all with dispersal. To briefly sketch these other studies, I have to acknowledge working in passing (*i.e.* as a technical commentary) on the evolution of animal personalities (P2), working, in anticipation of my current collaboration with Florence Débarre, on an application of analytical methods to the evolution of local adaptation in uncertain environments (P19), and also working on a model of the evolution of phenological traits, here exploration time in search of a good breeding site, when good sites are scarce and the link between exploration time and the bias in the probability of finding a good site is nonlinear (the lottery being governed by a Wallenius non-central hypergeometric distribution, P23). Just a brief comment: this last publication is an incentive, if need be, for correctly doing one’s work as journal referee because I was invited to be one of the authors of this paper after a first round of reviews in which I participated as a referee...

To conclude on diversity studies, I would like to highlight the fact that, in the years to come and in spite of my personal inability to conduct experimental research, I am now engaged in at least three collaborations on real biological systems that might provide clues as to biodiversity patterns and/or the evolution of dispersal.

First, I am associated with Patrice David’s ANR project AFFAIRS, which focuses on metacommunity dynamics, trait evolution and niche displacement following species invasions in freshwater assemblages of molluscs in Guadeloupe. In this context, I have supervised the BSc.



internship of Thibaut L'Honoré who worked on an extension of Calcagno et al.'s (2006) model in which competitive ability traded off with colonisation rate and also with resistance to perturbation. Results of his model are currently being re-analysed, but these might help understand how the various mollusc species observed in the West Indies might coexist, as apparently some of them are able to resist drought (Lamy et al., 2012a) while others might be more competitive and a gradient of colonisation rates might also be compatible with existing data (Lamy et al., 2012b).

Second, together with Nicolas Loeuille, I have launched a new project, ARSENIC, funded by the ANR, which aims at uncovering what evolutionary signal could be gained by looking at the association of traits determining interaction affinity (*e.g.* size) and traits related to dispersal ability, both in plant-pollinator networks and food webs. One of the specificities of this project is to combine both theoretical models and empirical approaches to test them. Indeed, with the help of database experts (Colin Fontaine, Gérard Lacroix and others) and natural-born naturalists (Bertrand Schatz, Yves Piquot, Nina Hautekète, Eric Schmitt, Pierre-Olivier Cheptou...), this project will provide data to explore the patterns that will have been previously suggested by theoretical work as potentially informative.

Last, and not least, my arrival in Lille has connected me with a community which I did not know anything about but which is seriously relevant for anyone interested in empirically testing metapopulation models. Together with Aurélie Tasiemski and Didier Jollivet, we are planning to test several predictions stemming from the literature on the joint evolution of local adaptation and dispersal (Kisdi, 2002, Nurmi and Parvinen, 2011, Blanquart and Gandon, 2014), together with some of my past (P8, P19) and current work on the evolution of dispersal (Box 1, Box 3) using the marine annelid *Alvinella pompejana*. This marine worm is widely distributed along the East Pacific dorsal (Desbruyères et al., 1998, Le Bris and Gaill, 2007), but only at hydrothermal vents which pop on and off, following a metapopulation dynamics that is not unlike the perturbation process found in Levins (1969) metapopulation model (Jollivet et al., 1995, Plouviez et al., 2010). One interesting fact is that populations of *A. pompejana* display two different morphotypes, seemingly corresponding to a “pioneer” and a “follower” type, easily characterised by allozymes linked to thermo-tolerance (Piccino et al., 2004) and their life history traits (fecundity, size, etc.; Jollivet, pers. comm.). All in all, available data so far suggest that this species might display a polymorphism of dispersal traits, with a potential association of dispersal type with different local adaptations, especially through different thermo-tolerances. The exploration of such a model in the near future will provide a good empirical basis for tests of model linking the evolution of local adaptation and dispersal.

### 3. Complexity and functioning: towards spatial interaction networks

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Je suis les liens que je tisse avec d'autres.

Albert Jacquard, *Petite philosophie à l'usage des non-philosophes*

One of the intrinsic difficulties of biology, as a science, is that it is fraught with variability. Contrary to statistical mechanics, which generally deal with particles of the same type (even if they do not all share the same spin, velocity, etc.) or a few countable number of types, ecology and evolution must deal with inter-individual variability within and among species. From a contemplative naturalist viewpoint, such variability is a boon – think of whether birders would exist in a world in which bird variability would boil down to as few species as bosons and fermions... – but for a theoretician, this can turn into a nightmare of sorts, especially if one clings too strongly to the reductionist paradigm.

The title of a paper, which has been quite influential in my view of science, summarises well the paradigm of complex system science: “*More is different*” (Anderson, 1972). Because ecological systems are inherently variable, made of different parts and spatially fragmented, the large spatial scale dynamics of such systems – at evolutionary and ecological time scales – will not be accessible through a reductionist approach that would “scale up” within-patch dynamics to a whole metapopulation.

Clusters of individuals that interact preferentially, due to spatial segregation or otherwise, have intra- and inter-cluster dynamics. Both dynamics interact to shape meta-cluster dynamics. To give an evolutionarily motivated example, the existence of kin selection acting on the evolution of dispersal is a by-product of the spatial structure of populations; within each population, dispersal would not evolve on its own, it is only within the connected metapopulation that evolving dispersal acquires an evolutionary meaning. Because relatedness, which is the notion at the core of kin selection, is the product of a local quantity (local population size) and a property emerging from the spatial structure of the metapopulation (the immigration parameter), the notion of kin competition is meaningless in the absence of the notion of metapopulation, *i.e.* local selective pressures change with the scale of the system considered.

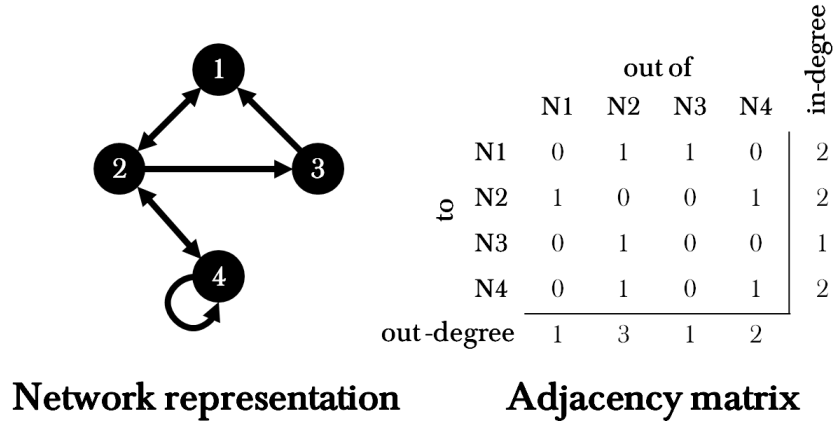
In the context of spatially structured ecological systems, one mathematical object that naturally arises is networks (Fig. 6). Networks represent the arrangement of nodes<sup>\*</sup> (or vertices<sup>\*</sup>) connected by links<sup>\*</sup> (or edges<sup>\*</sup>). In a sense, every situation in which interactions between “agents” can be represented as a pairwise affair (*i.e.* there are no three-way [or more complicated] interactions like chemical reactions of the type  $A + B + C \rightarrow ABC$ , but rather only pairwise interactions of the type  $A + B \rightarrow AB$ ) is amenable to a representation as a network. In ecology, the network representation is particularly fit to represent two different objects (P22, P26):

- a. When nodes are populations of the same species, living in different spatial patches, networks can be used to describe the exchange of migrants among populations (*e.g.* Economo and Keitt, 2008), *i.e.* spatial networks of nodes in which links represent diffusion / migration. All nodes are *a priori* of the same type, but links can be directed or undirected. Such models have been used, *e.g.* to represent spatially explicit metapopulations (Adler and Nuernberger, 1994, Hanski and Ovaskainen, 2000, Ovaskainen and Hanski, 2001, Gilarranz and Bascompte, 2012) or metacommunities (Economo and Keitt, 2008, 2010, Economo, 2011). Network approaches to spatially structured ecological systems have been applied to numerous questions in the past ten years. For instance, network structure modifies conditions for species persistence and coexistence at the regional scale, both in models based on neutral community ecology (Economo, 2011) or in those focusing on species occupancy *à la* Levins (Roy et al., 2008, Gilarranz and Bascompte, 2012). More generally, network-based approaches to spatially structured ecological systems bridge the gap between local and regional phenomena by describing the dynamics of large-scale objects as resulting from local persistence and dissemination processes.
- b. When nodes refer to different species, networks can represent biotic interactions among species, such as food webs or mutualistic networks, *i.e.* interaction networks in which nodes represent species (or populations thereof) and links stand for a given type of interaction between individuals of these species (*e.g.* predation, pollination, ...). Such networks can be multipartite<sup>\*</sup> (*i.e.* dividable into species groups with no interaction within a group) when guilds can be simply identified (*e.g.* plants *vs.* pollinators) or unipartite<sup>\*</sup> (*i.e.* not dividable as above) when it is less clear (*e.g.* food webs). Links can be directed when direction conveys meaningful information (especially in unipartite networks). Network representations have been the rule for food webs, plant-seed disperser associations, plant-pollinator associations (*e.g.* P25) and other types of interaction networks since seminal papers (Paine, 1966, Pimm, 1980, Yodzis, 1981, Briand and Cohen, 1984, Cohen and Newman, 1985, Jordano, 1987, Yodzis, 1998).

As a side note, one should also acknowledge other uses of networks in evolutionary ecology, *i.e.* when nodes are individuals, a network may describe different kinds of interactions among individuals of a group, such as pedigrees, social interactions (Wasserman and Faust, 1994) and clustering (Dupont et al., 2011), or be used to model their evolutionary dynamics (Le Galliard et al., 2005, Ohtsuki et al., 2006, Zhong et al., 2013, Débarre et al., 2014a).

Functional ecology is a sub-discipline within ecology focusing on the “roles” of the different species within communities. The role of a given species is most often inferred from the knowledge of species

traits (Lavorel and Garnier, 2002, Ackerly and Cornwell, 2007). In that vein, ecosystem functioning can be defined as the set of “roles” or functions represented in a given ecosystem and the dynamics of such functions. For practical reasons, empirical approaches to ecosystem functioning have often been restricted to the study of a single trophic level – most often, primary producers.



**Fig. 6** – Introduction to networks. The left-hand side panel depicts a directed network connecting four nodes. The right-hand side panel summarises the same information using the adjacency matrix of the network. In this matrix, a “1” represents an existing link, a “0”, the absence of such a link. Summing elements on a single row yields the in-degree (*i.e.* the number of incoming links) of the corresponding node; summing elements on a single column corresponds to the node’s out-degree (*i.e.* the number of outgoing links).

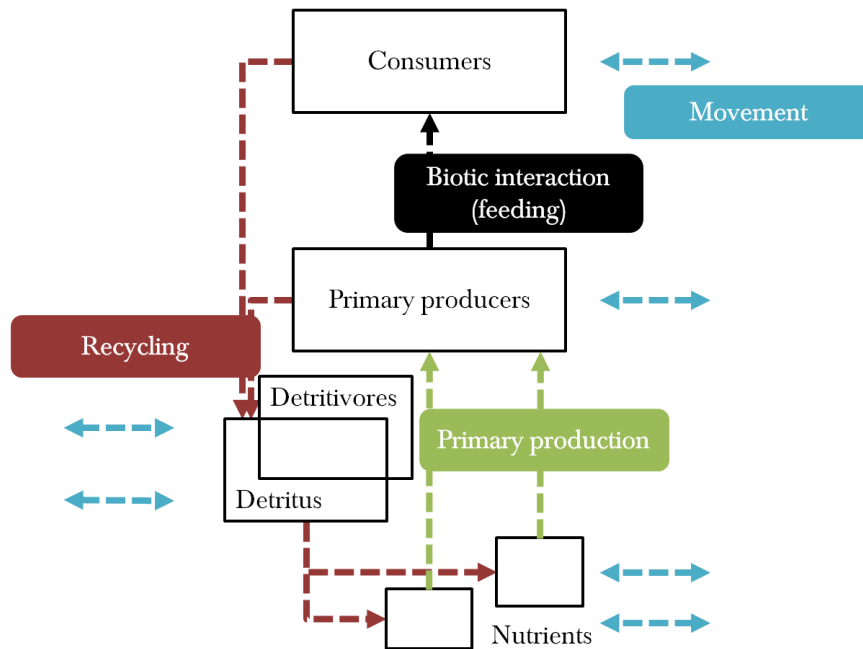
Most of these functions can be classically summarised as fluxes and stocks resulting from processes moving matter and energy among the different agents of a spatially structured ecosystem (P11, P21; Fig. 7) – *e.g.* food web functioning is characterised by the dynamics of matter and energy fluxes among trophic levels. To make a long story short, these fluxes (Fig. 7) can be due to:

- a. transfer of matter from the abiotic compartment to the biotic compartment through primary production,
- b. biotic interactions between individuals (*e.g.* transfer of matter due to feeding or mutualism),
- c. the death and subsequent recycling of an organism by another organism (*i.e.* not a direct interaction, but feeding through decomposition of dead organic matter), or
- d. the physical movement of living individuals from one place to another, or the physical movement of inorganic matter or detritus between locations (Loreau et al., 2003, Duffy et al., 2007).

Because all these fluxes are controlled by species traits, quite a large part of functional ecology has historically focussed on the study of species traits as proxies for the evaluation of ecosystem functioning (Violle *et al.*, 2007). By extension, the distribution of such traits among species from the same guild or trophic level is expected to reflect a more or less efficient functioning of the system, *i.e.* a more or less intense transfer of matter across trophic levels. The impacts of perturbations – be they press or pulse – on the functioning of steady state ecosystems may be mathematically studied through linearising the ecosystem’s dynamics and looking at its Jacobian matrix.

I have only begun to work on networks and their functioning since I finished my PhD, but developments on these aspects have greatly benefited from my interaction (no pun intended) with Julia Astegiano (post-doc at the CEFÉ between 2012 and 2013, responsible for P25, and with whom I am still remotely collaborating on plant-pollinator metacommunities), Dominique Gravel (professor at the Université du Québec à Rimouski on the other side of the Atlantic, who spent a year at ISEM just when I was finishing my PhD, and with whom I worked on P11, P13, P16 and P17) and two working groups funded by the Réseau National des Systèmes Complexes (RNSC), focusing on the modelling

of biodiversity networks in space (DyBRES working group) and the modelling of seed exchange networks in agroecosystems (MIREs working group).



**Fig. 7** (excerpt from P21) – Schematic description of possible matter and energy fluxes in spatially structured ecosystems (note that mutualistic and symbiotic interactions are omitted for clarity as this scheme mainly describes food webs). Open rectangles correspond to biotic and abiotic compartments; filled boxes, to processes creating fluxes (see main text for details).

The following subsections focus on aspects of my work pertaining to the question of network complexity and functioning in ecological systems, *i.e.* the use of network approaches to model spatially structured ecological systems and questions related to the complexity of interaction networks. In conclusions & perspectives, I briefly present project ARSENIC, recently funded by the ANR, and which is designed to tackle questions related to the spatial structure of interaction networks, thus bridging a conceptual gap between interaction networks and network approaches to metapopulations.

### 3.1. Spatial network and metaecosystem approaches

#### 3.1.1. Discontinuous habitats and metapopulations

A major practical challenge in ecology is to characterise habitat fragmentation and heterogeneity within a given landscape, and make predictions linking such landscape characteristics with local and regional persistence of organisms (Semlitsch and Bodie, 1998, Fahrig, 2002, 2003). Indeed, each species displays specific needs in terms of resources and environmental conditions fit for survival and reproduction – what is usually covered under the broad concept of the ecological niche (Hutchinson, 1957). Assessing habitat fragmentation and heterogeneity is thus synonymous with mapping geographic areas in which environmental conditions might be suitable for the founding and subsequent persistence of populations. These areas often form a discontinuous whole (because of habitat fragmentation), so that suitable areas are generally separated from one another by areas that are unsuitable for population persistence. A discontinuous habitat can implicitly define a network in which vertices are fragments of habitat (potentially harbouring populations) and links represent fluxes of individuals or genes among habitat fragments.

Understanding the dynamics of spatially structured ecological systems requires linking local and regional scales. At the local scale (the fragment scale), individual organisms can immigrate, reproduce, live and die; at the regional scale (metapopulation scale), populations can be founded, persist for a time and go extinct. Concepts and models linking local and regional dynamics have been historically defined using the Greek prefix “meta”, by analogy with the first such concept, metapopulation. A metapopulation is a population of populations, *i.e.* it is a spatial network in which each vertex can harbour a population of a given species (Levins, 1969, Levins, 1970, Hanski and Gaggiotti, 2004). As a population is defined by demographic processes (birth and death), a metapopulation can be defined by its own demographic processes, at larger spatial and temporal scales, *i.e.* “births” and “deaths” of populations. In the context of metapopulation models, the terms colonisation and extinction are often used to describe such processes.

### ***3.1.2. Metacommunities and metaecosystems***

By extension of the metapopulation concept, a metacommunity is a spatial network in which each vertex can harbour a community, *i.e.* a set of individuals from different species sharing some limiting factors (Leibold et al., 2004, Holyoak et al., 2005, Economo and Keitt, 2008). When these species are structured as interaction networks or more generally as an ecosystem, the terms meta-network, spatial interaction network or metaecosystem (Fig. 8) are also used (Holt, 1997a, Loreau et al., 2003; P11). Because the definition of metaecosystems is very general, it encompasses other less general models such as spatial interaction networks (everything but recycling and nutrient/detritus dynamics) and metacommunities (only competitive interactions are accounted for, and the dynamics of abiotic components are implicit). Spatially structured food web modules (Amarasekare, 2008), for instance, can be understood as some sort of simplified metaecosystems. Describing a metaecosystem usually means accounting for:

- The network of ecosystems and their hierarchical structure, especially relative to organism dispersal and nutrient/detritus diffusion. For instance, a series of lakes along a watershed displays some amount of hierarchy insofar as upstream lakes “give” more than they “receive” from downstream lakes in terms of nutrient/detritus diffusion and also in terms of organism dispersal for species that disperse passively;
- The intrinsic habitat heterogeneity, *i.e.* the variation in process rates among different ecosystems. For instance, some habitats might be more or less prone to nutrient leaching or detritus recycling through abiotic processes (erosion, etc.);
- The “template ecosystem” detailing all potential interactions between all potential partner pairs. Each local ecosystem is then an instantiation of this template, given the local conditions in the habitat patch. In the case of a food web, such template equals the knowledge of the whole food web at the regional scale (*e.g.* P13).

Historically, the driving pressure behind building metaecosystem models instead of just investigating metacommunities was (i) a need to account for the nutrient balance at the regional scale (Loreau et al., 2003, Loreau and Holt, 2004) and (ii) a way to investigate the effect of different movement rates between plants, detritus and nutrients (Gravel *et al.*, 2010a). From the ecosystem ecology side, there is also quite a substantial motive for putting ecosystems in spatially structured models, most notably the fact that landscape ecosystem models (Running et al., 1989, Turner and Romme, 1994), though sometimes incorporating the diffusion of nutrients and material across locations, were quite coarse in their treatment of the different abiotic compartments and did not account at all for the dispersal of plants and consumers.

Metapopulation, metacommunity and metaecosystem concepts are tailored to answer different questions. For instance, to study the persistence of a threatened species, the metapopulation concept will help assess conditions for species survival. When the topic of interest is to preserve a species-rich tropical forest, metacommunity models will bring answers for the conservation of biodiversity.

**Box 4: Tilman's resource ratio theory in metaecosystems**

in collaboration with **Tanguy Daufresne, Dominique Gravel, Mathew Leibold and Nicolas Mouquet**

The interaction between community assembly and ecosystem attributes depends on many distinct processes including nutrient consumption, recycling, export and import of materials by the biota. It is even more complex because stoichiometric relationships constrain how processes involving one element may be connected to another. For instance, nitrogen and phosphorus fluxes are strongly linked through various processes such as plant uptake or mineralisation. Recent work has revealed important consequences of stoichiometric mechanisms within ecosystems (Sterner and Elser, 2002). Export and import of materials and organisms between ecosystems will also be important as ecosystems are embedded in spatial networks called metaecosystems. Spatial fluxes of nutrients will strongly affect local stoichiometric constraints and ecosystem dynamics although their effects have not been well studied yet (but see Ryabov and Blasius, 2011, Haegeman and Loreau, 2014).

The resource-ratio theory of plant coexistence (Tilman, 1982, 1988) provides an adequate framework to study the intimate linkage between ecological stoichiometry, community assembly and ecosystem functioning (Daufresne and Loreau, 2001). The theory applies to two resources the  $R^*$  principle of competition theory. Its main prediction is that the stable coexistence of two species requires a particular ratio of the two most limiting resources (*i.e.* nutrients). Owing to its accessible graphical representation, the theory has a central position in most ecological textbooks (*e.g.* Begon et al., 2006). It was also further developed to derive a vast array of secondary predictions such as the impact of resource heterogeneity and fertilisation on species richness and successional dynamics (Tilman, 1982, 1985). Leibold (1995) extended the theory to include the effect of herbivory on species coexistence, and Chase and Leibold (2003) built on the graphical representation to integrate the concepts of Eltonian and Grinnellian niches. Daufresne and Hedin (2005) recast the theory using consumer-resource mathematical formalism and included the effect of nutrient recycling on plant coexistence. While resource ratio theory is implicitly spatial in its original formulation, there are few attempts at integrating this theory within metacommunity ecology (see *e.g.* Miller et al., 2004, Mouquet et al., 2006, Kato et al., 2007).

In this study, we extend the resource ratio theory of competition to heterogeneous metaecosystems. We consider two consumer species growing on two essential resources in a spatially heterogeneous metaecosystem of two patches (Gravel et al., 2010a). We account for internal resource recycling within each patch (Daufresne and Hedin, 2005) and for diffusive exchanges of nutrients, detritus and consumers between the two patches. Our main question is to understand how such exchanges alter the coexistence of consumer species. As a first step, we looked at whether diffusion of each of the three compartments affected the consumption vector, detritus recycling vector, supply point and zero net growth isoclines (ZNGI; Daufresne and Hedin, 2005).

The system of equations describing the dynamics of consumer species  $i$  in patch  $x$  ( $P_{ix}$ ), detritus pool due to the death of individual from species  $i$  in patch  $x$  ( $D_{ix}$ ) and nutrient pool of resource  $j$  in patch  $x$  ( $N_{jx}$ ) is:

$$\frac{dP_{ix}}{dt} = G_{ix}(N_{1x}, N_{2x})P_{ix} - m_i P_{ix} - d_p (P_{ix} - P_{jy}) \quad (B4.1)$$

$$\frac{dD_{ix}}{dt} = m_i P_{ix} - r D_{ix} - d_D (D_{ix} - D_{jy}) \quad (B4.2)$$

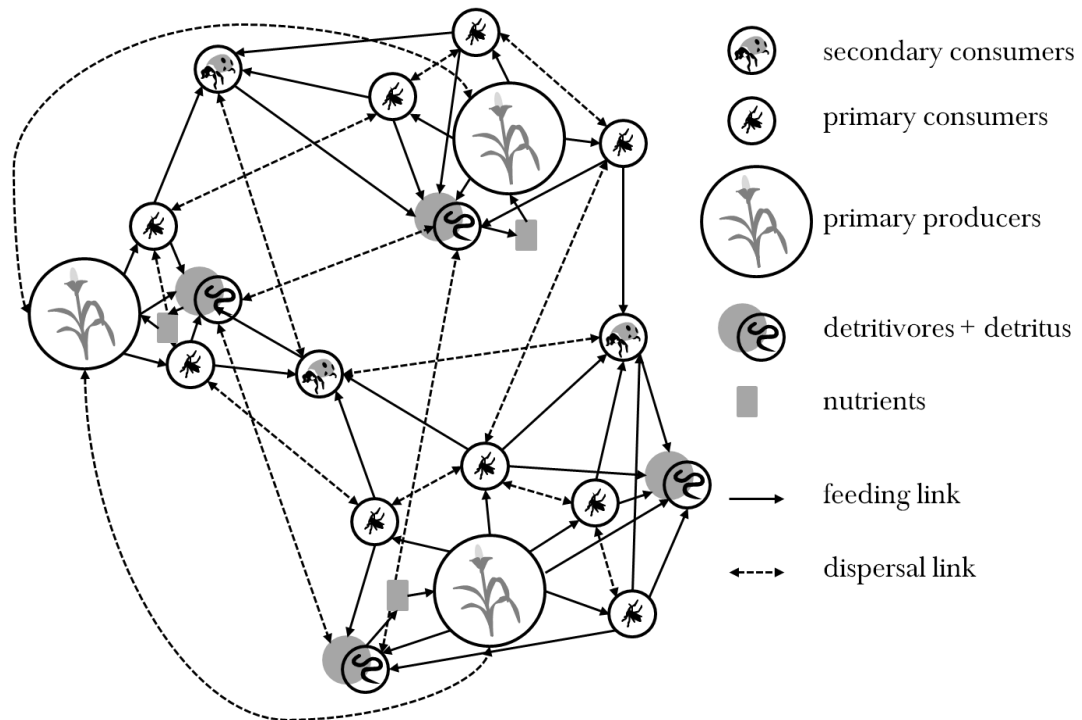
$$\frac{dN_{jx}}{dt} = S_{jx} - e N_{jx} - \sum_{i=1}^s q_{ij} G_{ix} P_{ix} + \sum_{i=1}^s r(1 - \phi) q_{ij} D_{ix} - d_{N_j} (N_{jx} - N_{jy}) \quad (B4.3)$$

where  $G_{ix}(N_{1x}, N_{2x})$  is the growth function of species  $i$  in patch  $x$ ,  $m_i$  is mortality rate of species  $i$ ,  $d_p$  is the diffusion rate of consumers,  $d_D$  is the diffusion rate of detritus,  $d_{N_j}$  is the diffusion rate of resource  $j$ ,  $r$  is the recycling rate,  $e$  is the rate of nutrient leaching out of the system,  $q_{ij}$  is the quota of resource  $j$  within the total biomass of consumer  $i$ , and  $\phi$  is the fraction of inorganic nutrient lost during the mineralisation process.

Setting diffusion rates to be positive one at a time, we were able to obtain the following results:

- Consumer diffusion has an indirect effect on both the consumption and detritus recycling vectors and a direct effect on ZNGIs;
- Detritus diffusion has an indirect effect on the consumption and detritus recycling vectors and on ZNGIs;
- Nutrient diffusion has a direct effect supply points and both vectors, and an indirect effect on ZNGIs;
- Setting different diffusion rates for the different nutrients induced a rotation of the consumption and recycling vectors.

Our results so far suggest that the different diffusion rates might have quite different effects on the coexistence of species under the resource ratio theory.



**Fig. 8** (excerpt from P21) – Schematic representation of a metaecosystem. The underlying ecosystem is assumed to consist solely of detritivores, primary producers, primary consumers and secondary consumers. Directed solid arrows represent feeding links between populations of different species while reciprocal dashed arrows stand for dispersal links between populations of the same species.

Spatial approaches to the functioning of ecosystems, based on metacommunity and metaecosystem theory, have proved useful to understand several ecologically relevant phenomena. For instance, coupling nutrient recycling dynamics among different locations, at the scale of a metaecosystem, taking into account detritus and raw nutrient fluxes, leads to richer theoretical predictions on the dynamics of such systems (Gravel et al., 2010a, Gravel et al., 2010b). The integration of food webs in a spatial context also fostered a richer theory able to take the spatial and temporal variability of observed food webs into account (Rooney et al., 2008, Pillai et al., 2011; P12, P13).

### 3.1.3. *Metaecosystem principles and assumptions*

As a theory trying to explain general features of ecological functioning, metaecosystem theory relies on a few principles and assumptions (Loreau et al., 2003; P11). Some of them are just translations of more general principles and assumptions to the field of ecosystem ecology – and should generally apply to all situations. Other principles and assumptions should be seen as guidelines for a more general, but less precise (*sensu* Levins, 1966), way of building an ecosystem model (P11, P21):

**Patch models.** Metaecosystem models have been designed as an extension to models already used in a metacommunity context. Therefore, most metaecosystem models are based on a discrete perception of space where each ecosystem is equated with a single patch (Loreau et al., 2003; P11).

**Mass balance.** A first principle that potentially entails large consequences for the functioning of metaecosystems is that of mass balance (Loreau *et al.*, 2003). This amounts to noting that everything that flows in must flow out when looking at a sufficiently large system on a sufficiently long period. When dealing with a large and somewhat autonomous metaecosystem, mass inputs must equal mass outputs at the metaecosystem scale. One important consequence of this principle is that sources and sinks rarely coincide for plants and their resources (Loreau et al., 2003; P17).

**Stoichiometric balance and constraints.** Ecological stoichiometry, *i.e.* the study of nutrient quotas in abiotic pools and in living organisms (Elser et al., 2000, Sterner and Elser, 2002, Loladze and Elser,

2011) is being extended to spatially structured contexts (Miller et al., 2004, Kato et al., 2007, Lenton and Klausmeier, 2007, Danger et al., 2008, Yoshiyama et al., 2009). Spatial ecological stoichiometry is an extension to the aforementioned mass balance principle (P11), taking into account the fact that inputs and outputs must be balanced element-wise, *i.e.* for Carbon (C), Nitrogen (N), Phosphorus (P) and other elements as well (Sterner and Elser, 2002, Miller et al., 2004). Because the building blocks of life (*i.e.* mitochondria, DNA, RNA, ribosomes, etc.) have tightly constrained chemical compositions, it is expected that the fluxes of elements within a metaecosystem will be constrained by the mass balance principle as well as by the inability of life to be sustained under certain stoichiometric conditions. From another perspective, the very fact that heterotrophic organism's stoichiometry is less plastic than those of primary producers (Van de Waal *et al.*, 2009) and the fact that certain components of life require a given ratio of P:N elements (Loladze and Elser, 2011) are two other constraints that are bound to affect the occurrence of sources and sinks for a particular element. Advances are needed to understand how stoichiometry is influenced by spatial structure, *e.g.* through the existence of biogeochemical hotspots (McIntyre *et al.*, 2008) or by stoichiometric imprinting of dominant organisms (Van de Waal *et al.*, 2009). Resource ratio theory (Tilman, 1982) has been one of the dominant recurring models to explain the coexistence of species with different ecological niches, especially among primary producers. In Box 4, a model currently developed to understand resource ratio theory in a spatial context is presented.

**Natural selection in metaecosystems.** Because metaecosystem theory is not solely geared towards understanding the functioning of ecosystems, but also solidly grounded in the foundations laid out by metapopulation and metacommunity theories, the movement of biotic agents within a metaecosystem are bound to be governed by how organisms perceive their environment and where they thrive. Essentially, this means that biotic flows are more likely expected from regions offering low fitness to regions offering high fitness, *i.e.* from evolutionary sinks to sources (Abrams, 1997, Holt, 1997b, Abrams, 2000, Kawecki, 2004). Such 'habitat assessment' or foraging behaviour can lead to what has been dubbed as the 'ideal free distribution' (Krivan, 2003), or at least to a non-random distribution of individual organisms across the landscape. Such a distribution is bound to alter ecosystem processes through either trait- or material/energy-based effects (Abrams, 2000; P11).

**Sources and sinks.** Understanding the spatial structure of ecological systems naturally leads to considering the notions of "sources" and "sinks", *i.e.* of certain locations being net exporters or importers of certain species or abiotic components (Pulliam, 1988, Kawecki, 2004; P17). When dealing with a single species living in a metapopulation, source and sink concepts are important to understand population genetics and the origin of immigrants in future generations – and thus the evolutionary dynamics of the focal species – with source populations contributing more than sink populations, in proportion to the reproductive values of these populations (Rousset, 1999, Holt et al., 2003, Holt, 2011). In metacommunities and metaecosystems, a location can be simultaneously a source and a sink, but at different biotic or abiotic compartments (Mouquet and Loreau, 2003, Gravel et al., 2010a) – for instance, a location can be a net exporter of herbivores and a net importer of carnivores. This conceptual sophistication is needed to model and understand matter and energy fluxes between different types of habitats, *e.g.* between aquatic and terrestrial ecosystems (Polis and Hurd, 1995, Srivastava and Jefferies, 1996, Nakano and Murakami, 2001, Helfield and Naiman, 2002).

**Keystone ecosystems.** In the vein of source/sink studies, metaecosystem theory offers the opportunity to study the importance of different ecosystem patches in relation to a particular metaecosystem property. For instance, certain habitat patches could have a large beneficial and disproportionate effect on metaecosystem productivity, *i.e.* qualify as keystone ecosystems (P16) or key habitats (Davidar *et al.*, 2001).



### 3.1.4. Network approaches to spatially structured systems

In spite of their exaggerated simplicity, “meta” concepts might help understand complex dynamics. In models inspired from these concepts, the structure of the habitat is represented as vertices within a network with a simplified geometry, and links yield a simplified representation of fluxes between vertices. Network topology is bound to affect the dynamics of such systems, *e.g.* through the distribution of degrees\* among vertices (Newman, 2002) or, almost equivalently, through the dominant eigenvalue of the adjacency matrix of the underlying graph (Ovaskainen and Hanski, 2001, Chakrabarti et al., 2008). One important question is then to understand what kind of network emerges from the spatial heterogeneity in habitat quality and the intrinsically 2D nature of suitable habitat maps – still an open question that approaches inherited from physics, such as percolation models, might help solve in the years to come (Huth et al., 2014). Another useful advance in our understanding of spatially structured ecological systems comes from the concept of network modularity (Newman, 2004b, Newman, 2006a, b): as populations exchange migrants preferentially at a certain spatial scale, spatial networks are intrinsically modular (Fletcher et al., 2013) and this might, in turn, affect the persistence of such metapopulations or metacommunities. In Box 5 (see also Fig. 9), I describe a model currently under study which extends the dispersal evolution model studied in (P8) to account for the modular nature of metapopulations.

Regional dynamics are governed by two types of processes: local persistence of a population at a vertex and dissemination between vertices. For instance, in a metapopulation, local persistence is defined by the probability that a population gets extinct during a given time interval while dissemination is represented by the probability that an initially empty vertex becomes colonised by a nearby vertex. The common goal of such models is generally to assess under which conditions a non-trivial equilibrium of vertex occupancy can emerge and allow species persistence on sufficiently long time scales (Gurney and Nisbet, 1978, Eriksson et al., 2013, Barbillon et al., 2015). Whatever the ecological object under study, two big classes of models have been studied (Hanski and Gyllenberg, 1993), in a way that is reminiscent of the distinction between micro-canonical, canonical and grand canonical ensembles in thermodynamics:

- a. Autonomous networks, governed solely by local persistence and dissemination rules that are internal to the network;
- b. Forced networks, in which local persistence is still an internal process, but dissemination is mainly seen as an external forcing factor.

The model proposed in Box 6 is a mix of these two approaches insofar as it deals with a metapopulation model fed both by exchanges of migrants between connected vertices and also by external immigration from an unknown source – a class of models usually denominated as  $\varepsilon$ -SIS or SISa models (Hill et al., 2010, Van Mieghem and Cator, 2012).

## 3.2. Interaction networks

Communities of interacting species, be they interacting as predators and preys, mutualist partners, hosts and pathogens, can be represented as networks. The study of the complexity of these networks then boils down to (i) understanding the rules governing the topology of these interactions and (ii) assessing how the structure of these networks drives ecological dynamics. Food webs are probably the most intuitive ecological concept to the general public: the concept of chains representing “who-eats-whom” can be simply used to teach why the presence of predators might benefit plants through limiting pullulation of herbivores (Hairston et al., 1960, Oksanen et al., 1981). However, food webs appear simple on the surface only; as soon as phenomena such as omnivory, detritivory or nutrient recycling are taken into account, food webs paint a richer, more complex picture (Polis and Strong, 1996, Moore et al., 2004). Moreover, food webs are inherently spatially structured, *i.e.* trophic interactions have specific spatial scales – foraging spatial scales – which might differ from the scales at which individual interact within their own species (*e.g.* reproduction or dispersal scales) and define the spatial framework of predator-prey interactions (Holt, 1997a, 2002; P11).

### Box 5: Two connected metapopulations and an evolutionary phase transition

in collaboration with **Fabien Laroche**

In classic, spatially implicit, models of dispersal evolution (*e.g.* Hamilton and May, 1977, Comins et al., 1980, Frank, 1986), one neglected aspect is the effect of the spatial arrangement of patches on the evolution of dispersal. Others have tried to remedy this by casting their models as spatially continuous and explicit, and thus focusing on the evolution of dispersal kernels (Bolker, 2010, Cantrell et al., 2010, North et al., 2011, Fronhofer et al., 2015). However, such models are often analytically intractable, thus difficult to completely grasp without resorting to a high dose of computer simulations.

In this study, our objective is to connect a model of the evolution of dispersal in a landscape with heterogeneous carrying capacity (P8) with the fact that such heterogeneity might be spatially explicitly structured. To do so, as in (P8), we consider a null-sum ecological model in which each dead individual is immediately replaced by a new one, randomly chosen out of a pool of local and immigrant juveniles. Carrying capacity is assumed heterogeneous ( $K$ ) with given statistical moments ( $\bar{K}$ ,  $\gamma_2$ ,  $\gamma_3$ ). We assume the existence of two separate “modules” within the metapopulation (Fig. 9), the first one being characterised by moments indexed by  $p$ , the second one characterised by moments indexed by  $q$ . Let  $c_0$  be the cost of dispersal within a module and  $c_1$  the cost of dispersal among modules. We assume that parameter  $\varphi$  determines the proportion of migrants remaining within their natal module, and that this proportion is the same in both modules. Parameter  $\varphi$  can help mimic a completely modular metapopulation ( $\varphi = 1$ ) or a bipartite metapopulation ( $\varphi = 0$ ).

The general fitness criterion for this model can be obtained as the leading eigenvalue  $\lambda$  of the  $R_m$  matrix (Diekmann et al., 1990; P3), here noted  $\mathbf{R}$  and given as:

$$\mathbf{R} = \begin{pmatrix} \pi R_p & 0 \\ 0 & (1-\pi)R_q \end{pmatrix} \begin{pmatrix} \frac{(1-c_0)\varphi}{\pi} & \frac{(1-c_1)(1-\varphi)}{\pi} \\ \frac{(1-c_1)(1-\varphi)}{1-\pi} & \frac{(1-c_0)\varphi}{1-\pi} \end{pmatrix} \quad (\text{B5.1})$$

where  $R_p$  and  $R_q$  are partial metapopulation fitness in modules  $p$  and  $q$ , and  $\pi$  is the proportion of patches belonging to module  $p$ . The  $\pi$  and  $1-\pi$  at denominators in the right-hand side matrix represent the effect of patch numbers within modules: the expected number of immigrants landing in a focal patch within module  $p$  is proportional to one over the total number of patches in this module, *i.e.* to  $1/\pi$ . Using the same techniques and calculus described in (P8), we can obtain the partial invasion fitness for the mutant type  $d_m$  with resident  $d$ :

$$R_p(d_m, d) = \sum_K \frac{{}_2F_1\left[1, 1-K; 2-K - \frac{dL_p}{1-d}; \frac{1-d_m}{1-d}\right] d_m K \pi_{K,p}}{(1-d)(K-1) + dL_p} \quad (\text{B5.2})$$

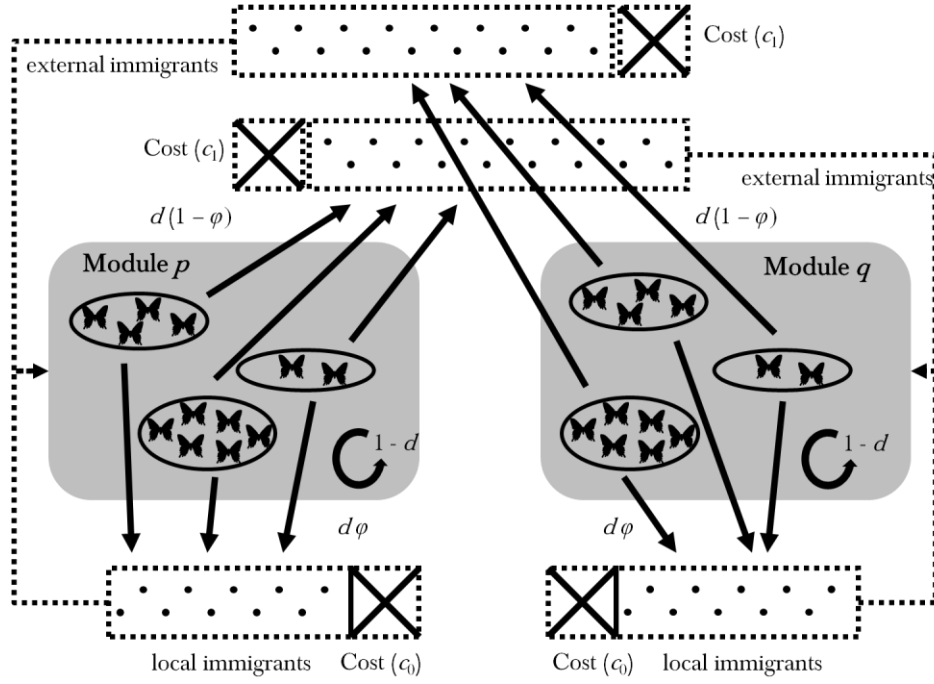
where  $L_p$  is the effective immigrant pool as seen from module  $p$ :

$$L_p = (1-c_0)\varphi \bar{K}_p + (1-c_1)(1-\varphi) \left(\frac{1-\pi}{\pi}\right) \bar{K}_q \quad (\text{B5.3})$$

Our results so far point at an interesting result: even with non-skewed distributions of population sizes in both modules and overall (*e.g.* putting two uniform distributions of carrying capacity, but with different means), a high modularity score ( $\varphi \approx 1$ ) can lead to disruptive selection on dispersal, as would have been the case in the initial, non-modular model with positively skewed distributions of carrying capacity (P8). In the light of Fabien Laroche’s PhD results (see subsection 2.1.2), especially the fact that in the non-modular model, one expects a statistical association of dispersal rates with carrying capacities, this result suggests that varying values of the “modularity-inducing parameter” ( $\varphi$ ) might affect this association and possibly induce phases transitions between at least three different states:

- (no modularity, ESS) A state in which individuals disperse at random between modules and the overall distribution of carrying capacity is not skewed enough, so that selection leads to a unique dispersal ESS;
- (no modularity, branching) A state in which individuals disperse at random between modules and the overall distribution of carrying capacity is skewed, thus inducing branching of dispersal rates and an association between small patches and high dispersal.
- (modularity, ESS) A state with selection towards two different ESS (one for each module), and thus an association between high dispersal and all patches of the module with the lower average carrying capacity.

One could also imagine more complicated and organised states, *e.g.* in metapopulations that are strongly modular and in which each module induces evolutionary branching of dispersal rates.



**Fig. 9** – Structure of the metapopulation model used to study the evolution of dispersal under a variable distribution of carrying capacity in two metapopulation modules,  $p$  and  $q$  (model presented in Box 5). Ovals indicate patches, with variable carrying capacity, butterflies are individuals. Dotted boxes represent the different propagule pools, after applying the cost of dispersal, which removes a certain fraction of propagules (indicated as “cost”). Solid arrows represent the flows of offspring (a proportion  $d$  is dispersed, and  $1 - d$  remains in the natal patch; among the dispersed fraction, a proportion  $\phi$  goes to the local propagule pool and the rest goes to the propagule pool emigrating towards the other module). Dotted arrows correspond to the flows of propagules (dispersed offspring).

In a spatially structured context, tackling the questions of interaction network complexity and dynamics requires modelling species interaction networks in a fragmented habitat (Fortuna and Bascompte, 2006, Amarasekare, 2008, Gravel et al., 2010b; P11, Box 7). The question of network structure and complexity with spatial structure (or at least, with replicates of networks of similar type) is a current “bandwagon” in ecological research, with more and more studies proposing new views and methods on how to best tackle practical matters, such as the beta-diversity of links among networks (Poisot et al., 2012), ways to integrate different types of interaction within a multiplex ecological network, *i.e.* a network with more than one type of interactions (Kéfi et al., 2012) or the expected link between modularity and nestedness\* measures (Fortuna et al., 2010). As already mentioned, models developed so far suggest that the spatial structure of food webs might result in certain patterns observed in nature, such as the upper bound to food chain length (Pillai et al., 2011; P12) or the link between diversity and connectance\* in food webs (P13).

When dealing with spatially structured food webs, a fundamental and recurrent question is to understand how the combination of bottom-up and top-down controls of species abundance or occupancy, the number of predator and prey species per focal species (*i.e.* their in- and out-degrees in a directed network of “who-eats-whom”) and the dispersal ability of each species shape the resulting distribution and abundance of the different species. In this context, two specific questions arise:

- Does trophic specialisation affect species occurrence? Can a species’ occurrence be reliably predicted from its diet breadth?
- Do bottom-up and top-down controls affect the complexity of realised food webs? Is the number of trophic levels constrained by these processes at large spatial scales?

## Box 6: Directed networks as models for seed exchange... or metapopulations

in collaboration with **Maxime Dubart, Francisco Laso and Doyle McKey**

In the field of ethnobotany, an important is to understand how the diversity of traditional varieties of cultivated crops is maintained *in situ*. One possible answer to this question comes from considering the networks of seed and other plant material circulation among farmers (P15). For theoretical ecologists accustomed to metapopulation and metacommunity models, a set of farmers exchanging seeds looks very much like a metapopulation, with the notable exception that exchanges might actually be directed (although this might actually be a desirable property to model metapopulations of marine organisms, e.g. Jollivet et al., 1999), *i.e.* it may be possible for a variety to be shared by farmer A with farmer B while the reverse would be impossible, for social, cultural, familial or hierarchical reasons.

Francisco Laso worked with me and Doyle McKey on such a problem during his second-year MSc internship at the CEFE in 2012 – 2013. This year, Maxime Dubart is going to re-code this model and launch simulations of the model to confirm/infirm certain analytical predictions that I have made.

The dynamics of the focal variety on the exchange network is modelled as a discrete-time two-event cycle. At the beginning of each cycle, all patches are subjected to possible extinction. Each patch loses its current population with probability  $e$ . Following extinction, each empty patch can obtain a new population of the focal variety, either through patch-to-patch diffusion (each incoming link from a patch where the focal variety is present has a probability  $c$  of bringing the entity back into the patch) or through background diffusion (regardless of connectivity to other patches, each empty patch has a small probability  $d$  of obtaining the focal variety). In terms of model family, the model used here is akin to  $\varepsilon$ -SIS and SISa models, *i.e.* epidemics models with external sources (Hill et al., 2010, Van Mieghem and Cator, 2012), but with potentially directed edges.

In practical terms, extinction corresponds to the loss of a given variety at a local scale, patch-to-patch diffusion represents seed sharing or buying, and background diffusion subsumes all possible means of recovering a lost variety through *e.g.* foraging in surrounding fields or natural areas, help from local NGOs, regional scale market, etc.

Theoretical predictions obtained so far concern three main points:

- The existence and computation of an “epidemics threshold” dividing parameter space into parameter values inducing a very low occupancy of the network and values inducing the existence of a giant “infected”/occupied component. Following arguments quite close (but not exactly alike) to those of Chakrabarti et al. (2008), we found that very low occupancy occurred when (see also Fig. 10)

$$\forall \lambda_{\mathbf{A}} \in \text{Sp}(\mathbf{A}), \left| \lambda_{\mathbf{A}} + \frac{1}{c[1-(1-e)d]} \right| < \frac{1}{c(1-d)(1-e)[1-(1-e)d]} \quad (\text{B6.1})$$

When the dominant eigenvalue of the adjacency matrix ( $\mathbf{A}$ ) is assumed to be real, the criterion boils down to those found elsewhere in the case of symmetric networks (Chakrabarti et al., 2008, Van Mieghem and Cator, 2012).

- Approximations of the occupancy of the network at equilibrium (Fig. 10). Using the “N-intertwined” approximation (Van Mieghem, 2011), we found that the equilibrium occupancy,  $p$ , could be approximated by:

$$p \approx 1 - (1-d)(1-c)^{\rho_{\mathbf{A}}(1-e)p} [1 - (1-e)p] \quad (\text{B6.2})$$

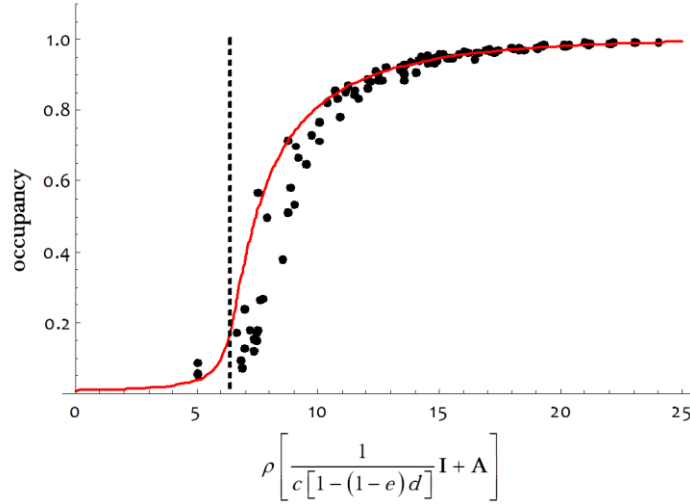
where  $\rho_{\mathbf{A}}$  stands for the spectral radius of the adjacency matrix depicting the exchange network.

- Determination of the asymptotic behaviour of the model for very large networks. Given the importance of the dominant eigenvalues of the adjacency matrix, both in equations (B6.1) and (B6.2), to understand the dynamics of the model, assessing the asymptotic behaviour of the dominant eigenvalues of large-sized directed adjacency matrix seems to be a relevant topic. Specifically, we looked at the asymptotic properties of  $\rho_{\mathbf{H}}$  with  $\mathbf{H} = \mathbf{A} + \alpha \mathbf{I}$  for a random adjacency matrix  $\mathbf{A}$  describing a directed graph and a given  $\alpha > 1$ . In the case of a directed Erdős–Rényi network (*i.e.* each link had the same probability of existing), we found that:

$$\rho_{\mathbf{H}} \approx \alpha + \bar{\delta} + \left( 1 + r - \frac{2\bar{\delta}}{N-1} \right) \sqrt{\frac{\bar{\delta}}{N-1-\bar{\delta}}} \quad (\text{B6.3})$$

where  $r$  is the reciprocity of edges,  $N$  is the number of nodes and  $\bar{\delta}$  is the average degree in the graph.

The objective of Maxime’s internship is to check the validity and robustness of the approximations obtained so far, especially with respect to assumptions on the degree distribution within the network. The methodology that he will follow corresponds broadly to the one presented by Gilarranz and Bascompte (2012), *i.e.* simulating networks with different topologies (regular, Erdős–Rényi, preferential attachment, etc.) and run the dynamical model on such networks.



**Fig. 10** – Some theoretical results already obtained for the model presented in Box 6. Abscissas depict the spectral radius of matrix  $\mathbf{A} + \mathbf{I} / c [1 - (1 - e) d]$ , ordinates represent occupancy of the network. The red line depicts the approximation given by equation (B6.2), the dashed line indicates the value of the epidemics threshold given by inequality (B6.1), and black dots correspond to simulations of Erdős-Rényi networks of 20 nodes with various degrees of reciprocity. Other parameter values:  $c = 0.2$ ;  $e = 0.2$ ;  $d = 0.01$ .

Using two different models (P12, P13), I have tackled these questions in a spatially structured ecological context. The model of (P12), which deals with constraints on food chain length induced by metacommunity dynamics, are described in more details in section 4. In this section I will focus on the trophic theory of island biogeography model described in (P13).

An important, classic question in ecology is to predict species diversity at a given location. While it is always possible to make this problem a correlative approach, using whatever environmental variable available to predict the occurrence of each potential species at a given location, such methods are not general insofar as they are not economical in degrees of freedom spent to explain patterns and what is learned about one species or community is never transposable to another one. To make things more simple, MacArthur and Wilson (1967) devised a famous model to predict species richness in insular systems (true islands, lakes, mountain tops, etc.). Constraining such a study to islands makes things easier because islands can be considered as “forced” systems in a “metacommunity bath” on which island diversity has no feedback. MacArthur and Wilson (1967) considered factors such as island size (the larger, the less prone to lose species) and its distance to the continent (the farther, the more difficult to colonise) as determinants of extinction and colonisation rates (Holt, 1997a, Holt et al., 1999), which are assumed identical for all species. Thus, in MacArthur and Wilson’s (1967) model, the probability  $p$  that any given species is present on a given island follows dynamics given by:

$$\frac{dp}{dt} = c(1 - p) - ep \quad (3.1)$$

where  $c$  is the colonisation rate and  $e$  the extinction rate.

At equilibrium, summing this equation over all the  $N$  available species at the metacommunity/continental scale, and setting its left-hand side to zero, we obtain the relation between realised species richness  $S$  and the extinction-colonisation ratio:

$$S^* = \frac{N}{1 + e / c} \quad (3.2)$$

Equation (3.1) cannot predict differences in occupancy among species – following the philosophy of the “*Theory of Island Biogeography*”, such differences are only due to historical contingencies, not to important deterministic factors.

## Box 7: Metacommunities of plants and pollinators

in collaboration with Julia Astegiano, Pierre-Olivier Cheptou and Paulo R. Guimarães

In comparison with food webs, very few network models have addressed the dynamics of mutualistic webs. Some recent studies have investigated ecological dynamics of mutualistic webs (Bascompte et al., 2006, Okuyama and Holland, 2007, Bastolla et al., 2009, Thébault and Fontaine, 2010), but they still generally disregard important biological processes linked with plant-animal interactions (Valdovinos et al., 2013). Incorporating biologically meaningful traits in such models is crucial to allow comparisons with patterns measured in the field – in other words, to obtain a testable model – and to correctly predict the effect of habitat loss (Aguilar et al., 2006; P25). Moreover, incorporating biological traits will ensure an adequate, mechanistic representation of mutualistic network dynamics that is currently lacking. Global changes affect species differently depending on their traits and position in plant-pollinator webs (Biesmeijer et al., 2006, Aizen et al., 2011) and we need appropriate models to understand and investigate these results further.

During her post-doc between Paulo Guimarães' laboratory in São Paulo and the CEFÉ in Montpellier, Julia Astegiano devised an extension to Fortuna and Bascompte's (2006) model of plant-pollinator metacommunities. The model deals with the occupancy dynamics of plants (occupancy of plant species  $i$ ,  $p_i$ ) and pollinators (occupancy of animal species  $j$ ,  $a_j$ ), assuming that (see also Fig. 11):

- each plant has a specific dispersal rate,  $\alpha_i$ , self-reproduces in proportion  $c_i$ , gets extinct at rate  $e_i$ , and depends on the set  $A_i$  of pollinators for pollinator-driven reproduction (thus, the degree of species  $i$  is equal to the cardinality  $|A_i|$ );
- each pollinator has a specific colonisation rate  $\beta_j$ , gets extinct at rate  $\gamma_j$ , and depends on the set  $P_j$  of plants for survival (*i.e.* it cannot colonise patches that do not contain at least one of these plant species);
- plant occupation patterns are assumed independent;
- self-reproduction entails a cost,  $\delta$ , due to inbreeding depression;
- pollinator species  $j$  pollinates plant  $i$  at rate  $s_{ij}$ ;
- as in Nee and May (1992), habitat can be partially destroyed so that only a fraction  $h$  of habitat patches is available for plant colonisation.

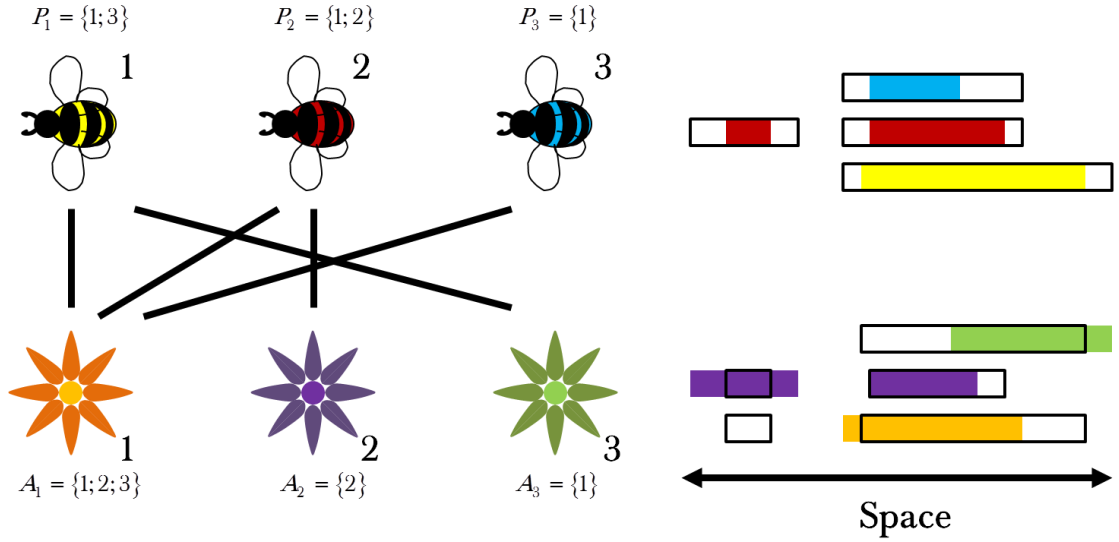
Accounting for all these assumptions, the dynamics of plants and pollinators thus read as:

$$\frac{dp_i}{dt} = \alpha_i \left[ (1 - \delta) c_i + (1 - c_i) \sum_{j \in A_i} \frac{s_{ij} a_j}{1 - \prod_{k \in P_j} (1 - p_k)} \right] (h - p_i) p_i - e_i p_i \quad (\text{B7.1})$$

$$\frac{da_j}{dt} = \beta_j \left[ 1 - \prod_{i \in P_j} (1 - p_i) \right] a_j - \gamma_j a_j \quad (\text{B7.2})$$

To evaluate how breeding system and dispersal ability influence plant-pollinator robustness to habitat loss, we constructed eight different scenarios to account for potential covariances between  $\alpha_i$ ,  $c_i$  and  $|A_i|$  among plant species, while putting all pollinator parameters at constant values (*i.e.* no interspecific variability among pollinators, except for  $P_j$ ). To do so, we first constructed random networks based on two different algorithms, one based on expected degree distribution, *a priori* modularity and nestedness (Thébault and Fontaine, 2010), the other based on an optimisation algorithm assuming that evolved plant-pollinator networks tend to be more nested than expected under random assemblage (Suweis et al., 2013). Once networks were drawn at a given size and connectance,  $\alpha_i$  and  $c_i$  were assigned at random following log-normal and logit-normal distributions, possibly conditioned by  $|A_i|$  (depending on scenario). In certain scenarios,  $\alpha_i$  and/or  $c_i$  were fixed for all species or allowed to vary among species. We envisaged both scenarios in which  $\alpha_i$  and  $c_i$  would correlate positively (as expected under Baker's law, Baker, 1955) and scenarios in which they would covary negatively (as supported by Auld and Rubio de Casas, 2013 and following results from P5, P9).

Our results so far indicate that variability in dispersal rate among plant species increases the number of plant species that can coexist in a given metacommunity. Autonomous self-pollination ( $c$ ) tends to negatively affect the occupancy of pollinators, as well as metacommunity diversity in general. This last pattern also interacts strongly with the assumption made on the covariance between  $\alpha_i$  and  $c_i$ , with less disparity between pollinator and plant occupancy patterns under a negative covariance pattern. The effect of habitat destruction (*i.e.* decreasing  $h$  from 1 to 0) is currently being investigated, but with no solid result so far.



**Fig. 11** – Schematic representation of the model presented in Box 7. On the left-hand side: a  $3 \times 3$  plant-pollinator network, displaying the sets  $P$  and  $A$  for pollinator and plant species, respectively. For instance, pollinator species 1 (yellow species) pollinates plant species 1 and 3, while plant species 1 (orange species) is pollinated by the three pollinator species. On the right-hand side: a representation of spatial occupancy by species (top = pollinator species, bottom = plant species, by colour). Solid coloured rectangles represent actual occupancies; open black rectangles represent the co-occupancy of partners (*i.e.* the sum of the occupancy of all pollinators for plants, the sum of the occupancy of all plants for pollinators). The occupancy of plants is a strict constraint for the occupancy of pollinators, but the reverse need not be true because plants can self-fertilise in the model.

Interactions among species are absent from the picture painted by MacArthur and Wilson's theory of island biogeography. Yet, the combination of dependencies between species occurrence, induced by species interactions, and colonisation/extinction dynamics within an island might produce non-trivial patterns, and quite intuitively, a narrow diet might restrict the occurrence of a species, as suggested by existing data (Beck and Kitching, 2007). Indeed, if the occurrence of a given species requires the presence of another species, its colonisation rate is effectively reduced – but in which proportion? Focusing on food webs (but see Box 7 for an ongoing study on plant-pollinator networks), one can make two basic assumptions about how a food web occupancy model should work (Fig. 12):

- A predator can only colonise the island if at least one of its prey species is already present (*cf.* open rectangles in Fig. 12);
- When the last prey species of a predator goes extinct, the predator also goes extinct (*e.g.* dashed line in Fig. 12).

Based on these two assumptions, Dominique Gravel, Elsa Canard, David Mouillot, Nicolas Mouquet and I proposed an extension to MacArthur and Wilson's (1967) model (P13) which makes use of the information contained in the regional food web, but uses no extra degree of freedom.

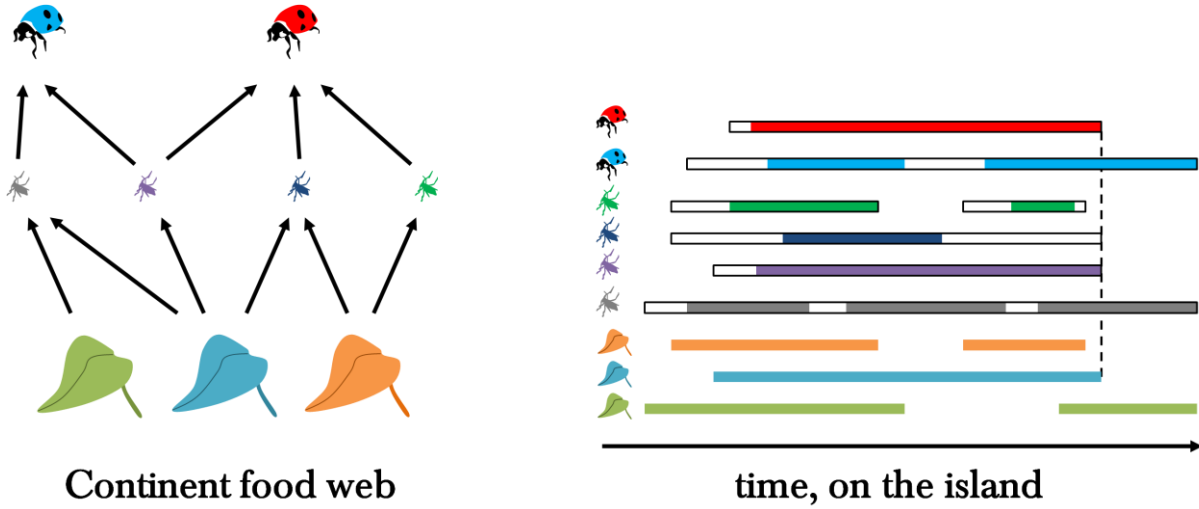
The formalisation of this model can be approximated as follows. Each species has a given diet breadth,  $g$ , which is equal to its number of prey species in the regional food web. The probability that a species with diet breadth  $g$  occurs on the island,  $p_g$ , is modelled as resulting from the processes of species colonisation (rate  $c$ ) and extinction ( $e$ ), modulated by the probability that at least one of its prey species is present ( $q_g$ ) and the extra extinction rate due to the loss of its last prey species ( $\varepsilon_g$ ):

$$\frac{dp_g}{dt} = c(1 - p_g)q_g - (e + \varepsilon_g)p_g \quad (3.3)$$

Analytical developments of this model lead to an equation linking species occupancy at equilibrium with  $\alpha = c/e$  and  $\beta$ , the average of  $\log(1 - p_g)$  weighted by diet breadth frequencies on the continent, assuming that predator occurrence had no effect on the occurrence of their preys:

$$p_g^* = \frac{\alpha(1 - e^{\beta g})}{1 + \alpha(1 - e^{\beta g})(1 + ge^{\beta g})} \quad (3.4)$$

From a mathematical viewpoint, introducing food web topology changes the shape of the curve linking occupancy to the colonisation-to-extinction ratio: introducing trophic dependencies means that the curve shape changes from concave to sigmoid. In other words, when colonisation to extinction ratio is too low, it becomes even more difficult for species to enter the island because their prey species cannot make it there first. The intensity of this effect depends on the diet breadth of the species considered. A more precise, but less tractable, approximation than equation (3.4) can be obtained assuming statistical dependence of predator and prey occurrence, but neglecting the statistical dependence among preys of the same predator (see supplementary information of P13). In both cases, this model makes species-wise predictions on occurrence without adding any parameters to MacArthur and Wilson's (1967) model.



**Fig. 12** – Schematic representation of the trophic theory of island biogeography model from (P13). On the left-hand side: the food web available on the continent. Different colours indicate different species (here, of plants, aphids and ladybirds). On the right-hand side: time series of occurrence of the different species on the island. As in Fig. 11, solid coloured rectangles represent actual occupancies; open black rectangles represent the co-occurrence of species needed to sustain the focal species (*i.e.* the sum of the occupancy of all prey species). The vertical dashed line shows an example of cascading extinctions: as the blue plant species go locally extinct on the island, so do the purple aphid species and the red ladybird species.

The model described by equation (3.3) can yield a probability of species occurrence solely based on species diet breadth; at no point in the approximation does trophic level affect the result for  $p_g$ . To compare approximation (3.4) with a more realistic (yet as parsimonious) version of the model, we confronted three models to the species occurrence data of Havens (1992) and Piechnik et al. (2008):

- MacArthur and Wilson's original model;
- The analytical approximation of the trophic model presented above;
- A simulation model using the whole network structure (thus, not predicting the same probability of presence for two species with the same diet breadth if they did not share exactly the same diets) and based on the two same assumptions as the analytical approximation.



Results of this model comparison exercise suggest that trophic information adds much to the model's explanatory power, especially in the case of Havens' (1992) freshwater food web data.

As a closing word on this model, the "biased sampling" of food webs implied by the trophic theory of island biogeography drives an intriguing relationship between diversity and the number of links within the realised food web. Indeed, when varying the parameter  $\alpha$  and starting from the regional food web, which is obtained for infinite  $\alpha$  values, one can compute the expected diversity and number of links at any given level of  $\alpha$ . The relationship we obtained was intermediate between a linear richness-number of links relationship, as under Cohen and Briand's (1984) link scaling law, and a squared richness-number of links relationship, as under Martinez' (1992) constant connectance law.

### 3.3. Conclusions & perspectives

Compared to the emergence and coexistence of genetic and species diversity, the topic of complexity and functioning of spatially structured ecological systems is a more recent endeavour in my academic life. As it can be seen from boxes 4-7, this is a topic that I want to explore more in the near future. Two funded projects that I coordinate aim at assessing certain properties of complex spatially structured ecological systems:

- The aim of project COREIDS (working group with post-doc, funded by the FRB and TOTAL) is to assess causative links between a species traits, its location within a food web and its ability to invade other food webs at remote locations over the world. This project feeds much conceptually on the recent work published by Tamara Romanuk's group (Romanuk and Kolasa, 2005, Beisner et al., 2006, Romanuk et al., 2009a, Romanuk et al., 2009b, Romanuk et al., 2010, Carscadden and Romanuk, 2012, Murphy and Romanuk, 2012, 2014). In practical terms, the group's post-doc, Grégory Mollet, is currently collating data on invasions and/or food webs (preferably both) from all the working group participants in order to make analyses from empirical data. At the same time, participants are engaged in devising theoretical models to explain (i) the propensity of food webs to be invaded, (ii) the propensity of certain types of species to invade, and (iii) the intensity of havoc wreaked by species invasions depending both on the type of invaders and the topology of the invaded food web.
- In project ARSENIC (funded by the ANR), the goal is to understand the consequences of global changes (warming, eutrophication, fragmentation...) through accounting for species interactions and their coevolution in a spatially structured context. In practical terms, this general question will be tackled through an integrative approach combining coevolutionary models and analyses of empirical datasets, existing or to be obtained during the course of the project. On the "modelling side", we will build evolutionary models of spatially structured antagonistic and mutualistic networks to understand how evolution affects (i) the association of traits in interacting species (in a fashion similar to P5 and P9 on the association of dispersal and selfing in plants, but focusing more on traits determining interaction affinity and dispersal), (ii) the dynamical properties of ecological networks, like robustness to invasions or extinctions, network stability, etc., and (iii) the dynamics of species' ranges when embedded in a network of interactions, *à la* Norberg et al. (2012). These models will hint at how and why some specialisation traits can be evolutionarily associated with higher dispersal, and thus suggest trait associations within and across networks that can be tested. Effects of natural selection on the stability of feasible ecological equilibriums will also be studied in the context of May's diversity-stability paradox (section 4). Finally, studying the dynamics of species' ranges in networks will allow us to make predictions of how trait evolution shapes the geographical distribution of mutualistic or trophic partners (section 5).

Both projects combine the use of empirical data with the development of theoretical models. These projects will deal with issues that I have not tackled so far (*e.g.* evolution in complex networks) but which are strongly connected to some of my past work (*e.g.* on the evolution of dispersal syndromes, P5, P9, and on the assembly of complex networks, P12, P13). In the more distant future, I envisage

developing new research on spatially structured ecosystems to tackle the evolution of symbiotic association *sensu lato*, *i.e.* both host-pathogen and mutualistic symbioses. I think the role of host dispersal as a means of symbiont dispersal has been generally overlooked in models connecting organism dispersal with ecosystem functioning, although it is now known that *e.g.* endophytes can disperse with seeds, hence the colonisation of a new field by certain plants can directly change the functioning of the colonised soil (Knoch et al., 1993, Saikonen et al., 1998). In the same vein, one can imagine that dispersal of annelids between hydrothermal vents can affect and be affected by microbial community through the worm's ability to produce antibiotics and its preferential association with certain chimio-lithotrophic bacteria (Chevaldonné et al., 1997, Tasiemski et al., 2014).

#### 4. Ecological dynamics and the stability issue

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Les hommes qui ressentent douloureusement la fuite du temps ne supportent pas la sédentarité. En mouvement, ils s'apaisent. Le défilement de l'espace leur donne l'illusion du ralentissement du temps, leur vie prend l'allure d'une danse de Saint-Guy. Ils s'agitent.

Sylvain Tesson, *Dans les forêts de Sibérie*

Although diversity studies characterise the number of compartments (biotic or abiotic, species, populations or communities), and functioning studies describe the fluxes of matter and energy among these compartments, these are not sufficient to characterise the dynamics of species' abundances within the ecosystem, for the main reason that a few organisms getting fatter or small organisms getting more numerous can theoretically represent the same change in matter/energy stocks within a given compartment. The study of the “demographics” of ecosystem agents – be they biotic or abiotic – is thus another needed pillar of ecosystem studies.

“Ecological dynamics” is an inclusive term which encompasses different topics dealing with the temporal evolution of individual counts (demographics) or species abundances (community ecology). This field of study has benefited from mathematical developments on probabilities and dynamical systems. A central notion in this context is ecological (or demographical) equilibrium, *i.e.* a steady state that keeps on being the same if left undisturbed. Other steady states of dynamical systems *i.e.* stable cycles and chaos, are also important notions, but have resulted in a less prolific literature in ecology than questions pertaining to the stability of ecological equilibriums.

In spatially structured systems, such as metacommunities or metapopulations, ecological dynamics can be considered at different spatial scales:

- a. At the local (patch) scale, populations or communities may display different dynamics based on species birth, death, immigration and emigration rates, and might also go extinct depending on perturbation rate;
- b. At the regional (metapopulation/metacommunity) scale, a set of populations or communities presents a dynamics of its own, based on the rates at which individual populations or communities get “started” (*i.e.* colonisation), “rescued” (*i.e.* immigration) or “finished” (*i.e.* extinction).

Because of a potential mismatch between the rates of processes occurring at local *vs.* regional scale, especially the slow/fast dynamics that might arise when the perturbation rate is way lower than demographic (birth and death) rates, the question of ecological dynamics in spatially structured systems can give rise to two different kinds of problems:

- a. When community assembly and disassembly within local patches are driven by stochastic processes (*i.e.* colonisation and extinction), what is the observed spatial variability of ecological metrics associated with local communities, *e.g.* species diversity, food chain length, food web connectance, etc.?

- b. When communities are linked by species dispersal among communities, can the ecological equilibrium at the metacommunity scale be stable when ecological equilibria at the local scale are unstable?

The following two subsections present two studies that deal with these two problems. In 4.1, I present a patch occupancy model predicting constraints to food chain length arising from metacommunity dynamics; in 4.2, the focus is given on an unpublished (yet completely analysed) model linking spatial structure to the geometry of eigenvalues of Jacobian matrices describing large communities (Box 8).

#### 4.1. Metacommunity assembly and food chain length

An important puzzle in ecology is how food web topology, and in particular food chain length, is determined (Hutchinson, 1959, Pimm, 1982, May, 1983, Cohen and Briand, 1984, Stenseth, 1985, Cohen and Newman, 1988, Williams and Martinez, 2000, 2004). Food chain length is a measure of the number of feeding links between resources and top predators (*e.g.* Sabo et al., 2009). Ecological theory has long tried to understand why food chains should have limited length (Hutchinson, 1959, May, 1972, Hastings and Conrad, 1979, Pimm, 1982, Menge and Sutherland, 1987). For instance, the energetic constraint hypothesis (Hutchinson, 1959) invokes imperfect transfers of energy and resources along food chains, the dynamics constraint hypothesis (May, 1972, Pimm and Lawton, 1977) considers that long food chains are more vulnerable to perturbation than short ones, and the community area hypothesis combines the diversity-area relationship obtained by the theory of island biogeography (MacArthur and Wilson, 1967) with the link scaling law (Cohen and Briand, 1984) to predict a concave increase in food chain length with habitat area (Cohen and Newman, 1991). Recent empirical studies have identified three major determinants of food chain length: productive space, disturbance, and ecosystem size (Post, 2002). While confirming the roles of resource limitation and perturbation, these results argue against single explanations, and also stress the need to incorporate space in theoretical models. Indeed, despite ample evidence that food chain length correlates with habitat area or ecosystem size (Schoener, 1989, Cohen and Newman, 1991, Post et al., 2000, Takimoto et al., 2008), spatial processes are still understudied in theoretical models of food webs (Holt, 2002, Amarasekare, 2008).

At the end of my PhD, together with Vincent Calcagno, and helped by Patrice David, Nicolas Mouquet and Philippe Jarne, we developed a simple, analytical patch-occupancy model to understand the links between spatial structure and constraints on food chain length (P12, Fig. 13). The model, inspired by seminal models by R. Holt (Holt, 1997a, 2002, Holt and Hoopes, 2005) and by Morton and Law's (1997) conceptual model of community assemblage, considered a simple food chain in which the occupancy  $p_i$  of every trophic level  $i$  obeyed some kind of Levins (1969) metapopulation model, generally defined as:

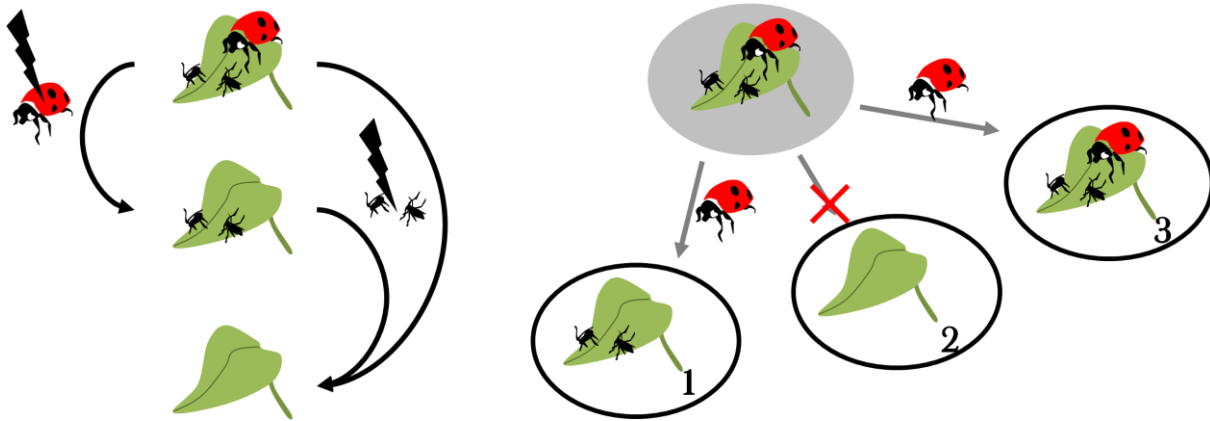
$$\frac{dp_i}{dt} = c_i p_i (h_i - p_i) - (e_i + \mu) p_i \quad (4.1)$$

where  $c_i$  is the average colonisation rate of species  $i$  (averaged over all the patches inhabited by species  $i$ ),  $h_i$  is the proportion of patches inhabitable by species  $i$ ,  $e_i$  is the average specific extinction rate of species  $i$  (also averaged over occupied patches) and  $\mu$  is the catastrophe/perturbation rate (such perturbations being able to wipe a patch clean of all its inhabiting species).

In order to be as general as possible, we incorporated the following ingredients to the model (P12, Fig. 13):

- a. Perturbations of species within patches could stem from either patch-level perturbation ( $\mu$ ) or species-specific extinction ( $e_i$ );
- b. When a given trophic level went extinct in a patch, all upper trophic levels also went extinct as a result of bottom-up control;

- c. Predators could have any type of top-down effect on the colonisation and extinction rates of prey populations (Fig. 14). In other words, the presence of one's immediate predator species could increase or decrease extinction or colonisation rates, depending on modelling choice;
- d. Dispersal could be non-random, *i.e.* predator (or prey) propagules could possess some level of habitat selection.

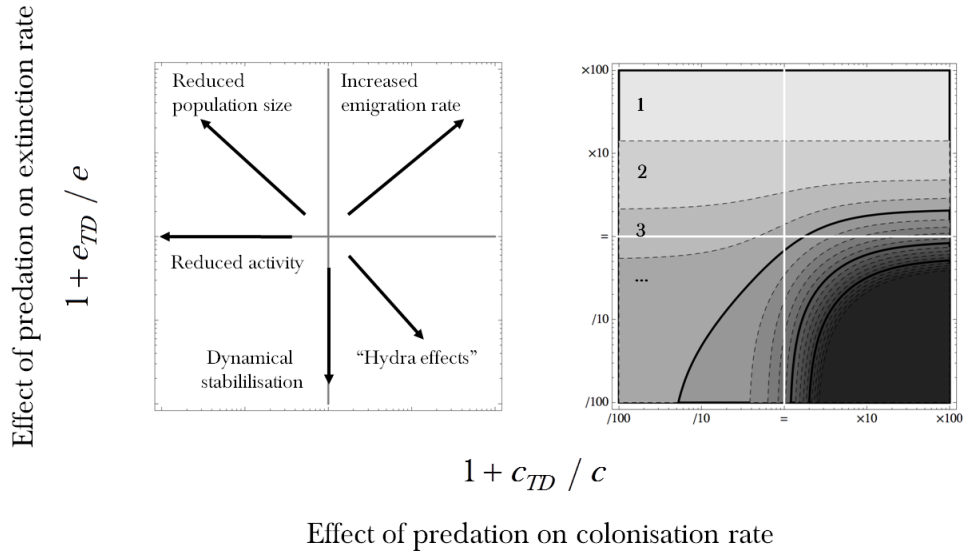


**Fig. 13** – Schematic representation of the food chain metacommunity model from (P12) illustrated with a three-level food chain (plant, aphid, ladybird). On the left-hand side: co-extinction dynamics along the food chain (lightning symbols represent extinctions). The arrow on the left shows the transition from a complete food chain to one without ladybirds as this species goes locally extinct; the arrows on the right show the transitions to a plant-only community as aphids go locally extinct (and so does the ladybird species if present). On the right-hand side: possibility of ladybird colonisation (grey arrows) from a patch where it occurs (gray oval) to different kinds of patches. Ladybirds can colonise patches where both plants and aphids are present (1) and patches where all three species are present (3), but the latter type of colonisation event does not change ladybird occupancy at the landscape level; however, ladybirds cannot colonise patches where aphids do not occur (2).

Through a complete analysis of the model, we identified two distinct constraints on food chain length arising from metacommunity structure. First, finite colonisation rates limit predator occupancy to a subset of prey-occupied sites. Second, intrinsic (*i.e.* species-specific) extinction rates accumulate along trophic chains. Both processes thus concur to decrease maximal and average food chain length in metacommunities. Our model predicts that:

- a. Food chain length can be very variable in space, so that the average chain length can be much smaller than the maximum.
- b. Food chain length is more limited when species-specific processes rather than patch-level catastrophes cause extinction;
- c. The decrease in maximal (and average) food chain length is mitigated if predators track their prey during colonisation (habitat selection) and can be reinforced by top-down control of prey vital rates (especially extinction);
- d. Top-down control of extinction is more critical to food chain length than top-down control of colonisation (Fig. 14);
- e. Strong negative top-down control of colonisation can produce counterintuitive patterns, such as food chain length increasing with perturbation rate, or decreasing with foraging efficiency. Specifically, top-down control of colonisation and foraging can interact to produce a counterintuitive positive relationship between perturbation rate and food chain length.

Our results show how novel limits to food chain length emerge in spatially structured communities. Connections between these constraints and the ones commonly discussed (*e.g.* Post, 2002) can be made and suggest ways to test for metacommunity effects in food webs.



**Fig. 14** (excerpt from P12) – Effect of top-down control of colonisation ( $c_{TD}$ ) and extinction ( $e_{TD}$ ) on maximal food chain length. At the centre of the graph  $c_{TD} = e_{TD} = 0$ , *i.e.* the presence of a species' predator has no effect on extinction and colonisation rates. The range of values amounts to dividing or multiplying the rates by a factor 100 (right-hand side panel, logarithmic scales). Darker shades of gray indicate that longer food chains can persist. Contour lines indicate changes in maximal food chain length (dashed lines at every trophic level; solid lines every four levels). The left-hand side panel represents mechanisms generating different signs for top-down control of colonisation (abscissas) and extinction (ordinates), *e.g.* increased emigration rate due to predator presence would generate positive  $c_{TD}$  and  $e_{TD}$ . Other parameters: catastrophe rate = 0.1; species-wise extinction rate = 0.1; foraging efficiency = 0.5.

## 4.2. The stability-complexity question

The diversity of species within natural communities and the complexity of their interactions in nature have fascinated ecologists at least since Darwin. More than 40 years ago and contrary to previous intuition (MacArthur, 1955, Margalef, 1963), R. May predicted that diversity and complexity should destabilise ecosystems (May, 1972, May, 1973a). The common observation of highly diverse communities has consequently been a major puzzle for ecologists.

May (1972) studied the dynamical properties of randomly assembled ecosystems using randomly assembled Jacobian matrices (Wigner, 1958). He found that stability should decrease with the number of species and interactions between them because, for random Jacobian matrices following the circular law (Tao et al., 2010), their empirical spectral distribution forms a disk centred at the average feedback coefficient among species (*i.e.* average diagonal coefficient in the Jacobian matrix) of radius proportional to the standard deviation of non-diagonal elements of the Jacobian matrix (see also Allesina and Tang, 2012). By varying the number of species  $S$ , the connectance  $c$  (the proportion of potential interactions among all pairs of species that are realised), the standard deviation of interspecific interaction strength ( $\sigma$ ) and the average intraspecific interaction strength ( $m$ ), this theory indicates that for a community to be stable, it must respect the following inequality (May, 1972, modified by Allesina and Tang, 2012):

$$\sigma \sqrt{c(S-1)} < m \quad (4.2)$$

*i.e.* to be stable, a community should display average intraspecific feedback greater than the squared root of the connectance  $\times$  species richness  $\times$  variance in interaction strength product.

## Box 8: The stability-complexity issue in space

in collaboration with **Dominique Gravel** and **Mathew Leibold**

A number of hypotheses have been proposed to resolve May's diversity-stability paradox (McCann, 2000, Ives and Carpenter, 2007, Donohue et al., 2013, Loreau and de Mazancourt, 2013) including the possibility that spatial dynamics may be strongly stabilising (Levin, 1974). However, no simple theory has yet been developed to quantify the stability of diverse "metaecosystems".

One of the most powerful hypotheses is that of spatial exchanges of individuals, energy and material between local ecosystems (McCann et al., 2005; P11). Spatial flows among local ecosystems are ubiquitous in nature, connecting not only similar habitats (*e.g.* patches of forest, lakes), but also very different ones (*e.g.* ocean/island, stream/forest, benthic/pelagic; Polis and Hurd, 1995). However, the strength and sign of this effect on stability is not clear. Most studies so far have focused on small food web modules (Amarasekare, 2008) or have been conducted with different measurements of stability that are not directly comparable to May's local stability (Gravel et al., 2011, Pillai et al., 2011).

We extend classic theory on the stability-complexity relationship to study the dynamics of ecosystems linked by dispersal of organisms and materials. Technically speaking, we expand the classic approach (May, 1972, 1973b) to look at the structure of the Jacobian matrix of the metaecosystem when placed in a spatial context (Svirezhev and Logofet, 1983). Jacobian matrices are obtained by linearising at equilibrium the system of equations describing the dynamics of all species making an ecosystem. A Jacobian matrix thus describes the direct interactions among all pairs of populations near this equilibrium. Stability is assessed from its largest eigenvalue and the system is stable when the real part of the largest eigenvalue is negative. The Jacobian matrix  $\mathbf{J}$  of a metaecosystem can be decomposed into a deterministic ( $\mathbf{M} + \mathbf{D}$ ) and a stochastic part ( $\mathbf{A}$ ):

$$\mathbf{J} = \mathbf{M} + \mathbf{D} + \mathbf{A} \quad (\text{B8.1})$$

where  $\mathbf{M}$  is the diagonal matrix that represents intraspecific density-dependence, with value  $-m$  along the diagonal and 0 in the rest of the matrix,  $\mathbf{D}$  is the matrix that represents the dynamics of dispersal among patches, and  $\mathbf{A}$  is the collection of local Jacobian matrices, arranged as diagonal blocks that describe dynamics due to interspecific interactions within each local communities. The sub-matrices of  $\mathbf{A}$  together with  $\mathbf{M}$  are equivalent to May's matrices, but now we combine them with matrix  $\mathbf{D}$  to form a metaecosystem. There are  $n$  patches (or ecosystems) and consequently the size of  $\mathbf{J}$  is  $n \times S$ .

Assuming that both  $S$  and  $n$  are large and that  $d$  is also sufficiently large, we obtain the following stability criterion (see also Fig. 15):

$$\sigma \sqrt{c(S-1) / n_e} < m \quad (\text{B8.2})$$

where  $n_e = n / [1 + (n-1)\rho]$  is the effective number of ecologically independent patches in the metaecosystem and  $\rho$  is the correlation among elements of  $\mathbf{A}$  among different patches. Equation (B8.2) results from the statistical thinning of the variance of the 'average ecosystem' obtained by linking all ecosystems through dispersal (*i.e.* as an instance of the central limit theorem). This result indicates that dispersal can stabilise metaecosystem dynamics in proportion to its ecological size (the number of effectively independent habitat patches). When  $d$  is small (and  $S$  and  $n$  large), however, the effect of dispersal is very different. The criterion corresponding to equation (B8.2) in this situation is approximately (see also Fig. 15):

$$\sigma \sqrt{c(S-1)} < m + d \quad (\text{B8.3})$$

In this case, stability increases with  $d$ , regardless of the value of  $n_e$  and it does so additively (at least in cases where  $d$  is very small) in comparison with the criterion for isolated ecosystems. In this case, environmental heterogeneity is not important – emigration alone is the factor improving the stability of metaecosystems.

Further work (designed by Dominique Gravel) allowed us to explore whether large simulated spatially structured Lotka-Volterra systems confirmed theoretical predictions made on Jacobian matrices. Based on this numerical exploration, we found that stability first increased with dispersal, peaking at intermediate rates, and then slightly dropped and became almost insensitive to dispersal at high levels. The increase in stability agrees with the theoretical results presented above. However, new mechanisms arise from the simulations: on average, the correlation between elements of  $\mathbf{A}$  among patches increases with dispersal, thus decreasing the effective number of patches as dispersal increases. Overall, a mixture of stabilising and destabilising effects of dispersal makes stability peaks at intermediate rates.

Our model confirms that spatial dynamics in metaecosystems can be a remarkably strong stabilising force that can facilitate coexistence among many interacting species (Levin, 1974). This work paves the way for extensions aimed, *e.g.* at understanding how the network structure of metaecosystem might affect stability.

In practice, assuming non-trivial values for  $c$  and  $\sigma$  and their independence, this means that ecosystems are likely to be relatively small, so that the common observations of hundreds to thousands of species are difficult to explain (May's so-called 'paradox of diversity', Neutel et al., 2007).

Since then, numerous hypotheses to explain this paradox have been invoked (McCann, 2000, Ives and Carpenter, 2007, Otto et al., 2007, Donohue et al., 2013, Loreau and de Mazancourt, 2013), some of which rely on re-tailoring the mathematical notion of stability for the purpose of ecology (Lehman and Tilman, 2000, Wang and Loreau, 2014). Most, if not all, of ecological explanations for the apparent stability of ecosystems have some empirical support, but their absolute or relative importance is not well understood.

I recently took part in two different studies tackling the issue of stability in complex ecosystems, which I will briefly present here. In a first (still unpublished) study, from Claire Jacquet's second-year MSc internship with Dominique Gravel, we investigated whether empirical patterns obtainable from 119 quantitative food webs, sampled worldwide, from marine, freshwater, and terrestrial habitats corroborated, or not, May's theory. A broader objective was to identify the non-random characteristics of natural ecosystems that allow them to persist despite their complexity. Food webs were compiled using a standard methodology to build Ecopath mass-balance models, *i.e.* biomass dynamics models at equilibrium developed for fishery studies (Christensen and Pauly, 1992). We then translated parameters of the Ecopath models into interaction coefficients of the Lotka-Volterra interaction model following the same approach as de Ruiter et al. (1995).

Our analysis reveals that classic descriptors of complexity (species richness, connectance and variance in interaction strengths) do not affect stability in natural food webs. Food web structure, which is far from random in real communities (Yodzis, 1981), reflects another form of complexity that we found dramatically influences the stability of real communities. Using randomisation of interaction strengths, interaction strength distribution or interaction signs, we tested whether certain features of observed food webs could be responsible for their stability. Our general conclusion is that the occurrence of complex communities is possible *in natura* owing to their trophic structure and the distribution of interaction strengths (see also Tang et al., 2014).

In a second study (Box 8, Fig. 15), Dominique Gravel, Mathew Leibold and I undertook the project of recasting May's (1972) initial stability-complexity model in the context of spatially structured ecosystems. In line with previous work linking dispersal and the stability of ecological systems (Levin, 1974, Freedman and Waltman, 1977, Doebeli, 1995), we found that dispersal among sufficiently heterogeneous patches stabilised metacommunity dynamics, mainly through two effects (Fig. 15):

- a. At low dispersal, dispersal stabilises dynamics through artificially increasing the negative feedback of species on themselves. Graphically, this leads to a displacement of the empirical spectral distribution towards the left of the complex plane (Fig. 15b);
- b. At high dispersal, dispersal stabilises dynamics through thinning the variance of the average patch-wise Jacobian representing species interactions, which determines the radius of the right-most eigenvalue disk (Fig. 15c). This thinning occurs only when patch-wise Jacobians are sufficiently uncorrelated, so that averaging them amounts to using a central limit theorem and thus divides the overall variance by a factor equal to the effective number of patches (see Box 8 for more details).

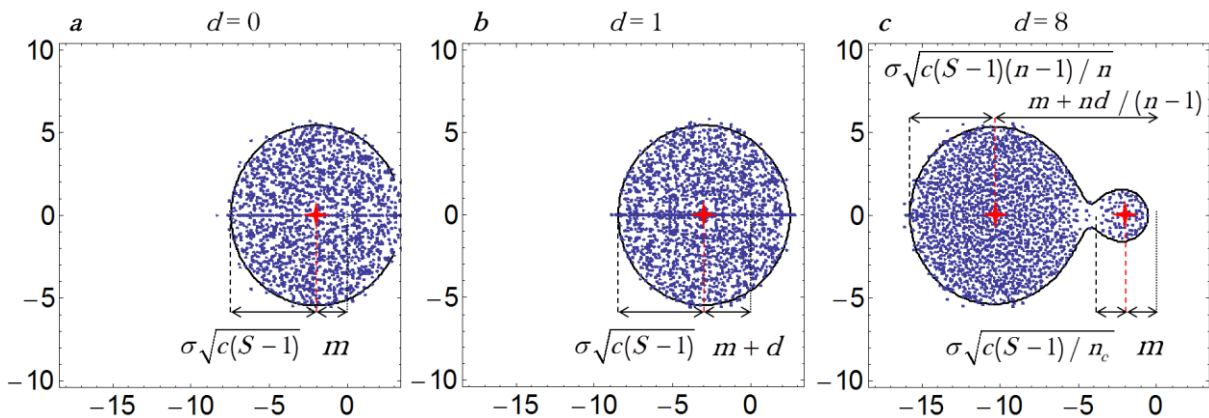
Details on the model and the nature of results obtained are provided in Box 8.

### 4.3. Conclusions & perspectives

The different studies dealing with the ecological dynamics of spatially structured systems have familiarised me with a variety of questions that deserve further treatment in the near future. Through projects like COREIDS, ARSENIC and MIRES, I hope to be able to treat some of these points soon:

- The work developed with Vincent Calcagno on food chain length in metacommunities (P12) could be extended to more general food webs, to provide a picture of spatial food web assembly complementary to the one derived by Pillai et al. (2011). Notably, incorporating top-down control of species colonisation rate and predator foraging might complexify the results of Pillai et al.'s model.
- Together with colleagues from Paul Painlevé mathematics laboratory in Lille, we discussed the possibility of extending the work on the stability of metacommunities (Box 8) through incorporating network structure among patches, *à la* Jansen and Lloyd (2000). This approach might help feed the current debate on the respective roles of network modularity and nestedness on system stability (Thébault and Fontaine, 2010, Allesina and Tang, 2012, James et al., 2012, Rohr et al., 2014), albeit in a spatial, rather than interaction, context.
- Recasting the question of stability in both ecological and evolutionary contexts, a synthesis of results obtained on the conditions inducing stability in ecological systems (McCann, 2000, Kondoh, 2003, Kondoh, 2006, Ives and Carpenter, 2007, Otto et al., 2007, Donohue et al., 2013, Loreau and de Mazancourt, 2013) and more recent work linking dimensionality to evolutionary diversification (Doebeli and Ispolatov, 2010, Débarre et al., 2014b, Svandal et al., 2014) might lead to new insights on the dynamics of ecological speciation and extinction due to dynamical instability. Such an “asymptotic” theory of ecology and evolution might also help understand the link between species evolution and ecological stability (Loeuille, 2010) or between ecological instability and subsequent evolutionary branching of ecologically relevant traits.

Although my work so far has only tackled stability and local *vs.* regional dynamics “in passing”, I think that understanding these issues will prove crucial to advance questions linked to evolving spatially structured networks, as envisaged in project ARSENIC.



**Fig. 15** – Illustration of the effects of increasing  $d$  on the distribution of eigenvalues in the complex plane for the model presented in Box 8. Distribution of eigenvalues of matrix  $\mathbf{J}$  in the complex plane when  $\sigma = 1$ ,  $n_e = n = 20$ ,  $S = 100$ ,  $c = 0.3$ ,  $m = 2$ , and (a)  $d = 0$ , (b)  $d = 1$  and (c)  $d = 8$ . Solid lines indicate predictions from asymptotic distributions of eigenvalues under the circle law (Tao et al., 2010); individual points indicate eigenvalues obtained from a random drawing of individual Jacobian matrices following a Gaussian distribution for non-diagonal elements. Red stars indicate the position of the centres of eigenvalue distributions.



## 5. Predicting species distributions

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People look down on stuff like geography and meteorology, and not only because they're standing on one and being soaked by the other. They don't look quite like real science. But geography is only physics slowed down and with a few trees stuck on it, and meteorology is full of excitingly fashionable chaos and complexity. And summer isn't a time. It's a place as well. Summer is a moving creature and likes to go south for the winter.

Terry Pratchett, *Feet of Clay*

Ongoing global change is strongly affecting biodiversity, with numerous species currently becoming extinct, shifting in range, and/or changing their phenotype. Global species extinctions linked to climate change have already been observed (*e.g.* Parmesan, 2006), and many more are expected in the coming decades, even under the overoptimistic scenario of unlimited dispersal (Thomas et al., 2004a). Global changes involve perturbations acting on large spatial scales, therefore not only on local communities, but also on neighbouring potential habitats, creating intense selective pressures (Moran and Alexander, 2014) that threaten many species (Thomas et al., 2004b). Such global changes include climate changes, eutrophication, pollution, fragmentation and loss of natural habitats, overexploitation of species, etc. (Vitousek, 1994). These disturbances vary in intensity in space and time and interact in complex ways (Reich et al., 2006, Munday et al., 2013). They also interact with smaller-scale disturbances like local pollution events. In the face of such multiple, and large-amplitude changes, one goal of ecology is to provide society and policy makers with forecasting tools that will allow relevant decisions to preserve the future of ecosystems and to manage the ecosystem services they provide for human well-being (Rockstrom et al., 2009, Compton et al., 2011).

With the advent of modern numeric cartography, satellite imaging and the creation of massive databases of naturalist observations, the quantity of data on the spatial distribution of species has literally exploded. Such data have allowed new taxonomic discoveries, *e.g.* through identifying potential habitat areas for certain species which, once explored, revealed yet unidentified sister species (Raxworthy et al., 2003). This data is also routinely used to make projections of species distribution shifts due to climate change (Clark, 1998, Chuine and Beaubien, 2001, Thuiller et al., 2011).

Currently, models used in forecasting distributions rely on a statistical description of ecological niches to project species distribution in space and time under a given perturbation scenario. A good example of such an approach is the use of “climate envelope models” (Pearson et al., 2002, Thomas et al., 2004a). They gather climatic data over the range of a given species, define the species niche out of this data, and, using climate forecasts under greenhouse gas emission scenarios, project the future possible distribution of the species accordingly. Such models make several strong assumptions (Davis et al., 1998, Ladle et al., 2004). They assume that:

- a. Species occurrence represents the species fundamental niche, which may not be true for many different reasons (*e.g.* source-sink dynamics Pulliam, 1988, extinction debts, Tilman et al., 1994);
- b. The niche is evolutionarily conserved, although several observations suggest that niches may evolve fast (Lavergne et al., 2010);
- c. Dispersal is assumed non limiting (Thuiller et al., 2011);
- d. Future environmental conditions are assumed to be “reducible” to a mix of environmental conditions observable currently or in the past.

While such assumptions may provide a first guess, we need to move from such statistical approaches to mechanistic ones for a finer understanding of the fate of ecosystems during the next few decades.

The study of species distributions raises the question of the mechanisms inducing observed occurrence patterns (*e.g.* Gaston, 2003, Sexton et al., 2009). Is a species restricted to a given geographic range because of a limited amount of suitable habitat, by the distribution of competing species, by the distribution of its natural enemies (predator, parasite, ...), by the distribution of its preys or resources, or even by maladaptation to certain types of habitat due to gene flow?

Extinction due to climate change can be avoided or delayed either through distributional range displacement or through trait evolution. Polewards shifts in distributional ranges are observed in many species, due to local population extinctions at low latitudes and/or colonisation at high latitudes (reviewed in Parmesan, 2006, Hill et al., 2011). Plastic responses (Parmesan and Yohe, 2003, Chevin and Lande, 2010, Chuine, 2010) and/or genetic responses (Bradshaw and Holzapfel, 2001, Umina et al., 2005) could enable species to sustain environmental changes while not necessarily displacing their ranges.

In the following, I present two studies I have been involved in, both dealing with predicting species distributions in the face of changing environment. In the first study (P18), we present a method to combine forecasts on species distributions from different models and to study the uncertainty associated with the variety of models used. In the second study (P14), we study a theoretical model explaining limited species distributions through a combination of maladaptation on different traits, and explore in particular the effect of genetic and selection covariances among traits determining local adaptation on the ability of species to follow shifting environmental gradients.

### 5.1. Species distribution models

When trying to build precise and realistic models (*sensu* Levins, 1966), species distribution models (SDMs) can be classified as follows (Peterson et al., 2011):

- a. Correlative SDMs use correlations between current species occurrences and various environmental descriptors to infer future distributions of species under realistic scenarios of environmental descriptor shifts (*e.g.* Thuiller et al., 2005). In other words, these models explore a species' limiting environmental variables across its realised niche and thus predict future distributions based on realised, rather than fundamental, niches;
- b. Process-based SDMs describe the responses of selected traits or processes (such as phenology, resistance to stress, resource acquisition) to environmental descriptors, based on empirical observations, and estimate proxies of occurrence, such as growth or fitness (Chuine and Beaubien, 2001, Kearney et al., 2009);
- c. Hybrid SDMs associate correlative models to describe habitat suitability and process-based models to describe relevant population dynamics characteristics (*e.g.* dispersal, demography).

Because correlative models rely on widely available occurrence and climatic data, they are largely used in the literature. However, their extrapolation to novel climates is uncertain. By contrast, process-based SDMs are assumed more robust to extrapolation to novel conditions (Morin and Thuiller, 2009, Dormann et al., 2012) because their parameterisation relies solely on experiments and observations independent of the data used for model validation.

Projections of future distributions vary according to the correlative model used (*e.g.* Pearson et al., 2006), and between correlative and process-based SDMs (Buckley, 2008, Morin and Thuiller, 2009, Kramer et al., 2010, Cheaib et al., 2012). Ensemble or consensus approaches, using information provided by different SDMs, have been advocated to tackle the problem of divergent forecasts and providing consensus maps (Araújo and New, 2007). Under such approaches, models can vote for the species' presence or absence, and votes are weighted by models' accuracies (*e.g.* Marmion et al., 2009), or combined using multi-model inference (Burnham and Anderson, 2002, see *e.g.* Gibson et al., 2004, Hartley et al., 2006). However, models may agree with one other for wrong reasons (Elith et al., 2010), potentially leaving systematic errors. Mapping the resulting uncertainty is therefore as important as mapping the consensual projection itself. Yet, few studies have provided uncertainty maps of SDM projections. Maps of model discrepancies (*e.g.* Hartley et al., 2006) only inform on the uncertainty associated with different model projections, not the uncertainty associated with the relevance of the climatic descriptors or the processes considered. Should an important environmental descriptor have been omitted in the individual SDMs, its variation would be absent from any multi-model, and even the best model among those considered would be unable to accurately project the species' range (Elith

et al., 2010, Dormann et al., 2012). The performance of conceptually different SDMs may vary with environmental conditions: each SDM may surpass the others in projecting a species' presence under a given set of climatic conditions, for the environmental variables or the processes it considers are more relevant in these conditions.

In a study led by Emmanuel Gritti, and involving Isabelle Chuine, Anne Duputié and myself, we built a simple consensus between SDMs relying on vegetation's physiological responses to climate to predict changes in the distribution of three tree species (*Fagus sylvatica* L., *Quercus robur* L. and *Pinus sylvestris* L.). The uncertainty of the consensus model was assimilated to its statistical deviance to observed occurrence maps. After calibrating and validating the consensus model, we model uncertainty as a function of composite, independent environmental descriptors, in a multi-model framework (Burnham and Anderson, 2002). This approach was applied using three conceptually different SDMs (one correlative with physiological basis, one hybrid and one process-based). Based on the model results, it was relatively straightforward to identify climatic types requiring more precise data to reduce uncertainty and to show that novel "climate types" had very divergent model predictions, thus paving the way for a more critical frame of mind when dealing with yet unknown environmental settings in SDMs.

## 5.2. The evolution of species distributions

Among the different hypotheses proposed to explain the finiteness of species range, evolutionary ecology has come up with a series of models aimed at assessing the effect of gene flow, spatial heterogeneity in fitness and environmental changes as factors driving species distributions (Pease et al., 1989, Garcia-Ramos and Kirkpatrick, 1997, Kirkpatrick and Barton, 1997, Barton, 2000, Barton, 2001, Alleaume-Benharira et al., 2006, Polechová et al., 2009, Norberg et al., 2012, Garcia-Ramos and Huang, 2013, Henry et al., 2015). Spatial heterogeneity may constrain species ranges because it leads to heterogeneous population density across the range (Garcia-Ramos and Kirkpatrick, 1997, Kirkpatrick and Barton, 1997). This generates asymmetric gene flow from central, dense populations towards peripheral populations with lower density. Such genetic swamping of peripheral populations may, in turn, prevent adaptation at the edge of the distribution range, and stop the expansion of the species. Even though the demographic importance of this migration load is unknown in natural settings (Sexton et al., 2009), empirical studies show that high migration rates prevent local adaptation, at least along steep gradients (*e.g.* Bridle et al., 2009). Along a constant linear environmental gradient, a cline is predicted to develop in the trait. If the gradient is sufficiently steep, the species has a finite range, which becomes smaller as genetic variance gets lower and/or the environmental gradient steeper (Kirkpatrick and Barton, 1997). When the phenotypic optimum also changes linearly in time, the trait is still predicted to form a linear cline. If the change in time is sufficiently slow that the species does not go extinct, its spatial distribution shifts, tracking the location where fitness is maximal (Pease et al., 1989). These results are not qualitatively altered by density regulation (Polechová et al., 2009). All these models, however, consider the adaptation of a single trait to changing environments.

Collaborating with Anne Duputié during her post-doc with Mark Kirkpatrick, Isabelle Chuine and Ophélie Ronce, we devised an extension of the initial model by Pease et al. (1989). We incorporated genetic covariance among traits under linear environmental gradients advancing linearly in time (P14). More specifically, we investigated the joint effects of multivariate genetic constraints and gene swamping on the demography and adaptation of a species faced with shifting environmental gradients. Building on the model by Pease et al. (1989), we focused on the evolutionary and demographic effects of

- a. The temporally and spatially varying adaptive landscape, modelled by a fitness function,  $r(\mathbf{z}, x, t)$ , which depended on space ( $x$ ), time ( $t$ ) and the vector of traits ( $\mathbf{z}$ ) as a quadratic function parameterised by  $r_0$ , the basic growth rate,  $\mathbf{b}$ , the slope of the environmental gradient in space,  $v$ , the speed of environmental change and  $\mathbf{W}$ , the selection variance matrix, as:

$$r(\mathbf{z}, x, t) = r_0 - \frac{1}{2} [\mathbf{z} - \mathbf{b}(x - vt)]^T \mathbf{W}^{-1} [\mathbf{z} - \mathbf{b}(x - vt)] \quad (6.1)$$

When averaged over genotypes, equation (6.1) entailed a mean fitness  $\bar{r}$  which depended on mean trait vector  $\bar{\mathbf{z}}$  and the phenotypic covariance matrix among traits,  $\mathbf{P}$ :

$$\bar{r}(\bar{\mathbf{z}}, x, t) = r_0 - \frac{1}{2} \text{Tr}(\mathbf{W}^{-1} \mathbf{P}) - \frac{1}{2} [\bar{\mathbf{z}} - \mathbf{b}(x - vt)]^T \mathbf{W}^{-1} [\bar{\mathbf{z}} - \mathbf{b}(x - vt)] \quad (6.2)$$

- b. Dispersal abilities through the diffusion rate of the population,  $\sigma$ , which influenced the dynamics of population density  $n$  at location  $x$  and time  $t$  through:

$$\frac{\partial n}{\partial t}(x, t) = \frac{\sigma^2}{2} \frac{\partial^2 n}{\partial x^2}(x, t) + \bar{r}(\bar{\mathbf{z}}, x, t) n(x, t) \quad (6.3)$$

- c. Multivariate genetic constraints through the genetic covariance matrix among traits under selection,  $\mathbf{G}$ , which influenced how mean trait vector  $\bar{\mathbf{z}}$  responded to the selection gradient,  $\boldsymbol{\beta}$ , as:

$$\frac{\partial \bar{\mathbf{z}}}{\partial t}(x, t) = \frac{\sigma^2}{2} \frac{\partial^2 \bar{\mathbf{z}}}{\partial x^2}(x, t) + \sigma^2 \frac{\partial \ln(n)}{\partial x}(x, t) \frac{\partial \bar{\mathbf{z}}}{\partial x}(x, t) + \mathbf{G} \boldsymbol{\beta} \quad (6.4)$$

with  $\boldsymbol{\beta}$  given by:

$$\boldsymbol{\beta} = \mathbf{W}^{-1} [\mathbf{b}(x - vt) - \bar{\mathbf{z}}(x, t)] \quad (6.5)$$

This model allowed us to answer the following questions (Fig. 16):

- When do genetic or selective correlations between traits limit a species' response to environmental change?
- What is the critical rate of environmental change that a species may sustain?

We found that the modeled species could track its phenotypic optimum with a constant lag, while all traits developed linear clines, *i.e.* the shape of  $n$  and  $\bar{\mathbf{z}}$  at evolutionary equilibrium were given by:

$$n(x, t) = \exp \left[ \rho t - (x - vt - L_n)^2 / 2 V_n \right] \quad (6.6)$$

and

$$\bar{\mathbf{z}}(x, t) = \mathbf{s}(x - vt) \quad (6.7)$$

where  $\rho$  is the population growth rate,  $L_n$ , the lag between the location where the species is optimally adapted and the peak in population density,  $V_n$  is the typical width of species range, and  $\mathbf{s}$  is the vector of slopes of traits in space.

Under the “strong migration load” assumption, *i.e.* when  $\|\mathbf{G} \mathbf{W}^{-1}\| \ll \sigma \sqrt{\mathbf{b}^T \mathbf{W}^{-1} \mathbf{b}}$ , dispersal increased, the distributional range of the species expanded and the population growth rate increased, while adaptation was prevented because of genetic swamping:

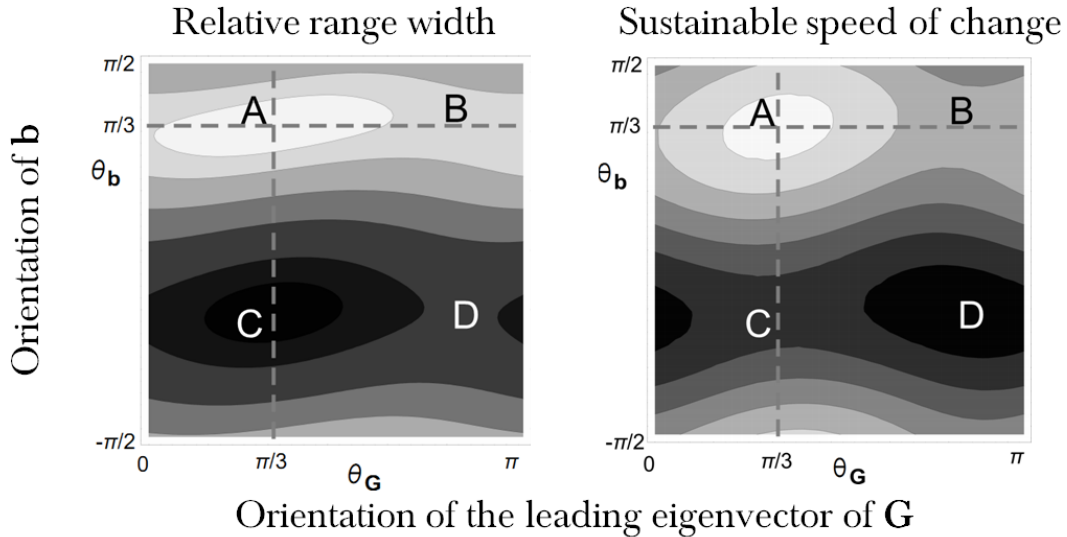
$$V_n \approx \frac{1}{\sqrt{\mathbf{b}^T \mathbf{W}^{-1} \mathbf{b}}} \left( \sigma + \frac{\mathbf{b}^T \mathbf{W}^{-1} \mathbf{G} \mathbf{W}^{-1} \mathbf{b}}{(\mathbf{b}^T \mathbf{W}^{-1} \mathbf{b})^{3/2}} \right) \quad (6.8)$$

$$\rho \approx r_0 - \frac{1}{2} \left( \text{Tr}(\mathbf{W}^{-1} \mathbf{P}) + \sigma \sqrt{\mathbf{b}^T \mathbf{W}^{-1} \mathbf{b}} + \frac{v^2}{\sigma^2} \right) + \frac{\mathbf{b}^T \mathbf{W}^{-1} \mathbf{G} \mathbf{W}^{-1} \mathbf{b}}{2 \mathbf{b}^T \mathbf{W}^{-1} \mathbf{b}} \quad (6.9)$$

$$\mathbf{s} \approx \frac{\mathbf{G} \mathbf{W}^{-1} \mathbf{b}}{\sigma \sqrt{\mathbf{b}^T \mathbf{W}^{-1} \mathbf{b}}} \quad (6.10)$$

Although the understanding of equations (6.8-6.10) does not seem simple at first sight, this was considerably eased by a geometric re-interpretation of the quantities  $\mathbf{b}^T \mathbf{W}^{-1} \mathbf{G} \mathbf{W}^{-1} \mathbf{b}$  and  $\mathbf{b}^T \mathbf{W}^{-1} \mathbf{b}$  in terms of eigenvalues and eigenvectors of matrices  $\mathbf{G}$  and  $\mathbf{W}^{-1}$ , respectively (Fig. 16, see P14 for details).

When most genetic variance (direction of the largest eigenvalue of  $\mathbf{G}$ ) occurred in a direction parallel to the selection gradient generated by the shifting optima ( $\mathbf{W}^{-1}\mathbf{b}$ ), and when the nonlinear selection pressures (stabilising and correlational selection) were weaker in that same direction (direction of the lowest eigenvalue of  $\mathbf{W}^{-1}$ ), the distributional range was wider, with a higher population growth rate, and better adaptation (Fig. 16). Extinction due to the speed of environmental change occurred for lower rates of environmental change when dispersal was lower and when the leading directions of genetic variance, of the nonlinear selection pressures, and of the selection gradient strongly differed (Fig. 16).



**Fig. 16** (excerpt from P14) – Demographic variables as a function of the orientations of  $\mathbf{b}$  ( $\theta_b$ , ordinates) and of the leading eigenvector of  $\mathbf{G}$  ( $\theta_G$ , abscissas) in the phenotypic space. Lighter shades indicate higher values. Intensities of the environmental change ( $\|\mathbf{b}\|$ ) and of genetic variance ( $\lambda_G$ ) are fixed, and  $\mathbf{W}^{-1}$  is fixed. Correlational selection acts so that the weakest stabilising selection occurs in the direction  $\theta_W = \pi/3$  of the phenotypic space. Points **A** and **B**: Selection is weakest in the direction of the environmental change, resulting in low spatial fitness contrast. Point **A**: best-case scenario; genetic variance is also amply available in that direction, conferring a large potential for adaptation, and leading to wide range and high sustainable rate of change. Point **B**: relative range width and sustainable rate of change are reduced compared to point **A**, because adaptation is slowed by the relative absence of genetic variance in the appropriate direction. Points **C** and **D** represent worst case scenarios, where spatial fitness contrast is high, resulting in large migration load. Point **C**: low genetic variance in the direction of the change in optimum results in a narrow range and low sustainable rate of change. Point **D**: genetic variance is available to sustain the environmental gradient. This results in slightly wider ranges than in **C**; however, the sustainable rate of change is even lower than in **C**, because this configuration generates standing loads exceeding the benefits of adaptation. Parameters used:  $\|\mathbf{b}\| = 1$ ;  $\lambda_{G_1} = 0.5$ ,  $\lambda_{G_2} = 0.1$ ,  $r_0 = 0.1$ ,  $\sigma = 1$ ,  $\nu = 0.01$ ,  $\mathbf{P} = 4\mathbf{G}$  and the coefficients of  $\mathbf{W}$  are  $w_{11} = 62.5$ ,  $w_{22} = 87.5$ ,  $w_{12} = 21.6$ .

Overall, this model highlighted the fact that genetic and selective covariances can severely constrain species distributions when genetic variance is not available in the main direction of selection and this selection is strongly stabilising (Fig. 16). Several other extensions of the model of Pease et al. (1989) are currently being considered and/or investigated. First, a model that would consider the evolution of the diffusion trait (Box 9) is needed to corroborate the huge amount of simulation models exploring the effect of dispersal evolution on range expansion and distribution dynamics (Phillips et al., 2008, Burton et al., 2010, Travis et al., 2010, Kubisch and Fronhofer, 2014).

In line with the work presented in 5.2 on constraints to species distribution due to local maladaptation and gene flow, a related question is to understand how the evolution of dispersal capacities may affect range limits. This question has stimulated many different models trying to link the evolution of dispersal to invasion wave speed and/or distribution range limits (Phillips et al., 2008, Burton et al., 2010, Kubisch et al., 2010, Henry et al., 2013, Kubisch et al., 2013, Bocedi et al., 2014, Kubisch and Fronhofer, 2014). However, these studies are based on simulation results and, to our knowledge, no clear analytic insight has been produced on this question yet.

We consider a population in continuous space ( $x$ ) and time ( $t$ ). Space and time are assumed to control population growth rate through extrinsic factors (*i.e.* not linked to local adaptation). The population is considered to be a mix of different genotypes (index  $i$ ) that have different diffusion rates,  $z_i$ , so that the local density  $n_i$  of genotype  $i$  obeys the following diffusion equation:

$$\frac{\partial n_i}{\partial t} = \frac{z_i}{2} \frac{\partial^2 n_i}{\partial x^2} + r_i n_i \quad (\text{B9.1})$$

The dynamics of  $n$ , the sum of all  $n_i$ , is obtained by summing this equation over all genotypes:

$$\frac{\partial n}{\partial t} = \frac{\bar{z}}{2} \frac{\partial^2 n}{\partial x^2} + \frac{\partial \bar{z}}{\partial x} \frac{\partial n}{\partial x} + \frac{n}{2} \frac{\partial^2 \bar{z}}{\partial x^2} + \bar{m} \quad (\text{B9.2})$$

In the same spirit as Pease et al. (1989), we can define a companion equation to equation (B9.2) that describes the dynamics of  $\bar{z}$ :

$$\frac{\partial \bar{z}}{\partial t} = \frac{\bar{z}}{2} \frac{\partial^2 \bar{z}}{\partial x^2} + \frac{\bar{z}}{n} \frac{\partial n}{\partial x} \frac{\partial \bar{z}}{\partial x} + \left( \frac{\partial \bar{z}}{\partial x} \right)^2 + \frac{1}{2} \frac{\partial^2 G_z}{\partial x^2} + \frac{1}{n} \frac{\partial n}{\partial x} \frac{\partial G_z}{\partial x} + \frac{G_z}{2n} \frac{\partial^2 n}{\partial x^2} + \text{Cov}[r_i, z_i] + D_\mu \bar{z} \quad (\text{B9.3})$$

where  $G_z$  is the genetic variance of trait  $z$ ,  $\text{Cov}[r_i, z_i]$  is the genetic covariance between trait  $z$  and fitness, and  $D_\mu$  is the diffusion in trait space due to mutation processes. To interpret equation (B9.3), one may note that:

- The first two terms,  $\frac{\bar{z}}{2} \frac{\partial^2 \bar{z}}{\partial x^2} + \frac{\bar{z}}{n} \frac{\partial n}{\partial x} \frac{\partial \bar{z}}{\partial x}$ , represent the average diffusion of trait  $z$  (as in Pease et al., 1989);
- $\text{Cov}[r_i, z_i]$  is the “Price equation” term (*i.e.* the selection gradient due to the local fitness gradient);
- $D_\mu \bar{z}$  is the mutation term due to the fact that diffusion is a strictly positive trait (hence, biased to mutate towards higher values on average);
- The sum of all the other four middle terms corresponds to  $\text{Cov}\left[z_i, \frac{z_i - \bar{z}}{2n_i} \frac{\partial^2 n_i}{\partial x^2}\right]$ , which could be

interpreted as the “Price equation” term applied to the excess fitness in equation (B9.1) due to the deviation in the diffusion rate of genotype  $i$ . This implicitly defines a “local fitness”  $\rho_i$  attributable to the dispersal trait, which can be written as:

$$\rho_i = \frac{z_i - \bar{z}}{2n_i} \frac{\partial^2 n_i}{\partial x^2} \quad (\text{B9.4})$$

What equation (B9.4) means in biological terms is that the effective growth rate of a genotype is increased by higher than average dispersal when the density of the focal genotype is locally spatially convex, *i.e.* near a local density minimum. By contrast, higher than average dispersal leads to an effective decrease in growth rate when the density of the focal genotype is locally spatially concave, *i.e.* near a local density maximum.

In the next months, we plan to finalise the analysis of this model, mostly through closing equations at some point (in equation [B9.3], genetic variance in diffusion plays a role; genetic variance also varies in space and time as the result of variable  $r$  and diffusion). Two solving possibilities are being compared, the first based on making the assumption that the diffusion rate approximately follows a log-normal distribution at any point in space and time, the second is to solve the dynamic equation on the characteristic function of the probability distribution of  $z$  in space and time rather than working separately on the equations governing the dynamics of each of its statistical moments. We also plan to obtain numeric confirmation of analytic predictions, under different scenarios for the function  $r_i(z, x, t)$ , *i.e.* so that  $r_i(z, x, t)$  can actually reflect purely spatio-temporal variability in growth rate and/or represents maternal cost of dispersal, etc.

Second, the models inspired by Pease et al. (1989) and Kirkpatrick and Barton (1997) have all made the assumption of a linear spatial cline in the optimal trait value for local adaptation. With Thomas Lenormand, Florence Débarre and Fabien Laroche (following some early discussions I had with Anne Duputié during her post-doc), we discussed the possibility of recasting such models in the context of fluctuating sine wave-like optimums in space. Such a shape for optimal trait values would add to the difficulty of adaptation because humped-shaped optima (*i.e.* the need for a different optimum between two regions sharing another value of the optimum) can impede adaptation by providing persistence domains that are too narrow (Shigesada and Kawasaki, 1997, Débarre and Lenormand, 2011, Leroux et al., 2013). Moreover, if such humped-shaped patterns occur with a phase difference among traits (*i.e.* humps for trait 1 do not coincide with a hump in trait 2), genetic covariance among the traits can be a serious constraint on species range because it will inevitably conflict with adaptation at some location.

### 5.3. Conclusions & perspectives

In the other sections of this synthesis, space is considered implicitly, *i.e.* as an island model in which all populations are connected to all others or, in the more sophisticated versions presented in section 3, as a network of populations exchanging migrants with neighbouring populations. In this section, however, I consider space in a continuous fashion. The models presented here are thus a little disconnected from the rest of my work, but I think that bridging the gap between them and my core topics is a clear priority of my future work. In particular, developing the model on the evolution diffusion (Box 9) will make a link between the “evolution of dispersal” theme presented in section 2 and spatially explicit approaches, such as (P14). At some point in the future, linking the evolution of dispersal under heterogeneous carrying capacity (P8) with the evolution of diffusion (Box 9) will help make the theory developed in (P8) more useful for empirical tests. Moreover, such an extension of (P8) might also link the evolution of dispersal on invasion fronts with ecological constraints on the development of pioneer populations (hence, on their growth rates and carrying capacities), in line with models proposed in Box 3 and already existing approaches such as the one proposed by Burton et al. (2010).

In projects AREOLAIRE and ARSENIC, developments of evolutionary models in continuous space are planned to answer different questions:

- a. In AREOLAIRE, we will develop a model *à la* Pease et al. (1989) that will model the evolution of dispersal, local adaptation, self-fertilisation ability and/or pollinator affinity in populations of plants to predict what types of syndromes are expected to be found at trailing and leading edges of plant distributions, depending on their mating system (auto-compatible or not). This model will allow for comparison with existing data on selfing rates, inbreeding depression and plant-pollinator interaction networks at the core *vs.* margins of plant distributions or expansion fronts (Pujol et al., 2009, Réjou-Méchain and Cheptou, in press).
- b. In ARSENIC, we will make use of results obtained on the association of dispersal with traits driving interaction affinities to explore the consequences of trait associations on the biogeography of interaction networks. We will assess how trait evolution shapes the geographical distribution of partner species, extending existing approaches (Price and Kirkpatrick, 2009, Garcia-Ramos and Huang, 2013) to allow for the evolution of traits other than local adaptation. We want to uncover simple ecological settings in which the evolution of dispersal syndromes results in characteristic, testable patterns of patchy distributions. We will first strive to obtain predictions for a fixed homogeneous environment. These predictions will serve as a “null hypothesis” of how species’ ranges should be if species were to interact homogeneously in space. Unlike classic models for the evolution of species’ ranges, such a null hypothesis will take account of the evolution of dispersal and, thus, the possibility that dispersal ability can increase near range margins due to *e.g.* selection (Burton et al., 2010, Kubisch et al., 2013) or dispersal syndromes linking selfing rate and dispersal

(Sun and Cheptou, 2012). In a second step, we will alter the assumption of a fixed, homogeneous environment to predict how species' ranges will change with a gradual shift of environmental condition and also how heterogeneous patchy environments alter the above-mentioned null hypothesis.

Both of these projects will provide me with opportunities to continue making my work more “spatially explicit”, an aspect that is still lacking in most of my studies. They will also help me connect more strongly with empirical approaches by providing readily testable predictions. Both projects AREOLAIRE and ARSENIC combine theoretical models and empirical work; thus, in both cases, the models developed will be tested as part of the projects.

## 6. Perspectives

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All these theories, diverse as they are, have two things in common. They explain the observed facts, and they are completely and utterly wrong.

Terry Pratchett, *The Light Fantastic*

Finishing this habilitation document is not exactly like arriving at the end of a road – there is no “dead end” proving that a subject has been closed. Rather, I think this is probably some kind of crossroads opportunity, a time when reflecting on the best path to tread in the future is possible. As it can be seen from the diversity of topics covered in the previous pages, my attention has been drawn to a large host of questions, but under all these seemingly different questions there is an underlying theme: spatially structured ecological systems. While I might not be working on this topic in ten or twenty years, I want to continue ploughing the field of spatially structured ecological systems at least in the next few years, but perhaps in directions that I have not tried before or with the aim of consolidating the frail parts of their underlying theoretical framework.

The presentation of this document might suggest that my interests, in all the topics I am working on, are purely theoretical in nature. This would be a wrong impression – this presentation actually reflects the points that I feel more comfortable explaining rather than the only points I would find interesting to work on. In the theories I am trying to develop, even in the absence of data (or analysis of such data), I try to keep on the realistic side of the road as much as possible. This is not always easy because, as it is well known in the field of ecological modelling, at least since Levins (1966), generality, realism and precision have to trade off at some point during the formalisation of models. My orientation within this three-way trade-off has not varied since my PhD dissertation: I would go for generality and realism over precision every time except when precision is really essential (*e.g.* in SDMs, but even then there are ways to cope with problems of generality, P18). Because some crucial elements of realism are lacking in what I have done to this day, I feel the need to develop a few new axes of my research in the next few years.

With this need for ecological and biological realism in the back seat, the following four subsections detail four different “leads” that I think are worth pursuing (Fig. 17). First, as already mentioned repeatedly in the above sections, I am engaged in at least three funded projects that deal with the topic of evolution of meta-networks, *i.e.* the evolution of traits in spatially structured interaction networks, such as food webs and plant-pollinator networks. Second, I have contributed to tease apart the various processes, assumptions and limitations of metaecosystem theory in the past (P11, P21), and I now want to overcome some of the mentioned limitations by extending the theory in various ways, both conceptually and in the methods to use. Third, rubbing shoulders with slightly more down-to-earth researchers such as Dave Bohan or Sandrine Petit has made me more aware of the need for ecological theory to actually produce tools to be used for the management of human-affected ecosystems. In this vein, I want to develop network-based models to predict ecosystem services, at least in the context of agro-ecosystems first, and maybe to extend such approaches to other contexts. Last, but not least, my current immersion in the world of functional biology through a new collaboration with Aurélie



Tasiemski has made me realise that symbiotic interactions *sensu lato* (i.e. mutualistic symbiosis, commensalism and the various forms of parasitism) have been completely overlooked by metacommunity and metaecosystem theories alike (up to now, but see Seabloom et al., 2015). While this might seem an arguably forgivable mistake when goals are set on explaining energy fluxes among compartments, it is not acceptable when the topic of interest is the evolution of interactions, as symbionts are a major source of evolutionary innovations for many (almost all?) large organisms on Earth (Margulis, 1998).

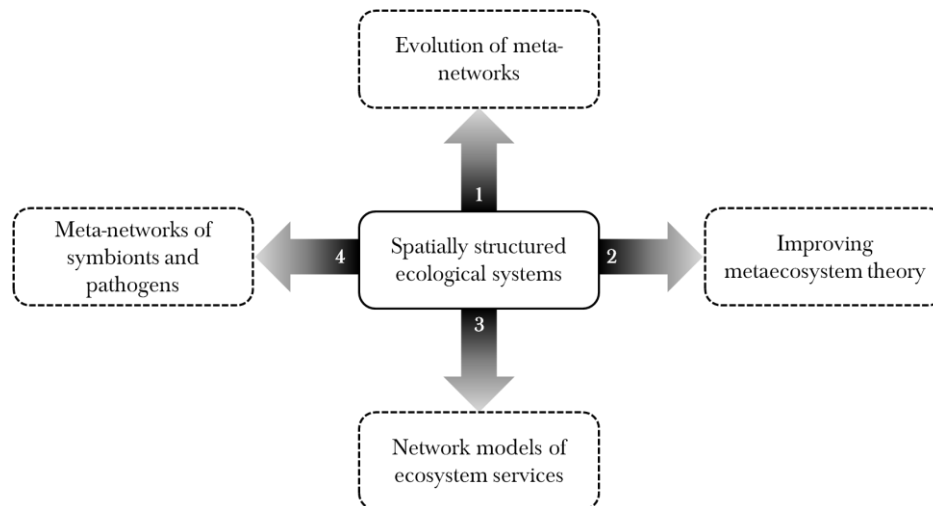


Fig. 17 – Perspectives for future work on spatially structured ecological systems.

### 6.1. Evolutionarily driven syndromes in spatial interaction networks

Thanks to projects ARSENIC, AREOLAIRE and COREIDS, my current research has clearly been shifted to the subject of meta-networks, *i.e.* spatially structured interaction networks, especially the question of how such networks evolve and what are the resulting evolutionary syndromes linking traits within and among species. These projects provide me with opportunities to develop several topics that I have been thinking about for quite a long time:

- a. Are there universal trait syndromes across interaction networks that emerge from the co-evolution of traits in different interacting species? For instance, is it a consequence of coevolution that mating systems and dispersal abilities might be somehow correlated in plants or animals or just a constraint stemming from a link between the morphology of reproductive systems and propagules?
- b. Can trait variation be linked to the position occupied by the species within the network? For instance, do self-compatible plants interact with more or fewer pollinator species and with more or less specialised pollinators and herbivores than self-incompatible plants?
- c. How strong is the role of spatial structure in driving the evolution of interaction networks? What are the predictions for the evolution of interaction networks when dispersal does or does not evolve?
- d. Is the spatial patchiness of ecosystems sufficient to explain the spatial heterogeneity of interaction networks, or does the spatial arrangement of dispersal fluxes play a role?
- e. Are co-evolved interaction networks more or less susceptible to invasions by exotic species than random networks? Are networks that co-evolved in a patchy landscape more or less susceptible to invasions than those co-evolved in a homogeneous well connected habitat? Does evolution lead to networks that are more or less prone to cascading extinctions? What is the typical scale of cascading extinction events in coevolved networks when compared with networks that would rely purely on external immigration for their build-up?

- f. How does network complexity evolve along an environmental gradient? Do nutrient-rich regions display different networks (and network topologies) from nutrient-poor regions? What happens to network topologies in colder/warmer environments? Does disturbance play a filtering role on species traits? Does this feed back on the evolution of dispersal abilities?
- g. Can the evolution of traits in interaction networks explain the stability of natural ecosystems? If so, what are the key selective pressures that determine this stability? Do these conclusions hold in general or only for spatially structured networks?
- h. Does the evolution of interaction networks lead to predictable patterns of ecosystem distributions on large scales? Can the patchiness of species distributions be the consequence of the local coevolution of interacting species, of their dispersal abilities or interaction traits?

The building of models addressing these questions will be a novel endeavour, of course, but it will find a strong theoretical basis in some of the work I have been involved in recently, especially on the evolution of dispersal (P5, P8, P9, P10, P20) and the dynamics of interaction networks (P12, P13, P21, P22, P25).

## 6.2. Improving metaecosystem theory

In two different papers (P11, P21), I identified, together with collaborators, two conceptual points (the proper definition of patches and limiting factors in metaecosystems) that I think deserve attention to improve the theory of metaecosystems. One of my goals in the next few years is first to make these points more understandable as potential sources of problems and then to try and improve the theory so that problems can be solved in theoretical models.

**Proper definition of patches.** Metaecosystem models have inherited the modelling habits of metacommunity ecologists, among which can be found a clear appeal towards discrete patch-landscape models. The inherent issue with such models is that they have hidden assumptions on the scales of processes acting within and among patches, *i.e.* whereas model presentation deals with patches as environmental constructs, there are very few natural settings that are clearly patchy by nature. Most of the time, patchiness should be thought of not as an environmental construct, but rather as a consequence of the biological processes at play.

A first instance of this issue occurs in models in which all organisms and nutrients perceive space with the same grain – movement rates parameterise movement on a trans-specific scale; this is bound to be false if *e.g.* a predator population shares several patches as its hunting ground (McCann *et al.*, 2005; P11). Assuming that, because a model is patch-structured, then all species should see the world as similarly patchy is an implicit yet drastic assumption.

A more complex understanding of this issue comes from the definition of a patch itself: when patches are geographically and physically limited (*e.g.* ponds), some organisms perceive the patch as a constraining unit for population growth (*e.g.* fish) while others can live over and among different ponds (*e.g.* adult dragonflies); when patches are not physically explicit, the existence of habitat patches is a model of reality. In this case, the spatial extent of a patch needs to be linked to the spatial extent of an important process. In metapopulation models, this is usually the stochastic extinction process because the assumption shared by all metapopulation models is that perturbations happen independently in different patches (Levins, 1969, Hastings, 1980, Tilman, 1994, Calcagno *et al.*, 2006). In metacommunities with local species sorting (Leibold *et al.*, 2004), the spatial extent of patches must be the spatial scale at which competition for limiting factors comes into play. Because “classic” metacommunities only consider competitive interactions, there is no intrinsic reason why this spatial scale should vary from one species to another (P11). However, in metaecosystems, many interaction types are considered, so that (i) the choice of interaction determining the spatial extent of patches is not trivial and (ii) the spatial scale of important interactions will vary from species to species.

**Limiting factors in metaecosystems.** In classic community ecology, it is widely admitted that species coexistence depends on the number of limiting factors, even though this idea holds problems of its

own (Hutchinson, 1961, Meszena et al., 2006). Essentially, each species must have its own “Hutchinsonian niche” in the space of limiting factors (Tilman, 1982, Leibold, 1996). However, from a metacommunity perspective, the addition of species dispersal makes the picture more complex because locally outcompeted species can persist thanks to high immigration from other patches (Mouquet and Loreau, 2002) – the so-called mass effect (Leibold *et al.*, 2004), which translates in metacommunity theory a source-sink phenomenon already known for single species metapopulations (Amarasekare and Nisbet, 2001, Kawecki, 2004).

In “limiting factor” parlance, organism dispersal among patches results in a shift of the supply point (*sensu* Tilman, 1982) along a direction parallel to the quotas of the different nutrients in the body of moving organisms (Box 4). This can result in either favouring or disfavouring the coexistence of species, depending on dispersal rates. If we were to extend such a theory to metaecosystems with more than one biotic trophic level, the various movement rates of inorganic nutrients, detritus, primary producers, etc. would all have a say on the coexistence of all species. In other words, the persistence of a given species in a given location depends on its “local niche” – which is a product of its local limiting factors (resources, natural enemies, ...) – and on its “regional niche” – which integrates the “fitness” subsidies obtained from the movement of all species and abiotic agents from other patches to the focal patch.

### 6.3. Towards models of ecosystem services

Regularly reading published calls for research projects, at the national and European levels, I have quickly become used to the fact that words like “impact”, “innovation”, “knowledge gap”, etc. often pave the way for calls that would readily see researchers in ecology as some additional pool of executive civil servants, capable of making assessments on whatever societal question is currently at stake in whatever environmental or socio-economic context. While this interpretation seems to be widespread – there is more than a seeming gap between what call funders believe research should be doing and what researchers believe their job is about –, it does not reflect all the reasons why a theoretical ecologist could feel uneasy when realising that what he/she is working on is not linked to societal issues.

Of course, academics that pursue their career up to the habilitation are often dead set on their conviction that either societal issues are a thing to take care of (what is usually called *applied research*) or that societal issues are yet another hurdle between the researcher and pure truth, a hurdle that must be dealt with only to obtain money necessary to carry out some “good” (understand: not applied) research. My first job after my PhD defence was at IRSTEA, an institute that takes pride in the fact that it is a leader in applied ecological research in France. While I was at IRSTEA, I kept on complaining that too much pressure was put on researchers to obey private companies’ whims to obtain funding (like counting fish near nuclear power plants). And yet, now that I have been delivered from such psychological shackles, I think that adding a little bit of applied ecology to my palette would not be a disservice to society.

One particular subject that David Bohan and I (and many others) think would deserve some attention from ecologists – and particularly from adepts of network approaches – would be the development of a framework to envisage how changes in the various anthropogenic disturbances occurring at the landscape scale affect the production of various ecosystem services, such as pollination, pest control by natural enemies or the maintenance of good water quality. The currently envisioned project, which would focus on this question from the viewpoint of agro-ecosystems, would not be purely theoretical, but would rather integrate modelling approaches with mesocosm and microcosm experiments, as well as field data collections. It would also cross disciplinary boundaries and comprise ecologists, social scientists and economists alike.

The precise reason why I think network approaches should definitely find an outlet in the world of applied ecology, and particularly on the topic of ecosystem services, is that, however the problem of

linking anthropogenic changes is being looked at, whatever the assumptions made on the processes underlying global changes or the production of ecosystem services, the systems underlying ecosystem services are inherently driven by pairwise interactions – plants and pollinators, farmers and land use, pest and their natural enemies, agricultural decisions and governmental incentives, etc. – and, thus, inherently prone to a description as a network, as evidenced *e.g.* by the variety of Bayesian belief network approaches developed specifically for ecosystem services (Landuyt et al., 2013).

The potential end result that I think could be feasible and satisfactory in the long run would be to develop such an integrative framework approach up to the production of “maps”, *à la* SDM, *i.e.* to be able to draw on a landscape map the “value” of different ecosystem services predicted from the knowledge of anthropogenic and environmental variables at a sufficiently fine spatial scale (Raffaelli et al., 2014). While the use of the word “value” in the context of ecosystem services is still subject to debate, it would be a good advance nonetheless to be able to map the state of ecosystem services in response to external drivers of change, to be able to make an assessment of the value of policies from the point of view of ecosystem services.

#### 6.4. Symbiotic associations and metaecosystem heterogeneity

For someone interested in interaction networks, coevolutionary dynamics and spatial structure, there is a topic which should draw a lot of attention, namely the evolution of spatially structured symbiotic interaction networks. The question of the evolution of host-symbiont associations finds most of its theoretical basis in two different principles, the coevolutionary arms race and Red Queen dynamics, which have been exemplified in population genetics through the gene-for-gene and matching-allele models, respectively (Gandon et al., 2008, Gandon and Day, 2009).

The topic of host-pathogen coevolution has recently benefited from three conceptual advances:

- a. While classic approaches used to focus on host-symbiont evolution as a one-on-one species problem, either as a virulence evolution or a local adaptation problem, the issue of parasite generalism/virulence trade-off has garnered much interest recently (Leggett et al., 2013);
- b. As epidemiological theory has moved from unstructured mean-field SIS and SIR models to network models that account for the variability of host neighbour size (Andersson and Britton, 2000, Britton, 2010), models of host-pathogen coevolution have moved from an unstructured setting to spatially structured ones (Sasaki et al., 2002, Débarre et al., 2012, Webb et al., 2013);
- c. Trait-based approaches to the coevolution of host resistance and pathogen infectivity have finally incorporated both gene-for-gene and matching-allele paradigms in a single unified framework (Boots et al., 2014).

Moreover, the issue of resistance evolution to antibiotics (or other means of defence) in pathogens, in which the main debate used to be focused on the intensity of antibiotic treatments (Read et al., 2011, Kouyos et al., 2014), now incorporates elements of ecological theory, *e.g.* by considering that resource limitation might be a factor affecting the cost of resistance, and thus the mutant strain’s absolute fitness (Day et al., 2015), in line with Tilman’s (1982) resource ratio theory.

While the current framework of host-pathogen coevolution seems to be getting along quite well without any interference from someone like me, I would like to contribute to this general theme in the years to come to unify mutualistic, commensalistic and parasitic symbiont-host coevolution in a spatially structured ecological context, for the following reasons:

- a. Most, if not all, clades of mutualistic symbionts also contain related species that are especially virulent pathogens, *e.g.* in endophytes (Carroll, 1988) or bacteria in various metazoans (Graf, 1999, Bäckhed et al., 2005, Yu et al., 2007, Nicholson et al., 2012).
- b. Empirical evidence, at least on plants and their endophyte or ectomycorrhizal “mutualists”, seems to indicate that high limiting nutrient levels break beneficial associations and might select for a switch from mutualism to commensalism or even parasitism in symbionts, or stronger

defence of the host, as the association between hosts and symbionts is disrupted by high nutrient inputs (Kiers et al., 2003, Kiers et al., 2007, Jackson et al., 2012). Of note, a recently published hypothesis explaining the high virulence of tuberculosis in humans is based on the speculation that *Mycobacterium tuberculosis* might have started out as a mutualistic tryptophan-providing symbiont, and that the associated mutualism might have been disrupted by the increase of meat in the human diet (Williams and Dunbar, 2013);

- c. In the same way, invasions may also disrupt such associations, *e.g.* in plant-fungus associations by affecting soil microbial communities (Brouwer et al., 2015);
- d. On the other hand, some plants can become myco-heterotrophic or parasitic of mycorrhiza (Hobbie and Höggberg, 2012);
- e. The evolution of virulence in pathogens and the evolutionary stability of mutualistic interactions both depend on relatedness (van Baalen and Sabelis, 1995, Ferrière et al., 2007, Vigneux et al., 2008, Bashey et al., 2012), and thus on the level of immigration within local symbiont communities, *i.e.* infectivity and the mode of transmission (see also Genkai-Kato and Yamamura, 1999).

Overall, mutualistic interactions between host and symbionts can be disrupted by a variety of external ecological factors, such as nutrient limitation, which also control the evolution of pathogen virulence (Hochberg et al., 2000).

All these observations pinpoint a lack of model to explain the coevolution of host defence intensity and dispersal and symbiont infectivity, competitiveness and/or transmission mode in a spatially structured context, with heterogeneity in resource supply among patches and considering that symbiont species can compete both through resource use *à la* Tilman (1982) and through direct interference competition, *e.g.* through antibiotic production or phage release. Such a microbial warfare within the host can also be regulated by the host natural antibiotic production, to control beneficial symbiont proliferation (Login et al., 2011) and resist against pathogenic symbionts (Tasiemski et al., 2004). The picture painted so far seems a bit confused and maybe overly complex, but I think it deserves some attempts at modelling to understand how and under which conditions beneficial associations can turn into pathogenic ones.

## 6.5. Conclusion

The nagging question that will inevitably arise – and I know I will have to deal with it somehow – is the following. Proposing new leads is obviously a tune that I have sung quite a number of times in the past, first during my Master internship, switching from a purely theoretical model on fish communities to the actual analysis of fish community data (leading to P1), then during my PhD, switching more drastically from local community models to metacommunities and the evolution of dispersal, and since then even more diversifying by incorporating network approaches, metaecosystems and spatially explicit models. But what if I had to cut down some branches in order to pursue new leads? At what point should I prioritise the different topics I am working on?

I must acknowledge I have always been reluctant to give up working on any given topic, but I have actually succeeded in such a “rehab” programme, my first academic subject having been the comparison of phylogenetic tree topologies under different modes of speciation... and now it has been more than twelve years since I last worked on this topic. Arguably, my incursions in the realm of fish community ecology (P1) or in the ecophysiology of trees under drought regimes (P6) were “one-night stands” that have not impinged much on the directions I have taken since then. Other such incursions, despite being collaborations not meant to be repeated afterwards, such as the study of ideotypic selection of cassava cultivars by Amerindian cultivators (P4), have made me aware of new doors (in this case, the door being Doyle McKey’s) leading to completely different interesting worlds.

Even in the process of finding one’s way among all the possible paths to tread in the ecological research world, serendipity is of the essence. I am not convinced that the success of future leads

depends on cutting loose some old ones, however filled up my schedule seems to be – or at least, this cutting loose need not be a conscious process, it will probably take care of itself. Putting too much emphasis on the fact that a researcher should be the driver behind the wheel rather than sitting on the passenger seat is a recurrent theme in academic mythology, but it obfuscates reality in more than one way. Research subjects are not always chosen, they often choose you. Rewriting history at academic job interviews is fine, but it does not mean the principles behind such rewriting are worth changing the way I am doing research.

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## GLOSSARY AND ABBREVIATIONS

Adaptive dynamics (adapted from P20)	A mathematical framework aimed at studying the evolutionary dynamics of phenotypic traits (Hofbauer and Sigmund, 1990, Dieckmann and Law, 1996, Champagnat, 2006). Adaptive dynamics relies on two main assumptions: (i) mutations are rare and (ii) of weak effect. Based on these two assumptions, analyses are performed so that, at any moment, the population consists of a given number of resident strategies (initially, one) and one mutant strategy equipped with a trait value infinitesimally close to one of the residents'. Evolutionary trajectories are obtained through the computation of the mutant fitness, the ensuing selection gradient (first-order derivative of the mutant fitness with respect to mutant trait value) which determines evolutionary trajectories through the 'canonical equation' (Dieckmann and Law, 1996), and second-order derivatives defining the convergence and evolutionary stability of the coalition of phenotypes (Geritz et al., 1998).
AD2M	Adaptation et Diversité en Milieu Marin In English: Adaptation and diversity in marine environments A laboratory located in Roscoff biological station.
ANR	Agence Nationale de la Recherche The French equivalent of the National Science Foundation in the US.
AREOLAIRE	Adaptation, Régression et Expansion en Limite d'Aire de Répartition Project funded by the FRB / Région Nord Pas-de-Calais programme for the period 2015 – 2018 and coordinated by Anne Duputié. The general aim of the project is to study the adaptation of organisms at the leading and trailing edges of their geographic distribution, both from theoretical and empirical standpoints.
ARSENIC	Adaptation and Resilience of Spatial Ecological Networks to human-Induced Changes Project funded by the ANR for the period 2014 – 2019 and coordinated by Nicolas Loeuille and me. The general aim of this project is to study evolutionary syndromes associating traits affecting interaction affinity and traits affecting dispersal ability in spatially structured interaction networks (plant-pollinator networks and food webs), both from theoretical and empirical perspectives.
ASN	American Society of Naturalists
BES	British Ecological Society
CEFE	Centre d'Ecologie Fonctionnelle et Evolutive (UMR 5175) In English: Centre for Evolutionary and Functional Ecology The laboratory I worked in during my PhD and between 2012 and 2014 (in Montpellier).
Centrality (P22)	A general term that refers to one of various measures of the 'importance' of the node within the network. Basically, all such measures are sophisticated extensions of the degree that account for the topology of the network around the focal node.
CESAB	Centre de Synthèse et d'Analyse de la Biodiversité The French equivalent to the US National Center for Ecological Analysis and Synthesis
CESCO	Centre d'Ecologie et de Sciences de la Conservation In English: Centre for Ecology and Conservation Sciences A laboratory hosted at the National Museum of Natural History, in Paris.
CIRB	Center for Interdisciplinary Research in Biology Interdisciplinary laboratory hosted at the Collège de France, in Paris.
CNRS	Centre National de la Recherche Scientifique In English: National Centre for Scientific Research
Connectance	Connectance (or density) measures the proportion of edges that exist in relation to the number of edges that can potentially exist (Wasserman and Faust, 1994). For obvious reasons, connectance is not well defined for weighted networks (P22).

COREIDS	<p>Predicting community resilience to invasions from diversity and network structure CESAB working group / project funded by the FRB and TOTAL for the 2014 – 2017 period and coordinated by Patrice David and me.</p> <p>The general aim of the project is to study the effects of biological invasions in food webs as well as the potential factors explaining the ease of invasions in certain food webs. This project relies on the use of a lot of existing databases on food webs and invasions. The “working horse” of the project is Grégory Mollot, CESAB post-doctoral fellow based at the CEFE in Montpellier.</p>
CS	<p>Convergence stable</p> <p>A singular strategy is convergence stable when the monomorphic evolution of strategies, through slow substitution sequences, can lead to this focal strategy. A singular strategy that is not CS is an evolutionary repeller.</p>
CSS	<p>Continuously stable strategy (Eshel, 1983)</p> <p>A singular strategy is continuously stable when it is simultaneously evolutionarily stable and convergence stable.</p>
Degree (P22)	<p>The degree (or connectivity) of a node is the number of edges connected to it. In directed networks, each node has an in-degree and an out-degree that respectively count the number of incoming and outgoing edges.</p>
DGSE	<p>Dynamique et Gouvernance des Systèmes Ecologiques In English: Dynamics and Governance of Ecological Systems</p> <p>The department of the CEFE I was recruited in. Now renamed Biodiversité et Conservation (Biodiversity &amp; Conservation).</p>
Dispersal (P20)	<p>Dispersal can be defined in different ways. The most commonly admitted definition of dispersal is ‘<i>any movement of individuals or propagules with potential consequences for gene flow across space</i>’ (Ronce, 2007). On the one hand, for zoologists, dispersal involves the movement of individuals, at any life stage, between the birth place (or a former breeding site) towards a new breeding site (Clobert et al., 2009). Botanists, and zoologists interested in sessile organisms, on the other hand, tend to consider dispersal as a two-sided process, with gamete dispersal and zygote dispersal being two sides of the same coin (Ravigné et al., 2006, Cousens et al., 2008). While the mode of dispersal in animals is almost always straightforward (but see Pradillon et al., 2001, Zakas and Hall, 2012), plants can use many different modes of gamete and zygote dispersal (see e.g. Ellner and Shmida, 1981 for a good glossary of terms). One difficulty linked to defining dispersal without any explicit relation to gene flow is that many animal species move all the time in search of food (foraging movements), so that definitions of dispersal based on spatial or temporal scales of movements are more difficult to formulate (P11).</p>
DyBRES	<p>Dynamique de la Biodiversité sur des Réseaux Ecologiques Spatiaux Working group funded by the RNSC in 2013 and 2014 and coordinated by Stéphanie Manel, François Munoz and me.</p> <p>The general aim of this working group was to discuss and think about the use of network approaches to model spatially structured ecological systems.</p>
ECMTB	<p>European Conference on Mathematical and Theoretical Biology.</p> <p>A series of conferences organised by the ESMTB (see below).</p>
EDB	<p>Evolution et Diversité Biologique In English: Evolution and Biological Diversity</p> <p>A big ecology laboratory in Toulouse.</p>
Edge / link (P22)	<p>An edge or link connects two nodes in a network. An edge can be undirected (the connection goes both ways) or directed (one way). In the case of energy pathways, directed links represents the elemental flux; in the case of mutualistic networks, a pair of directed links represents an interaction with mutual benefit, such as in the case of plant-pollination syndromes; in the case of classical (<i>i.e.</i> trophic) food webs, directed links go from the prey/resource to the predator/consumer.</p>
EEF	<p>European Ecological Federation Federation of ecological societies in Europe.</p>



EEP	Evolution, Ecologie et Paléontologie (UMR 8198) My current laboratory (in Lille) since 2013.
ENGREF	Ecole Nationale du Génie Rural, des Eaux et des Forêts In English: National School of forestry and water management The engineering school I went to after my 3 years at the Ecole Polytechnique
ESA	Ecological Society of America
ESEB	European Society for Evolutionary Biology
ESMTB	European Society for Mathematical and Theoretical Biology
ESS	Evolutionarily stable strategy (Maynard Smith and Price, 1973, Hofbauer and Sigmund, 1990) A singular strategy is an ESS if it is unbeatable by other strategies when settled as the resident strategy of the population.
FAPESP	Fundação de Amparo à Pesquisa do Estado de São Paulo In English: São Paulo Research Foundation
GDR	Groupe de recherche CNRS non-permanent structure aimed at animating and organising research on a given topic.
GEPV	Génétique et Evolution des Populations Végétales (UMR 8198) The old name (until the end of 2014) of my current laboratory in Lille (now EEP).
IEES	Institute of Ecology and Sciences of the Environment
INRA	Institut National de la Recherche Agronomique In English: National Institute of Agronomic Research
IPEF	Ingénieur des Ponts, Eaux et Forêts Civil servant for the French Ministries of Agriculture and Environment
IRSTEA	Institut national de Recherche en Sciences et Technologies pour l'Environnement et l'Agriculture In English: National research institute of science and technology for environment and agriculture
ISEM	Institut des Sciences de l'Evolution – Montpellier In English: Institute for Sciences of Evolution in Montpellier The “other” huge evolutionary ecology lab in Montpellier beside the CEFE. Although I have never been formally hosted at ISEM, many of my collaborators work there.
Kin competition (P20)	The process by which related individuals tend to compete with one another. Strong kin competition selects for dispersal following Hamilton’s rule (Hamilton, 1964a, b). It should be noted that relatedness is influenced by both dispersal and local population size, so that dispersal and relatedness feedback on one another (Frank, 1986).
Metacommunity (P26)	A set of communities linked together by exchange of migrants from the different species (Leibold et al., 2004, Holyoak et al., 2005, Economo and Keitt, 2008).
Metaecosystem (P26)	A set of ecosystems linked by fluxes of organisms and/or abiotic matter (Loreau et al., 2003).
Metapopulation (P20, P26)	A population of populations, <i>i.e.</i> a collection of populations subjected to the processes of colonisation and extinction (Andrewartha and Birch, 1954, Levins, 1969, Levins, 1970, Merriam, 1988, Hanski and Gilpin, 1997, Hanski, 1999, Hanski and Gaggiotti, 2004). By extension, in the context of dispersal evolution, subdivided populations ( <i>i.e.</i> sets of populations subjected to dispersal but not to extinctions) have been termed metapopulations ( <i>e.g.</i> P8).
MIRES	Méthodes interdisciplinaires pour les réseaux d'échange de semences Working group funded by the RNSC in 2013 and 2014, and now supported by INRA mathematics department. The group is coordinated by Pierre Barbillon, Sophie Caillon, Mathieu Thomas, Nicolas Verzealen and me. The general aim of the working group is to discuss and build new methods for the study of seed exchange networks. The group comprises both “field scientists” from ecology, anthropology, ethnology and geography, as well as a strong group of theoreticians from computer science, mathematics, population genetics and theoretical ecology.

Modularity (P22)	<p>The grouping of nodes in the network into modules. Modules are defined as consisting of nodes that are well connected to other nodes within modules, but less well connected to nodes in other modules. Given the knowledge of a network's modules (<i>i.e.</i> some groups of nodes), modularity <math>Q</math> is a score that is based on the density of links within modules when compared to their expectation under a random assignment of links (Newman, 2004a, Newman and Girvan, 2004, White and Smyth, 2005, Newman, 2006a):</p> $Q = \sum_i \sum_j \left[ a_{ij} - \frac{\left( \sum_k a_{ik} \right) \left( \sum_k a_{kj} \right)}{\sum_k \sum_l a_{kl}} \right] \delta_{ij} / \sum_i \sum_j a_{ij}$ <p>where <math>\delta_{ij} = 1</math> if and only if nodes <math>i</math> and <math>j</math> belong to the same module. This definition can even be extended to graphs that have negative edge weights (Traag and Bruggeman, 2009).</p>
Multipartite network (P22)	<p>A network is said to be bipartite if nodes can be put in two disjoint groups so that edges only connect nodes from different groups (<i>i.e.</i> there is no within-group links). It is tripartite if there are three disjoint groups. For instance, a plant-pollinator network is bipartite, while a plant-herbivore-parasitoid network is tripartite. Analysis of bipartite networks is well developed, especially within ecology. Analysis of tripartite networks is less well developed and usually is done on the individual, stacked bipartite networks.</p>
Nestedness (P22)	<p>A network is said to be perfectly nested if there is some reordering of vertices complying with the fact that node <math>i+1</math> can be connected to node <math>j</math> only if node <math>i</math> is connected to node <math>j</math>. Such a reordering must follow an ordering of vertices by decreasing degree. In bipartite networks, many different indices has been proposed to measure nestedness (Atmar and Patterson, 1993, Ulrich and Gotelli, 2007, Almeida-Neto et al., 2008, Ulrich et al., 2009, Fortuna et al., 2010, Baselga, 2012, Carvalho et al., 2012, Podani and Schmera, 2012), but the lack of formal definition of the concept makes it difficult to agree on a good general measure of nestedness. Recently, Staniczenko et al. (2013) have proposed that the spectral radius of the adjacency matrix could be used as a good proxy for nestedness.</p>
Node / vertex (P22)	<p>A node or vertex represents an individual component of a graph, <i>e.g.</i> a species in a species-species interaction network, such as a food web or a plant-pollinator network.</p>
RNSC	<p>Réseau National Systèmes Complexes In English: National network on complex systems Association of research institutes aiming at supporting work on complex systems</p>
SDM	<p>Species Distribution Model</p>
SFE	<p>Société Française d'Ecologie In English: French Society for Ecology</p>
SGDC	<p>Species-Genetic Diversity Correlation The correlation (among locations) of measures of diversity at the community level (<i>e.g.</i> species richness) and at the gene level within one focal species (<i>e.g.</i> allelic richness at one locus).</p>
SIAL	<p>Speciation In Ancient Lakes A series of conferences organised by researchers working on biodiversity of ancient lakes (Tanganyika, Victoria, Baikal, Ohrid, etc.). SIAL 3 (2002) was actually the first scientific conference I ever participated to.</p>
SIR	<p>Susceptible, Infected, Removed model of epidemics A model of epidemics in which individuals that were once infected and have recovered are not susceptible to the disease anymore (Kermack and McKendrick, 1927).</p>
SIS	<p>Susceptible, Infected, Susceptible model of epidemics The simplest epidemiological model, in which individuals that recover from the disease can be infected again.</p>
SSE	<p>Society for the Study of Evolution</p>

Syndrome (P20)	An association of values of different phenotypic traits due to selection. For a syndrome to exist, there should be at least one reason for divergent selection of different trait values across habitats. Syndromes should not be confused with standing genetic variances and covariances, which specify how traits co-vary (within a population or metapopulation) as a consequence of mutation (with potentially pleiotropic mutations affecting more than one trait at once), recombination (linked loci would statistically co-vary), selection, drift and migration. A syndrome does not emerge as a result of a trade-off either ( <i>i.e.</i> a constraint on trait values due to physical or chemical constraints).
Unipartite network (P22)	A network is said to be unipartite if nodes cannot be put in disjoint groups within which there is no interaction. For instance, a classical (multi-trophic) food web is often treated as being unipartite, although if trophic levels are distinct and the number of them is low then they are often treated as stacked bipartite networks. Much of network analysis outside of ecology is based on unipartite networks.



## WHO'S WHO

The names of the collaborators and students cited in the synthesis might not be familiar to every reader. I have thus taken the liberty of listing them here (sorted by surname), with their **current position** and laboratory.

Astegiano, Julia	Post-doc	Univ. São Paulo (São Paulo, Brazil)
Bohan, David	Research director, INRA	Agroécologie (Dijon)
Calcagno, Vincent	Researcher, INRA	ISA (Sophia-Antipolis)
Canard, Elsa	Post-doc	MIVEGEC (Montpellier)
Cheptou, Pierre-Olivier	Research director, CNRS	CEFE (Montpellier)
Chuine, Isabelle	Research director, CNRS	CEFE (Montpellier)
Cuvelliez, Rémi	MSc student	Lille
David, Patrice	Research director, CNRS	CEFE (Montpellier)
Daufresne, Tanguy	Researcher, INRA	Eco & Sols (Montpellier)
Débarre, Florence	Post-doc	CIRB (Paris)
Denton, Joseph	MSc student	Lille
Dubart, Maxime	MSc student	Lille
Duputié, Anne	Associate professor, Univ. Lille 1	EEP (Lille)
Fontaine, Colin	Researcher, CNRS	CESCO (Paris)
Gravel, Dominique	Regular professor, Univ. Québec	Univ. Québec (Rimouski, Canada)
Gritti, Emmanuel	Post-doc	SYSTEM (Montpellier)
Guimarães, Paulo R.	Professor, Univ. São Paulo	Univ. São Paulo (São Paulo, Brazil)
Hautekète, Nina	Associate professor, Univ. Lille 1	EEP (Lille)
Jacquet, Claire	PhD student	EcoSym (Montpellier)
Jarne, Philippe	Research director, CNRS	CEFE (Montpellier)
Jollivet, Didier	Researcher, CNRS	AD2M (Roscoff)
Kirkpatrick, Mark	Professor, Univ. Texas	University of Texas (Austin, TX, USA)
Lacroix, Gérard	Researcher, CNRS	iEES (Paris)
Laroche, Fabien	Post-doc	CEFE / Cirad (Montpellier)
Laso, Francisco	Staff at Ecology Project International	Galapagos, Ecuador
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L'Honoré, Thibaut	MSc student	Paris
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Mollot, Grégory	Post-doc	CEFE (Montpellier)
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Ronce, Ophélie	Research director, CNRS	ISEM (Montpellier)
Schatz, Bertrand	Research director, CNRS	CEFE (Montpellier)
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Tasiemski, Aurélie	Associate professor, Univ. Lille 1	EEP (Lille)



## POSTSCRIPT: MISCELLANEA

Puisse chacun être son propre historien. Alors il vivra avec plus de soin et d'exigence. Moi, toi, elle, lui, nous, vous ! Terminé.

Jean-Luc Godard, *Tout va bien*

While writing this document, a lot of questions emerged that have absolutely nothing to do with the scientific parts described in the serious sections. My feeling is that this memoir, to genuinely reflect the process of “growing up” from being a PhD to being a “habilitated” researcher, must somehow comprise traces of these questions and how I dealt with them. Here is a non-exhaustive sample, presented as some kind of FAQ (don't ask why).

**Q: Why the HDR now?**

A: Reading around, I've discovered that the recommendation for the HDR is to be defended at least five years after one's PhD. It's been seven years now since I had my last adrenaline surge due to an academic diploma, I think it's time for a new shot. More altruistically, having a high proportion of non-habilitated researchers and lecturers in laboratories is a burden because these do not “count” for many things at the university level (most notably, PhD grants).

**Q: Is it possible to explain what the HDR is to a non-French academic?**

A: Well, you have to imagine a system in which you would have to defend a second PhD dissertation before being allowed to actually advise PhD candidates. In the French system, the HDR is a psychological barrier that plays the role of regulating the number of applicants to professor and research director positions. I think it's really a psychological barrier because, deep down, people that have already been through a whole PhD, some post-docs, and have found a job in the French academics really have nothing to be afraid of about the HDR. When writing grant proposals, papers or reviews for manuscripts, we casually do the same kind of work we could be doing to write a HDR memoir – except, without the possibility of fancy typesetting and out of place remarks on academic life. Of course, it could be said it's a waste of time – but what isn't a waste of time in academics these days? And a last word: there are many things around in other countries that really look like the HDR (the two-dissertation system in Russia for instance, the *privatdozent* in the German-speaking countries, or the “tenure” custom in North America). In all cases, this boils down to a symbolic way to celebrate the passage of a researcher from one “caste” to another, nothing more.

**Q: Why not writing this synthesis in LaTeX?**

A: Because someone proved it would be a waste of my time (Knauff and Nejasmic, 2014)? No, just kidding. Partly because I am very far from the Linux-LaTeX-Beamer crowd (I am quite convinced that trying to convert the rest of the academic world to using your favourite tools is a waste of time), partly also because I wanted to experiment a little bit with Word typesetting capabilities (or at least trying to push them to their limits). What is within this document is much more important to me than the software I used to type it, I really don't care if it doesn't look geeky enough...

**Q: Was it a good move to start writing this document barely a month before the deadline?**

A: Not really, but at least it wasn't painful. And it was finished before the next GoT season began.

**Q: (very frequent question) Why defend in Lille rather than Montpellier?**

A: The HDR is not really “useful” by itself – as I wrote, it's a rite of passage. Why not make it an opportunity for insertion into the local academic landscape?





## ACKNOWLEDGEMENTS

The presence of those seeking the truth is infinitely to be preferred to the presence of those who think they've found it.

Terry Pratchett, *Monstrous Regiment*

The “acknowledgements” sections of PhD and HDR dissertations seem to be the most highly prized sections... It would be tempting to try and eschew such a *passage obligé*, just for the sake of not yielding to social pressure. However, this will not be the path I choose as I think being thankful costs very little and does good to both the thankful and the thanked. The only risk is to forget to name someone that should be named. I'll try to be as exhaustive as possible here (at the cost of not writing much for everyone, sorry...) because it's probably better to give undue credit than not giving credit when credit is due.

To begin with, I'd like to thank the jury for accepting to take part in this lengthy endeavour. So, my many thanks go to **Dries Bonte**, **Joël Cuguen**, **Annick Lesne**, **Hélène Morlon**, **Nathalie Niquil** and **Jean-Christophe Poggiale**.

The second round of applause will go to the pillars of stability with whom it has been a pleasure working with for quite a long time now. I thus would like to thank **Sophie Caillon**, **Vincent Calcagno**, **Pierre-Olivier Cheptou**, **Patrice David**, **Philippe Jarne**, **Mathew Leibold**, **Doyle McKey** and **Nicolas Mouquet** for their enduring support. Getting to meet such good-hearted, open, interesting folks in academics is something rare. Thanks for your advice and help, and I hope I'll be able to work with you for long.

Beside those long-term collaborators, there is also a group of very stable, wise and open researchers that I have had the pleasure to know but with whom I have worked less often. My education in evolutionary ecology would not have been the same if I had not met **Isabelle Olivieri**, **Michel Raymond**, **Ophélie Ronce** and **François Rousset** at ISEM, **Claire de Mazancourt** and **Michel Loreau** at the CBTM in Moulis, and also **Jérôme Chave** and **Eric Vindimian**. Good advice, especially from people that are not directly involved in the work you are discussing, is a truly generous gift.

Next to these series of wise ones, I would like to thank the brave soldiers that have had to suffer me as a mentor of some sort. I know I am impossible to work with, always on the run and quite distracted all the time, so I want to express all my gratitude to **Julia Astegiano**, **Rémi Cuvelliez**, **Joseph Denton**, **Maxime Dubart**, **Mélie Durecu**, **Claire Jacquet**, **Maxime Jacquot**, **Nina Joffard**, **Thomas Koffel**, **Francisco Laso**, **Thibaut L'Honoré**, **Grégory Mollot**, **Thomas Perrot**, **Julia Radoszycki**, **Alban Sagouis**, **Diana Schleuter** and **Mathieu Thomas**. “At the end of the day”, among all the ones that have had to cope with my inefficiencies, above all I want to thank **Fabien Laroche**, my first doctorate student, who defended first-class last December in spite of my not being there when needed.

In-between my PhD defence and today, I have met a lot of interesting people with whom it has been a pleasure to collaborate.

At the time when I was finishing my PhD, I began interacting with a young PhD candidate that was asking a lot of relevant (and difficult) questions on tough subjects like P. Chesson's coexistence theory papers. Today, I am really thankful to have been able to work with **Florence Débarre** – I consider myself lucky to have encountered such a paragon of mathematical rigour (at last, someone to check my MATHEMATICA notebooks beside Vincent...). I hope our collaboration continues for long.

At some point at the end of my PhD, Nicolas Mouquet introduced me to a pair of brothers, both interested in ecology and interesting to chat with; as I finished my PhD and switched from the CEFE to IRSTEA, I actually shared office with one of them (well, not immediately, but soon afterwards)

while I regularly met the other one... in Knoxville, Tennessee! Today I want to thank **Martin** and **Tanguy Daufresne** for being what they are: humane researchers with the instincts of good naturalists, always ready to discuss ideas and capable of not inducing stress in others (a quality that is often lacking in young researchers). Without Martin and Tanguy, my life at IRSTEA would not have been improved, I owe them quite much.

Also thanks to Nicolas, I have had the pleasure to meet and to know one of my most frequent collaborators, **Dominique Gravel**. At some point, I even wondered whether I would ever run any project without Dominique... Anyway, he is one of the most energetic and enthusiastic ecologists I have had the opportunity to know and I owe him all my gratitude for being so patient and tenacious with me at the same time.

Over the years and thanks to the now famous “metaecosystem” workshops organised by Nicolas Mouquet in Saint-André-de-Buèges, I have been glad to know four brilliant young researchers from the “Parisian” school of evolutionary ecology (in opposition to the other big one, Montpellier...), namely **Colin Fontaine**, **Sonia Kéfi**, **Nicolas Loeuille** and **Elisa Thébault**. The making of the ARSENIC project owes them quite a lot, especially Nicolas. I am very thankful for now knowing at least a few researchers of my generation that share many of my academic interests and who are willing to discuss easily.

As already alluded to in the scientific synthesis, my moving to Lille has accidentally brought me in contact with some hydrothermal annelid-obsessed researchers with whom it has been delightful to exchange. With **Aurélie Tasiemski** and **Didier Jollivet**, I have met two complementary characters working on the same vents: Didier, the wise and relentless, passionate about his work and always a wise counsel; Aurélie, the enthusiasm geyser, always ready for a quick chat over coffee in-between two sessions of writing papers or proposals, or organising missions around the world. I have had little time to know you, but what I have experienced leaves me hopeful for the rest of the journey along the road to understanding dispersal in marine annelids.

In June 2012, as I was just ready to move from Aix to join the CNRS in Montpellier, I received an intriguing e-mail from a yet unknown person asking whether I would be ready to join a workshop on networks and interaction in agriculture. As I answered in the affirmative, hoping that this would be another opportunity to discuss with researchers I already knew (spoiler: this was not the case... and it did me a lot of good), I did not know that I was to engage in a long eventful collaboration with **David Bohan**, probably the most talented proposal/workshop organisers I have ever met. The ease with which Dave navigates through the different networks of European laboratories, how he simply connects people that should have been working together when you look at what they’re doing, the sheer number of e-mails he can send when he is seemingly overwhelmed (I mean, I would be if I were walking in his shoes), and how he always keep the faith in spite of administrative hurdles are just fascinating.

Speaking of good organisers, in Lille, there is a very special person among the new crowd I have had to rub my shoulders with, **Diala Abu Awad**, who brilliantly defended her PhD last December. Diala is simply the one person who knows what should be done at the level of the laboratory to improve the general mood. Beside the fact that she shares my addiction to the books of the late Terry Pratchett, I also admire Diala because she literally *animates* the lab – which makes me all the more anxious about the day she will move from Lille to Montpellier...

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During my post-doc at Mathew Leibold's lab, Mathew came up one day with the idea that "we should propose something about food webs" to the recently created NIMBioS centre in Knoxville, Tennessee. This is what we did with **Chris Klausmeier** and **Robert Sterner**, and that's how the "stoichiometry in metaecosystems" / "food web" working group started. The numerous open-ended discussions we had were animated by patient and passionate people whom I'd like to thank now, so beside Chris, Tanguy, Dominique, Mathew and Bob, and hoping I don't miss anybody: **Laura Jones, Yang Kuang, Elena Litchman, Irakli Loladze and Kim Schulz**.

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AATT, APOF, ATDI, AYWKUBTTOD, CBP, HTDA, ICP, MSP, NIN, NMA, QOTSA, SY... Those are not amino acid sequences but the soundtrack of these pages.

\*\*\*\*\*

Pendant cinq années, j'ai rêvé à cette vie. Aujourd'hui, je la goûte comme un accomplissement ordinaire. Nos rêves se réalisent mais ne sont que des bulles de savon explosant dans l'inéluctable.

Sylvain Tesson, *Dans les forêts de Sibérie*

## A SELECTION OF PUBLICATIONS

### Article A 109

Massol, F. & Cheptou, P.-O. (2011) Evolutionary syndromes linking dispersal and mating system: the effect of autocorrelation in pollination conditions. *Evolution*, **65**, 591-598.

### Article B 121

Gravel, D., Massol, F., Canard, E., Mouillot, D., & Mouquet, N. (2011) Trophic theory of island biogeography. *Ecology Letters*, **14**, 1010-1016.

### Article C 135

Massol, F. (2013) A framework to compare theoretical predictions on trait evolution in temporally varying environments under different life cycles. *Ecological Complexity*, **16**, 9-19.

### Article D 151

Duputié, A. & Massol, F. (2013) An empiricist's guide to theoretical predictions on the evolution of dispersal. *Interface Focus*, **3**

### Article E 165

Laroche, F., Jarne, P., Lamy, T., David, P., & Massol, F. (2015) A neutral theory for interpreting correlations between species and genetic diversity in communities. *American Naturalist*, **185**, 59-69.

### Article F 185

Astegiano, J., Massol, F., Vidal-Morais, M. M., Cheptou, P.-O., & Guimarães, P. R. Jr. (2015) The robustness of plant-pollinator communities: linking plant centrality and sensitivity to pollinator loss. *PLoS ONE*, **10**, e0117243.





# EVOLUTIONARY SYNDROMES LINKING DISPERSAL AND MATING SYSTEM: THE EFFECT OF AUTOCORRELATION IN POLLINATION CONDITIONS

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Self-fertilization is classically thought to be associated with propagule dispersal because self-fertilization is a boon to colonizers entering environments devoid of pollinators or potential mates. Yet, it has been theoretically shown that random fluctuations in pollination conditions select for the opposite association of traits. In nature, however, various ecological factors may deviate from random variations, and thus create temporal correlation in pollination conditions. Here, we develop a model to assess the effects of pollination condition autocorrelation on the joint evolution of dispersal and self-fertilization. Basically, two syndromes are found: dispersing outcrossers and nondispersing (partial) selfers. Importantly, (1) selfers are never associated with dispersal, whereas complete outcrossers are, and (2) the disperser/outcrosser syndrome is favored (resp. disfavored) by negative (resp. positive) autocorrelation in pollination conditions. Our results suggest that observed dispersal/mating system syndromes may depend heavily on the regime of pollination condition fluctuations. We also point out potential negative evolutionary effects of anthropic management of the environment on outcrossing species.

**KEY WORDS:** Adaptive dynamics; evolutionarily stable strategy; joint evolution; metapopulation; self-fertilization.

Dispersal and mating system traits are key parameters that affect the fitness of organisms. As such, elucidating the mechanisms that determine these traits is an important issue in evolutionary biology. Empirical observations report a wide variation in dispersal strategies (Herrera 1995; Hazell et al. 2005) and mating systems (Goodwillie et al. 2005; Jarne and Auld 2006) among related taxa, in plants as well as in animals. Such a wide variability, both in dispersal and mating systems, raises the question of the evolutionary factors that determine these traits. Although general in evolutionary ecology, this subject has been particularly studied in plants.

Many factors have been proposed for the evolution of dispersal strategy, including, perturbations (Comins et al. 1980; Parvinen et al. 2003), habitat heterogeneity (Balkau and Feldman 1973; Hastings 1983), population dynamics (Holt and McPeck 1996; Cadet et al. 2003), inbreeding depression (Bengtsson 1978), kin competition (Hamilton and May 1977; Frank 1986), and dispersal cost (Hamilton and May 1977; Comins et al. 1980). Self-fertilization is favored by paucity of pollinators or low population density (Baker 1955) and the higher transmission rate of selfers over outcrossers (Fisher 1941; Lande and Schemske 1985), and

counter-selected by the deleterious effect of inbreeding depression (Lloyd 1979; Lande and Schemske 1985).

Until recently, the evolution of dispersal and the evolution of selfing have been considered as separate in models. However, Cheptou and Massol's (2009) theoretical model recently showed that pollination uncertainty affects the evolution of both dispersal and self-fertilization in a metapopulation and that accounting for the evolutionary feedback between dispersal and selfing allows predictions on evolutionarily stable syndromes of traits. Most notably, the existence of temporal fluctuations in pollination conditions selects for the association of selfing and zero dispersal on the one hand, and outcrossing and dispersal on the other hand (Cheptou and Massol 2009). This result seriously questions a common idea among plant biologists, which holds that good colonizers should self-fertilize (known as Baker's law, see Baker 1955; Baker 1967). Empirical data are unclear and, according to existing data, the evidence for the syndromes of traits implied by Baker's law (i.e., dispersing/selfing and nondispersing/outcrossing) is mixed (Price and Jain 1981). Self-compatible species may have larger ranges than self-incompatible ones (Van Kleunen and Johnson 2007; Randle et al. 2009) or be more likely to invade new environments (Van Kleunen et al. 2008). However, invasion success is better predicted by trait interactions (most notably traits on flowering, reproductive biology, and tolerance to environmental stress) than by self-compatibility (or any other trait) alone (Kuster et al. 2008), suggesting the importance of trait syndromes in explaining plant invasiveness. Besides, some studies that seemingly support the classical formulation of Baker's law deal with clonal reproduction rather than self-fertilization (Horandl 2008). Clear direct cases going against Baker's law have been pinpointed (Miller et al. 2008). Last but not least, the high incidence of dioecy on islands (Sakai et al. 1995; Barrett 1996) tends to support syndromes opposed to Baker's predictions.

In Cheptou and Massol (2009)'s model, pollination fluctuations are assumed temporally uncorrelated. However, the way pollination heterogeneity acts in Baker's model (in space or in time) is subject to interpretation. In natural populations, pollination may be variable both in space and time. Temporal variations can be autocorrelated, and this autocorrelation may be central for the selection of syndromes. For extreme positive values of temporal autocorrelation, pollination conditions become spatially heterogeneous only, some patch being always pollinated, others being never pollinated. Intuitively, temporal autocorrelation in pollination conditions might affect evolutionary syndromes (at least through dispersal evolution) because a static spatially heterogeneous environment is expected to select for low dispersal (Hastings 1983; Holt 1985).

In this article, we extend an earlier model (Cheptou and Massol 2009) through the incorporation of temporal autocorrelation in pollination condition. We analyze the model through

**Table 1.** Model notations.

Parameter/ Variable	Meaning	Value range
$s$	selfing rate	[0;1]
$d$	dispersal rate	[0;1]
$\delta$	inbreeding depression	[0;1]
$q$	survival of dispersed offspring	[0;1]
$e$	frequency of nonpollinated patches	[0;1]
$\varphi$	temporal autocorrelation of pollination conditions	$[\max(-\frac{e}{1-e}, -\frac{1-e}{e}); 1]$

direct comparisons of model predictions on evolutionarily stable strategies (ESS) and their feasibility conditions in the presence of positive or negative autocorrelation. We also check the robustness of our conclusions to the assumption of deleterious mutation purging. Our model generalizes the classical evolutionarily stable dispersal rate (Comins et al. 1980) to temporally correlated environments.

## Model

### MODEL BASICS

Our model is based on Cheptou and Massol's (2009). We consider a metapopulation consisting of an infinite number of patches, each containing an infinity of individuals (hence, the absence of kin competition). Modeled organisms are self-compatible hermaphrodites and can be thought of as annual plants, or any semelparous sessile organism. Individuals inhabit patches that may be either pollinated (frequency  $1 - e$ ) or nonpollinated (frequency  $e$ , see Table 1 for notations). At each generation, the pollination condition of each patch can change according to parameter  $e$  and to the temporal autocorrelation of patch state,  $\varphi$ . Parameter  $\varphi$  measures the correlation of pollination condition in the same patch between two successive generations. A pollinated patch remains so with probability  $1 - (1 - \varphi)e$ , or becomes nonpollinated with probability  $(1 - \varphi)e$ . Symmetrically, the probability for a nonpollinated patch to remain so (resp. to become pollinated) is  $1 - (1 - \varphi)(1 - e)$  (resp.  $(1 - \varphi)(1 - e)$ ). Because these probabilities are bound to remain between 0 and 1,  $\varphi$  must be greater than  $\max[-e/(1 - e), -(1 - e)/e]$ .

Individuals follow the same life cycle: (1) reproduction; (2) dispersal; (3) regulation (lottery competition: sites are assigned to genotypes according to their fitness). Individuals are characterized by the proportion of self-fertilized ovules ( $s$ ) and by the proportion of seeds dispersed to other patches ( $d$ ). All individuals have the same fecundity, which is assumed large enough so that no patch remains empty after the regulation stage. Offspring

produced by self-fertilization suffer from inbreeding depression ( $\delta$ ) due to the expression of recessive deleterious alleles. During the dispersal stage, all offspring have the possibility to disperse and an individual with dispersal trait  $d$  emigrates to other patches with probability  $d$ . Migrants incur a cost to disperse and only a fraction  $q$  survives the dispersal episode.

### MUTANT FITNESS

Assessing the outcome of evolutionary processes is performed by analyzing the fate (invasion or not) of a rare mutant phenotypically close to the resident (Hofbauer and Sigmund 1990; Geritz et al. 1998). A mutant selfer transmits one copy of its genes via its outcrossed seeds and its pollen, whereas its self-fertilized seeds contain two gene copies (cost of outcrossing, see Fisher 1941; Holsinger 2000). We assume that male gametes are very abundant and that there is no pollen discounting. The fitness is summed over the dispersing and nondispersing fractions.

We compute the fitness  $W$  of a rare mutant (with traits  $s'$  and  $d'$ ) in a metapopulation entirely occupied by a single resident type (with traits  $s$  and  $d$ ).  $W$  can be computed as the dominant eigenvalue of the mutant-type next generation matrix  $G$ . From the life cycle,  $G$  can be written as the product of four matrices:  $G = E.L.D.R$  where  $E$  is the matrix of environmental fluctuation,  $L$  is the lottery regulation matrix,  $D$  is the dispersal matrix, and  $R$  is the reproduction matrix. Detailed methods on the computation of  $W$  are given in Appendix S1. When  $\varphi = 0$ , the expression of  $W$  is equal to the fitness function used in Cheptou and Massol (2009).

### EVOLUTIONARY OUTCOMES

Based on selection gradients for both traits (i.e., partial derivatives of  $W$  with respect to mutant allele trait value), we can visually assess the outcome of evolution: the field of selection gradients gives the direction of selection at any point of the  $(s, d)$  plane (e.g., see Cheptou and Massol 2009). When singular points exist (i.e., combination of traits values for which both selection gradients vanish), two properties must be determined (Hofbauer and Sigmund 1990): (1) whether the singular point is convergence stable (i.e., an attractor of monomorphic substitution dynamics) and (2) whether it is evolutionarily stable (ESS, i.e., no similar combination of trait values can invade it). Convergence stability is easily seen on a two-dimensional field of selection gradients: when a singular point is convergence stable, it must be a stable node or focus. A singular point that is an unstable equilibrium is said to be an evolutionary repeller. Pseudo-singular points (i.e., combinations of trait values for which one of the selection gradient vanishes and the other trait has a boundary value, 0 or 1) are convergence stable when the vanishing selection gradient points toward the pseudo-singular point in its vicinity and the other selection gradient points “outwards” of the trait value limits (i.e., is positive for a trait equal to 1 or negative for a trait equal to 0). Any

convergence stable pseudo-singular point is evolutionarily stable (see Cheptou and Massol 2009).

### MODEL ROBUSTNESS TO THE PURGING OF DELETERIOUS MUTATIONS

We checked that our results were qualitatively robust to the assumption of purging, that is, a decrease of inbreeding depression with increasing selfing rate (e.g., Johnston et al. 2009). We tested this assumption using a simple, exponential model linking inbreeding depression to the propensity for selfing:  $\delta(s) = \delta_0 e^{-\beta s}$  where parameter  $\beta$  measured purging efficiency.

## Results

### TRAIT SYNDROMES

Depending on the value of  $q$ ,  $e$ ,  $\delta$ , and  $\varphi$ , three evolutionary outcomes (qualitatively equivalent to those found in Cheptou and Massol 2009) are possible

- (i) dispersal is selected for (with an ESS value  $0 \leq d^* \leq 1$ ) and selfing is selected against ( $s^* = 0$ , Fig. 1A);
- (ii) selfing is selected for ( $0 < s^* \leq 1$ ) and dispersal is selected against ( $d^* = 0$ , Fig. 1C);
- (iii) the two above-mentioned ESS exist, together with an interior evolutionary repeller. The actual evolutionary outcome depends on the initial value of  $s$  and  $d$  (Fig. 1B).

The dispersal/outcrossing syndrome present in cases (i) and (iii) displays the following ESS:

$$s^* = 0 \quad (1a)$$

$$d^* = \text{Min} \left[ \frac{e(1-\varphi)}{1-q(1-e)}, 1 \right]. \quad (1b)$$

Note that  $d^*$  is equivalent to Comins et al. (1980) result when  $\varphi = 0$ . As a consequence, our result generalizes the ES dispersal rates to temporally correlated environments.

This syndrome is feasible when condition (2) or condition (3) is verified

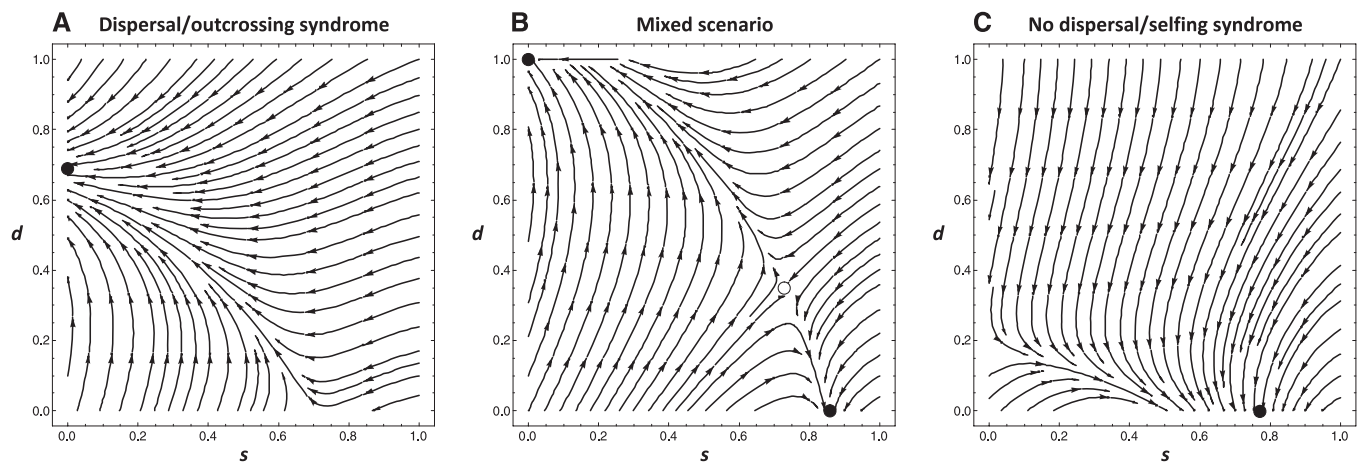
$$\varphi \geq 0 \text{ or } e < (1-q)/(1-q-\varphi) \quad (2a)$$

$$\text{and } \delta > 1 - \frac{(1-e)[1-q(1-e)]q}{2[(1-q)(1+e\varphi) + (2q-1)e]} \quad (2b)$$

$$e > (1-q)/(1-q-\varphi) \quad (3a)$$

$$\text{and } \varphi < 0 \quad (3b)$$

$$\delta > \text{Max} \left[ \frac{2(1-q)-\varphi}{2(1-q-\varphi)}, \frac{3e-1}{2} \right] \quad (3c)$$



**Figure 1.** Potential evolutionary outcomes. Abscissas indicate selfing rate, and ordinates indicate dispersal rate (i.e., the proportion of seeds dispersing from a patch). In all panels, filled circles represent the evolutionarily stable strategies, whereas the open circle in (B) represents the evolutionary repeller. Arrows indicate possible evolutionary trajectories. Parameter values: (A)  $\delta = 0.9$ ,  $q = 0.6$ ,  $e = 0.4$ ,  $\varphi = -0.1$ ; (B)  $\delta = 0.7$ ,  $q = 0.9$ ,  $e = 0.3$ ,  $\varphi = -0.4$ ; (C)  $\delta = 0.9$ ,  $q = 0.2$ ,  $e = 0.5$ ,  $\varphi = 0.7$ .

The no dispersal/selfing syndrome obtained in cases (ii) and (iii) has the following ESS selfing rate at high inbreeding depression ( $\delta > (1 - e)/2$ ):

$$s^* = \text{Min} \left[ \frac{2e}{2\delta - 1 + e}, 1 \right] \quad (4a)$$

$$d^* = 0 \quad (4b)$$

or, at lower inbreeding depression:

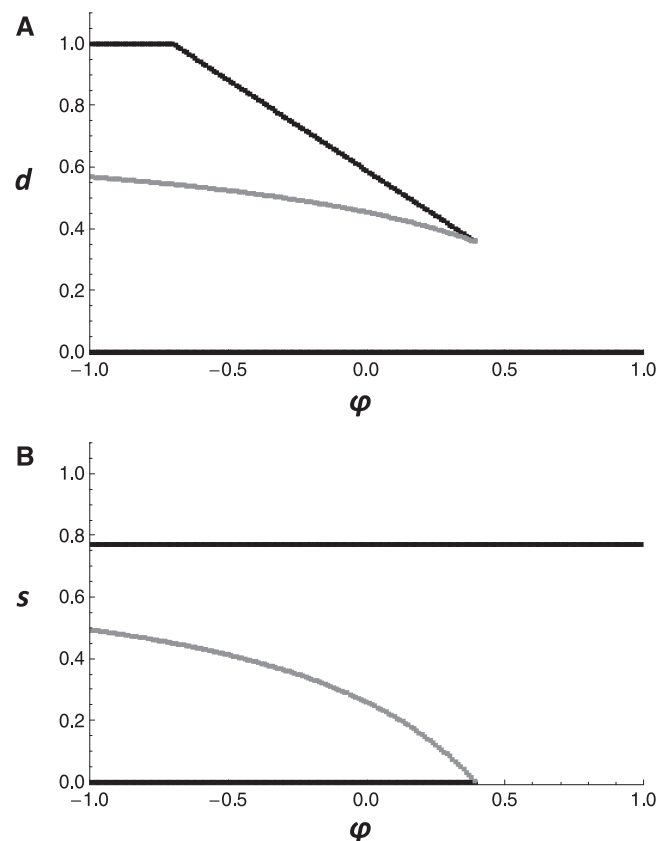
$$s^* = 1 \quad (5a)$$

$$d^* = 0. \quad (5b)$$

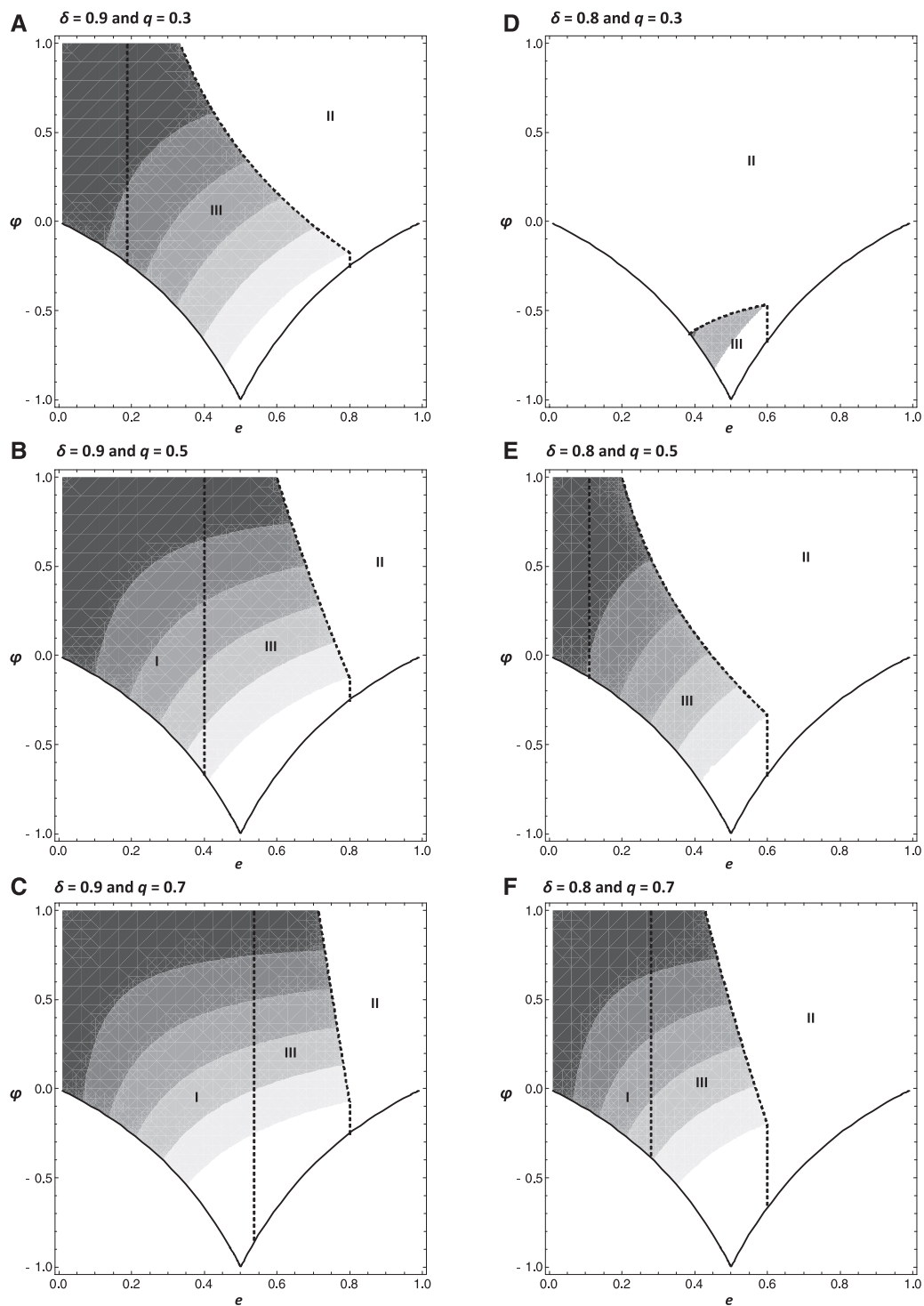
This syndrome exists as long as  $\delta < (1 - e)/2$  or  $q < 2(1 - \delta)(2\delta - 1)/[e^2 + (2\delta - 1)(1 - 2e)]$ . When both  $\delta > (1 + e)/2$  and  $q < 2(1 - \delta)(2\delta - 1)/[e^2 + (2\delta - 1)(1 - 2e)]$ , intermediate selfing rates ( $0 < s^* < 1$ ) are selected for.

### EFFECTS OF POLLINATION CONDITION AUTOCORRELATION

The ESS for dispersal associated with the dispersal/outcrossing syndrome decreases linearly with pollination condition autocorrelation ( $\varphi$ , eq. 1; Fig. 2A), potentially down to  $d^* = 0$  when  $\varphi = 1$ . Moreover, the conditions for the existence of this syndrome become harder to achieve when  $\varphi$  increases, and easier for negative  $\varphi$  values (inequalities [2 and 3]; Fig. 3). Under conditions that would strictly enforce the no dispersal/selfing syndrome in the absence of pollination condition autocorrelation (Fig. 3D, take  $\varphi = 0$ ), a decrease in  $\varphi$  may provoke the emergence of the dispersal/outcrossing syndrome. Because  $\varphi > \text{Max}[-e/(1 - e)]$ ,



**Figure 2.** Sensitivity of singular strategies to the autocorrelation of pollination conditions ( $\varphi$ ). Evolutionarily stable (ES) dispersal ( $d$ , ordinates in panel A and selfing rate  $s$ , ordinates in panel B) are presented as functions of  $\varphi$  [abscissas]). Black lines represent the possible ES trait values. Gray lines indicate the value of the evolutionary repeller. Parameter values:  $\delta = 0.9$ ,  $q = 0.3$ ,  $e = 0.5$ .



**Figure 3.** Evolutionary outcomes at fixed inbreeding depression and disperser survival. Evolutionary outcomes are presented as functions of the probability of pollen limitation ( $e$ , abscissas) and the autocorrelation in pollination condition ( $\phi$ , ordinates). In each panel, dashed lines indicate the boundaries between the dispersal/outcrossing syndrome (I), the mixed scenario (where the two syndromes are possible; III), and the no-dispersal/selfing syndrome (II). Thick lines at low  $\phi$  delimit feasible autocorrelation values (i.e., we must have  $\phi \geq \max[-e/(1-e), -(1-e)/e]$ ). Gray shades represent the selected dispersal rate in outcrossers (darker shades indicate lower dispersal values). Inbreeding depression is  $\delta = 0.9$  in panels (A–C) and  $\delta = 0.8$  in panels (D–F). Disperser survival is  $q = 0.3$  in panels (A) and (D);  $q = 0.5$  in panels (B) and (E);  $q = 0.7$  in panels (C) and (F).



$-(1 - e)/e]$ , this effect mostly happens for intermediate values of  $e$  (Fig. 3).

The no dispersal/selfing syndrome is not affected by  $\varphi$ : neither its selfing rate (eqs. 4 and 5), nor its feasibility condition are affected by the pollination condition autocorrelation (Fig. 2B). Because the emergence of the dispersal/outcrossing syndrome is facilitated by negative  $\varphi$  values, decreasing  $\varphi$  can only change a case (ii) scenario into a case (iii), not into a case (i) (Fig. 3).

### EFFECTS OF PURGING

The existence of the three generic scenarios was not altered by the assumption of purging effects (Figs. S1 and S2). Overall, purging only shifted the selfer/nondisperser ESS toward higher selfing rates (Fig. S2) and allows for larger portions of parameter space supporting the existence of two alternative ESS (Fig. S1).

## Discussion

Our model generalizes the evolution of syndromes between dispersal and selfing rates in heterogeneous pollination environments. Although Cheptou and Massol (2009) predicted a strict association between obligate outcrossing (resp. partial selfing) and dispersal (resp. absence of dispersal) under random pollination fluctuations, the introduction of temporal autocorrelation in pollination conditions mitigates this result. Importantly, the general association between mating system and dispersal still holds, but pollination autocorrelation modifies the conditions for the evolution of syndromes and the value of the ESS dispersal rate.

### NEGATIVE AUTOCORRELATION FAVORS DISPERSAL IN OUTCROSSERS

When the probability of being pollinated is spatially and temporally variable, two fundamental syndromes can be selected: the “dispersal/outcrossing” syndrome or the “no-dispersal/selfing” syndrome. In the absence of factors selecting for higher dispersal independently from the mating system, such as kin competition (Hamilton and May 1977; Frank 1986) or perturbations (Comins et al. 1980; Ronce et al. 2000), only the first syndrome displays a nonzero dispersal rate (as predicted by Balkau and Feldman 1973; Hastings 1983). The ESS value for dispersal in outcrossers decreases linearly with pollination condition autocorrelation (Fig. 3). Hence, temporally constant environments (spatial heterogeneity only;  $\varphi \approx 1$ ) have zero dispersal ESS, whereas regularly changing environments ( $\varphi \approx -1$ ) have higher dispersal ESS than predicted under random pollination fluctuations. This result is consistent with dispersal models showing that temporal variation is required for dispersal to evolve and spatial variation only cannot select for dispersal (Balkau and Feldman 1973; Hastings 1983; McPeck and Holt 1992; Holt and McPeck 1996; Doebeli and Ruxton 1997; Mathias et al. 2001) and pro-

vides the analytical ES dispersal rate under temporally correlated environment.

### THE NO-DISPERSAL/SELFING SYNDROME IS UNAFFECTED BY POLLINATION CONDITION AUTOCORRELATION

The existence of an evolutionary stable no-dispersal/selfing syndrome is guaranteed by either low inbreeding depression or a high dispersal cost (Cheptou and Massol 2009). Interestingly, we have proved in this study that pollination autocorrelation does not modify the conditions for the existence of this syndrome. Even more remarkably, the value of the selfing rate ESS is insensitive to the value of the pollination condition temporal autocorrelation. In short, at constant frequency of pollination, spatial or temporal heterogeneity are equivalent for the evolution of this syndrome. This is because selfers are under no pressure to disperse (there is no kin competition, nor perturbations, in the present model). Thus, the fitness of a mutant lineage only depends on the temporal geometric average of its fitness, whatever is the value of the temporal autocorrelation (i.e., the order in which pollination conditions are experienced does not matter in the long run). When selfing rate is zero, by contrast, the fitness of a mutant depends on how well it can track patches where outcrossing is possible: because dispersal is costly and pollination conditions fluctuate, the dispersal rate reflects this balance (decreases with increasing dispersal cost and increases with fluctuation regularity).

### POSITIVE AND NEGATIVE AUTOCORRELATION IN WILD POPULATIONS

Although previous studies have established that environmental heterogeneity has important consequences on mating system (Cheptou and Mathias 2001), on dispersal (Comins et al. 1980), and on syndromes of these traits (Cheptou and Massol 2009), this study points out that environmental autocorrelation is central in the selection of syndromes. Negative autocorrelation favors the outcrossing/dispersal syndrome whereas positive correlation makes its evolution more difficult. Although pollination fluctuations are widespread in natural populations (Burd 1994), we demonstrate that the characterization of pollination fluctuation regimes is central to interpret the association of mating system and dispersal traits. Data from natural populations are scarce, but different classes of factors may induce positive or negative autocorrelation. Directional changes in communities (e.g., successions) may radically change pollinator fauna through modifying plant species composition and functional traits (e.g., shade, vegetation height, etc.), and thus create a temporally negative autocorrelation in pollination conditions for a focal plant species. For example, Parrish and Bazzaz (1979) found differences in pollination niches during successional processes, which typically create negative autocorrelation. On the contrary, when populations of pollinators

need a large plant population to be viable, we expect a positive autocorrelation in pollination conditions, some plant populations being well pollinated (because of their size) whereas others are not. However, Kalisz et al. (2004) showed in the species *Collinsia verna* (Scrophulariaceae) that demographic attributes, such as the total number of flowers, do not explain the high annual variability in pollinator activity. This result suggests that pollination fluctuations may be at least partly uncorrelated with plant population state and, thus, temporally uncorrelated.

The question of dispersal and mating system association has traditionally been considered in the light of Baker's law, which emphasizes the selective advantage of selfing for colonizers. However, theoretical predictions based on pollination fluctuations tend to favor the opposite association of traits (Cheptou and Massol 2009). The present study mitigates these predictions by pointing out that pollination condition autocorrelation determines the outcome of selection. Nevertheless, the main conclusion is that dispersal is never associated with selfing, whatever the autocorrelation of pollination conditions in the metapopulation. This model points out a potential flaw in the logic of Baker's law and emphasizes the need to analyze the joint evolution of traits to draw conclusions about syndromes.

## IMPLICATIONS FOR CONSERVATION

From a conservation viewpoint, the fact that temporally constant pollination environments select against outcrossers has an obvious implication: when an outcrossing species lives in a fluctuating pollination environment such as one linked to successional processes (e.g., Fig. 3D), increasing the likelihood of pollination and stabilizing the environment (i.e., decreasing  $e$  and increasing  $\varphi$ ) may have the irreversible consequence of completely negating selection for outcrossing, and thus change mating systems (and dispersal rates) on an evolutionary time scale. This is a clear instance of a large trait shift due to a small environmental trigger (Scheffer et al. 2001). The most striking aspect of this phenomenon is that an outcrossing species can be wiped out through seemingly benign/beneficiary changes to the environment. Anthropogenic effects on the environment are often stabilizing in nature (e.g., preventing natural forest fires). Figuring out how not to harm outcrossing species is thus trickier than it seems at first sight.

## ACKNOWLEDGMENTS

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## Supporting Information

The following supporting information is available for this article:

**Appendix S1.** Detailed model description.

**Figure S1.** Evolutionary outcomes at fixed inbreeding depression, disperser survival, and purging efficiency.

**Figure S2.** Sensitivity of singular strategies to purging efficiency.

Supporting Information may be found in the online version of this article.

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**Supplementary Material:**  
**Appendix A: Detailed model description**

The fecundities of a resident in a non-pollinated ( $w_{NP}$ ) or pollinated ( $w_P$ ) patch are assessed through selfing and inbreeding depression:

$$w_{NP} = (1 - \delta)s \quad (\text{A.1})$$

$$w_P = (1 - \delta)s + 1 - s \quad (\text{A.2})$$

whereas the fecundities of a mutant in a non-pollinated ( $w'_{NP}$ ) or pollinated ( $w'_P$ ) patch depend also on resident selfing rate through pollen transmission (Lande and Schemske 1985):

$$w'_{NP} = (1 - \delta)s' \quad (\text{A.3})$$

$$w'_P = (1 - \delta)s' + \frac{1 - s'}{2} + \frac{1 - s}{2} \quad (\text{A.4})$$

We note  $f_{NP}$  and  $f_P$  the quantity of offspring competing in NP and P patches respectively. These quantities are controlled by the resident phenotype (remember that each patch contains an infinity of individuals), hence:

$$f_{NP} = (1 - d)w_{NP} + dq[(1 - e)w_P + ew_{NP}] \quad (\text{A.5})$$

$$f_P = (1 - d)w_P + dq[(1 - e)w_P + ew_{NP}] \quad (\text{A.6})$$

Based on  $w$  and  $f$  quantities, we can compute the next generation matrix:

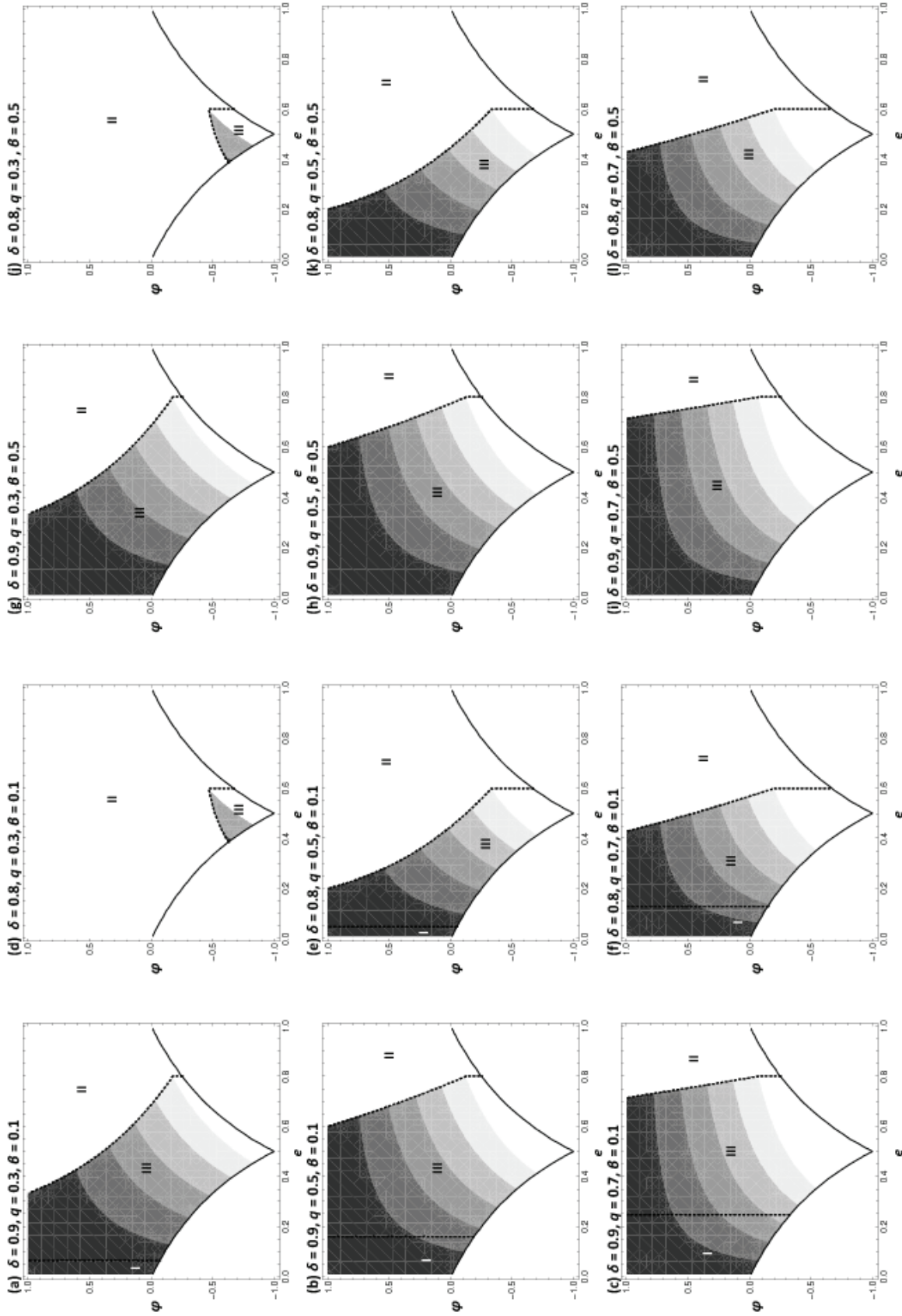
$$G = \begin{pmatrix} 1 - (1 - e)(1 - \phi) & e(1 - \phi) \\ (1 - e)(1 - \phi) & 1 - e(1 - \phi) \end{pmatrix} \cdot \begin{pmatrix} 1/f_{NP} & 0 \\ 0 & 1/f_P \end{pmatrix} \cdot \begin{pmatrix} (1 - d') + qed' & qed' \\ q(1 - e)d' & (1 - d') + q(1 - e)d' \end{pmatrix} \cdot \begin{pmatrix} w'_{NP} & 0 \\ 0 & w'_P \end{pmatrix} \quad (\text{A.7})$$

$W$  is then obtained as the dominant eigenvalue of  $G$ , *i.e.*

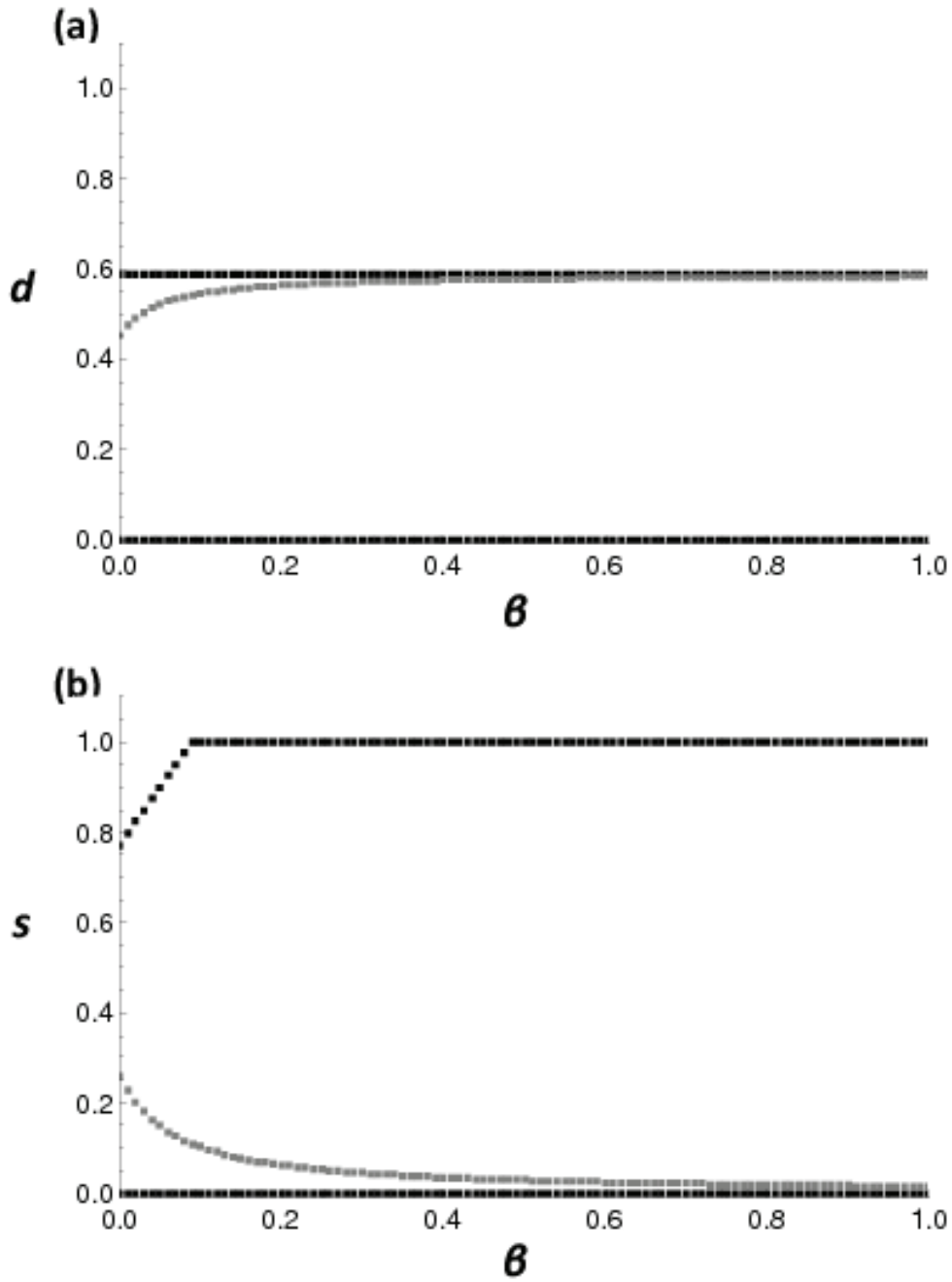
$$W = \frac{\text{Tr}(G) + \sqrt{\text{Tr}(G)^2 - 4\det(G)}}{2} \quad (\text{A.8})$$

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Lande, R., and D. W. Schemske. 1985. The evolution of self-fertilization and inbreeding depression in plants .1. Genetic models. *Evolution* 39:24-40.



**Fig. S1** – Evolutionary outcomes at fixed inbreeding depression, disperser survival, and purging efficiency. Evolutionary outcomes are presented as functions of the probability of pollen limitation ( $\varphi$ , abscissas) and the autocorrelation in pollination condition ( $e$ , ordinates). In each panel, dashed lines indicate the boundaries between the dispersal/outcrossing syndrome (I), the mixed scenario (where the two syndromes are possible; II), and the no dispersal/selfing syndrome (II). Thick lines at low  $\varphi$  delimit feasible autocorrelation values (*i.e.* we must have  $\varphi \geq \text{Max} \left[ -e/(1-e), -(1-e)/e \right]$ ). Gray shades represent the selected dispersal rate in outcrossers (darker shades indicate lower dispersal values). Inbreeding depression is  $\delta = 0.9$  in panels (a-c,g-i) and  $\delta = 0.8$  in panels (d-f,j-l). Disperser survival is  $q = 0.3$  in panels (a,d,g,j);  $q = 0.5$  in panels (b,e,h,k);  $q = 0.7$  in panels (c,f,i,l). Purging efficiency is  $\beta = 0.1$  in panels (a-f) and  $\beta = 0.5$  in panels (g-l).



**Fig. 2** – Sensitivity of singular strategies to purging efficiency ( $\beta$ ). Evolutionarily stable (ES) dispersal ( $d$ , ordinates in panel a) and selfing rate ( $s$ , ordinates in panel b) are presented as functions of  $\beta$  (abscissas). Black lines represent the possible ES trait values. Gray lines indicate the value of the evolutionary repeller. Parameter values:  $\delta = 0.9$ ,  $q = 0.3$ ,  $e = 0.5$ ,  $\varphi = 0$ .



## LETTER

## Trophic theory of island biogeography

Dominique Gravel,<sup>1\*</sup> François Massol,<sup>2</sup> Elsa Canard,<sup>3</sup> David Mouillot<sup>4,5</sup> and Nicolas Mouquet<sup>3</sup>

### Abstract

MacArthur and Wilson's Theory of Island Biogeography (TIB) is among the most well-known process-based explanations for the distribution of species richness. It helps understand the species–area relationship, a fundamental pattern in ecology and an essential tool for conservation. The classic TIB does not, however, account for the complex structure of ecological systems. We extend the TIB to take into account trophic interactions and derive a species-specific model for occurrence probability. We find that the properties of the regional food web influence the species–area relationship, and that, in return, immigration and extinction dynamics affect local food web properties. We compare the accuracy of the classic TIB to our trophic TIB to predict community composition of real food webs and find strong support for our trophic extension of the TIB. Our approach provides a parsimonious explanation to species distributions and open new perspectives to integrate the complexity of ecological interactions into simple species distribution models.

### Keywords

Complexity, ecological network, food web, island biogeography, metacommunity, species–area relationship.

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### INTRODUCTION

The elegance of the Theory of Island Biogeography (TIB; MacArthur & Wilson 1967) arises from its simplicity (Lomolino *et al.* 2009): species richness in a community is the result of a dynamic equilibrium between immigration and extinction processes, which are influenced by the area holding the local community and its connection via dispersal (MacArthur & Wilson 1967). It predicts the slope of the species–relationship, a fundamental pattern for ecology (Lomolino 2000) and conservation (May 1988; Guilhaumon *et al.* 2008; He & Hubbell 2011). This parsimonious classic theory comes, however, with some limitations: it only applies to well-defined trophic guilds, it does not explicitly consider the nature of interactions among species and it cannot predict their identity in local communities.

Ecological interactions are known to underpin species occurrence at large spatial scales (Gotelli *et al.* 2010). However, there have been surprisingly few theoretical developments on these limitations since the publication of the TIB (Holt 1996, 1997; Hanski & Gyllenberg 1997; Holt *et al.* 1999; Ryberg & Chase 2007) and development of metacommunity theory (Leibold *et al.* 2004). The success of the TIB, and its recent extension through the neutral theory of biodiversity (Hubbell 2001), is nonetheless strong assets for an elegant and synthetic theory of biogeography (Losos & Ricklefs 2009). Considering more realistic community structures and dynamics is now needed to reach process-based species distribution models (Guisan & Thuiller 2005; Araujo & Luoto 2007). Ecological communities generally display complex structures (Polis & Strong 1996) that are

challenging to integrate into a parsimonious and realistic model. Here, we show how integrating elements of food web theories (Pascual & Dunne 2006) into the TIB helps improve predictions of community structure across trophic levels and scales.

### MODEL ANALYSIS

Following the TIB, a local community is assumed to be a random sample of species drawn from a metacommunity (Leibold *et al.* 2004). The sampling process is non-specific: every species has the same probability  $p(t)$  of being included in the local community at any time  $t$ , independently of local and regional community structures (MacArthur & Wilson 1967). This probability, named occupancy, is the result of two processes: locally absent species immigrate into the local community at rate  $c$ , and locally present ones go extinct at rate  $e$ , yielding the following dynamics (Holt 1996):

$$\frac{dp}{dt} = c(1 - p) - ep \quad (1)$$

The equilibrium total occupancy is then  $p^* = \frac{\alpha}{1+\alpha}$ , where immigration and extinction rates are summarised under a single parameter,  $\alpha = c/e$ . The immigration rate  $c$ , and so the ratio  $\alpha$ , is hypothesised to be inversely related to the distance to the mainland (MacArthur & Wilson 1967). As the extinction rate  $e$  should be inversely proportional to population size (Hanski 1999; Lande *et al.* 2003), the ratio  $\alpha$  is also hypothesised to be related to local area or any environmental factor affecting local population density. The equilibrium local species

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richness  $S_L$  is reached when immigration equals extinction, and is given by  $S_L = P_T p^*$ , where  $P_T$  is the total species richness in the metacommunity (Fig. 1a).

The challenge of building a trophic TIB model is to use as few assumptions as possible to capture the inherent complexity of food webs, without losing the elegant simplicity of the classic TIB. We make two assumptions translating the concept of bottom-up sequential dependency, developed by Holt and others (Holt 1997, 2009; Dunne *et al.* 2002a; Calcagno *et al.* 2011; Gravel *et al.* 2011): (1) a consumer species can colonise a local community only when at least one of its prey species is already present and (2) a consumer species losing its last prey species in a local community (because of extinction or emigration processes) goes extinct. We consider a regional food web with  $P_T$  species, among which there are  $P_C$  consumer species, and which share  $L_R$  potential feeding links in the regional species pool. The number of potential prey species for a given consumer species is noted  $g$  (diet breadth). The average diet breadth of a consumer in the regional food web is  $\bar{g} = C_R P_T$ , where  $C_R$  is the regional directed connectance,  $C_R = L_R / P_T P_C$ . As the distribution of diet breadth is usually skewed (many specialists, few generalists, Dunne *et al.* 2002b), we need to take into account species-specific diet breadth. Let  $p_g$  be the occupancy of a consumer species having a diet of  $g$  prey species, we define  $q_g$  as the probability that a species with diet breadth  $g$  has one or more of its prey species present in the local community when it colonises it, and  $\varepsilon_g$  the rate at which a species with diet breadth  $g$  loses its last prey species (these variables are derived in the online supporting information). The TIB can thus be modified, yielding the following occupancy dynamics:

$$\frac{dp_g}{dt} = c(1 - p_g)q_g - (e + \varepsilon_g)p_g \quad (2)$$

The immigration rate  $c(1 - p_g)q_g$  increases with the probability of finding a prey in the local community ( $q_g$ ), while the extinction rate  $(e + \varepsilon_g)p_g$  increases with the probability of finding no prey. Equation 2 yields the following steady-state occurrence probability:

$$p_g = \frac{cq_g}{cq_g + e + \varepsilon_g} \quad (3)$$

The expected local species richness  $S_L$  at equilibrium is then obtained by averaging the equilibrium occupancies  $p_g^*$  over all diet breadths found in the regional species pool ( $S_L = \sum_{g=1}^{P_C} P_g p_g^*$ ).

We now need to express the quantities  $q_g$  and  $\varepsilon_g$  to derive the solution for the equilibrium occupancies  $p_g^*$  (the detailed derivations are provided in the online supporting information, here we just provide an overview of the approach). Let the random variable  $X_i$  indicate occurrence for species  $i$ , with  $X_i = 0$  when species  $i$  is absent from the local food web and  $X_i = 1$  when it is present. We note the expected occurrence probability  $p_i = E[X_i]$ . The indicator variable  $Y_i$  equals 1 when at least one prey of species  $i$  is present.  $Y_i$  may be expressed in terms of variables  $X_j$ 's:

$$Y_i = 1 - \prod_{j \in G_i} (1 - X_j) \quad (4)$$

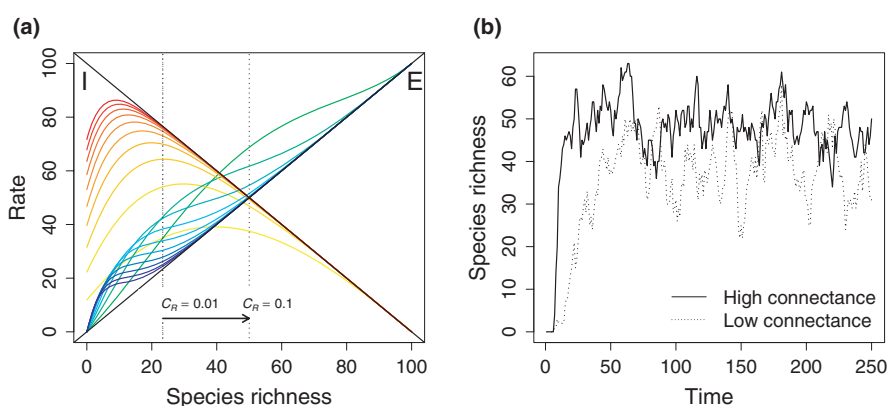
where  $G_i$  is the set of prey for species  $i$  (so that its cardinal  $|G_i|$  denotes the number of prey for species  $i$ , i.e. its diet breadth  $g$ ). Based on eqn 4 and assuming that the occurrence of a species is not affected by the occurrence of its predators and by the occurrence of species sharing its predators (similar results are obtained when relaxing this assumption), we can express  $q_i$  as the expectation of  $Y_i$  when species  $i$  is absent:

$$q_i = 1 - E \left[ \prod_{j \in G_i} (1 - X_j) \mid X_i = 0 \right] \quad (5)$$

$$q_i = 1 - \prod_{j \in G_i} (1 - p_j) = 1 - e^{\beta |G_i| \langle \log(1 - p_g) \rangle_p}$$

where  $\beta = \langle \log(1 - p_g) \rangle_p$  is the average value of the log-probability of absence, obtained from the regional food web.

We note  $e_i = e + \varepsilon_i$  to include the trophic constraint on the extinction rate for consumer species  $i$  resulting from intrinsic



**Figure 1** The trophic theory of island biogeography. (a) Adding a trophic constraint on species immigration and extinction affects the equilibrium species richness in a local community (note all consumer have the same diet breadth for the illustration). The classic TIB is depicted with the black lines. Species richness in a local community is found when the immigration rate equals the extinction rate (when the respective I and E curves cross, depicted by the vertical dotted lines). The coloured lines for the trophic TIB are obtained following the analytical approximation in the online supporting information. The connectance in the regional species pool is varied between 0.01 (yellow and green for the immigration and extinction curves, respectively) and 0.1 (red and blue curves, respectively). At connectance larger than 0.1, the trophic TIB no longer differs from the classic TIB for these immigration and extinction rates (see Fig. 2a). The parameter  $\alpha$  (ratio of intrinsic immigration to extinction rates) is set at 1 for the illustration. (b) Stochastic simulations (see online supporting information) show the assembly dynamics for local communities with low and high regional connectance ( $C_R = 0.05$  and  $C_R = 0.3$ , respectively). All consumer species have the same diet breadth  $g$  on both and the regional species pool consists of 10 primary producer species and 100 consumer species (both panels).



extinction ( $e$ ) and the extinction of its last prey species ( $\varepsilon_i$ ). The expression for  $\varepsilon_i$  is given by:

$$\varepsilon_i = E \left[ \sum_{j \in G_i} e_j X_j \prod_{\substack{k \in G_i \\ k \neq j}} (1 - X_k) \middle| X_i = 1 \right] \quad (6)$$

$$\varepsilon_i \approx \sum_{j \in G_i} e_j E[X_j] \prod_{\substack{k \in G_i \\ k \neq j}} (1 - E[X_k])$$

Solving for  $\varepsilon_i$  yields:

$$\varepsilon_i = e + \sum_{j \in G_i} e_j p_j \prod_{\substack{k \in G_i \\ k \neq j}} (1 - p_k) \quad (7)$$

$$\varepsilon_i \approx e + \left( |G_i| \left\langle e_g \frac{p_g}{1 - p_g} \right\rangle_P e^{|G_i| \langle \log(1 - p_g) \rangle_P} \right)$$

Using eqns 3 and 6, taking expectations over the whole food web and replacing species indices by diet breadths, we obtain the following expression which links the probability  $p_g^*$  that a species with diet breadth  $g$  occurs in a local community (using  $\alpha = c/e$ ):

$$p_g^* = \frac{\alpha(1 - e^{\beta g})}{1 + \alpha(1 - e^{\beta g})(1 + g e^{\beta g})} \quad (8)$$

Equation 7 cannot be solved in closed form, but a numerical solution can be found easily given  $\alpha$  and the distribution of  $g$  in the regional food web. The species richness for a diet breadth  $g$  is then simply  $S_g = \sum_{i=1}^{S_g} p_i$  (where  $S_g$  is the number of species with diet breadth  $g$  in the regional species pool). Note that this analytical derivation is a mean-field approach that does not consider food web topology. Previous metapopulation studies established that persistence and occupancy of a consumer is influenced by its trophic position (Holt 1997; Holt *et al.* 1999; Calcagno *et al.* 2011; Gravel *et al.* 2011). We thus performed stochastic simulations to better assess how topology influences predictions on occupancy (see Simulation Model).

Following this model, we found that trophic interactions fundamentally alter the way species richness varies with immigration and extinction rates. Under the classic TIB, the equilibrium species richness occurs when immigration and extinction rates are equal (in Fig. 1a: when the immigration and the extinction curves cross). We found that the immigration rate is lower for the trophic TIB than for the classic TIB, but increases with regional connectance (Fig. 1a) because immigrating consumers struggle to find a prey. Conversely, the extinction rate is increased at low connectance relative to the classic TIB because of secondary extinctions occurring when specialised consumers lose their last prey. The trophic TIB thus predicts that decreasing regional connectance reduces equilibrium species richness (Fig. 1a). Stochastic simulations illustrate the effect of trophic structure on immigration-extinction dynamics (see Supporting Information Data S1): a low regional connectance slows the assembly dynamics as primary producers, generalists and then specialists arrive sequentially (Piechnik *et al.* 2008; Fig. 1b) and also increases the temporal variability of assembly dynamics (Dunne *et al.* 2002a; Fig. 1b).

Regional food web structure has considerable effects on the resulting species–area relationship (Fig. 2a). The trophic TIB predicts that at a given area (proportional to  $\alpha$ ), local species richness increases with connectance of the regional food web because the average diet breadth increases with connectance, and thus fewer species are

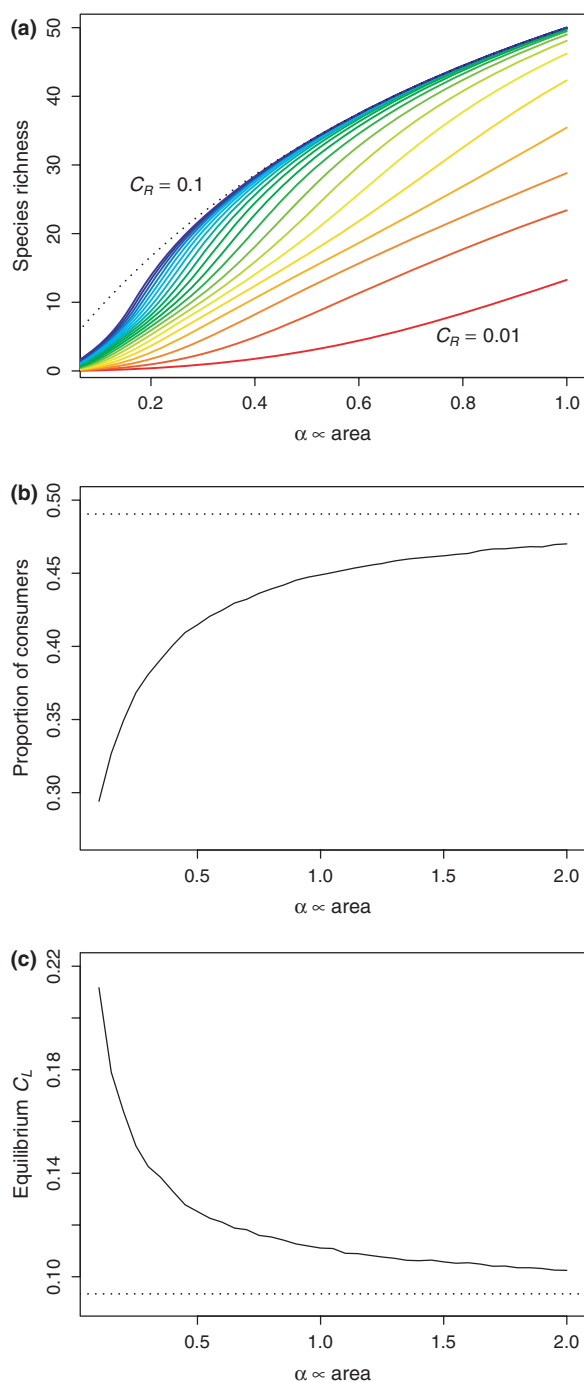
constrained to find a prey in the local community. It also predicts that the proportion of consumers increases with  $\alpha$  (Fig. 2b) because it is easier for them to find at least one prey in larger local communities with higher species richness. The species–area relationship displays a sigmoid shape (Fig. 2a) with a first phase dominated by primary producers (Fig. 2b), followed by a build-up of the consumer species richness. Immigration-extinction dynamics favour greater occupancy of generalists in small areas, so local directed connectance ( $C_L = L_L/S_L S_C$ , where  $S_C$  is local consumer species richness) is predicted to decline with area (Fig. 2c). As community complexity depends on both species richness (Fig. 2a) and connectance (Fig. 2c), our model provides a process-based prediction for the complexity–area relationship that has been derived from the combination of link–species and species–area scaling relationships and observed for various systems (Brose *et al.* 2004).

## TESTING THE THEORY

We investigated how the trophic TIB performs compared with the classic TIB to predict local community structure and composition using two published datasets of insular food webs. We collected local and regional food web data for pelagic organisms of 50 lakes of the Adirondacks (Havens 1992) and for the arthropod community from a classic defaunation experiment performed in the Florida Keys (Simberloff & Wilson 1969; Piechnik *et al.* 2008). The lake dataset has a lower regional connectance (0.09) than the island dataset (0.21). The trophic TIB thus predicts that the former will be more constrained by trophic interactions (Figs 1a and 2a). Starting with coarse analyses at the community-level scale and then moving to the species-level, we tested the following predictions derived from the trophic TIB: (1) link density and connectance in local food webs is higher than the expectation from the classic TIB, (2) connectance in local food webs increases with the extinction rate, (3) occupancy increases with species diet breadth.

The complete methodology for the sampling of the 50 lakes can be found in Sutherland (1989). The lakes were sampled once during the summer 1984. The potential predator–prey interactions among the 210 species of the regional food web were determined by Havens (1992) from the literature, precluding the potential effect of regional abundance (Krishna *et al.* 2008) and sampling effort on network structure (Martinez 1991). A feeding link between two species found in the regional food web was automatically assumed to occur when both species were present in a given lake. Each of the 50 lakes comprised 13–75 species, with 17–577 feeding links (Table 1). There are 2020 feeding links in this regional food web.

The methodology for the sampling of the island data is described in Simberloff & Wilson (1969) and Piechnik *et al.* (2008). Six islands from the Florida keys, 11–25 meters in diameter, were defaunated with insecticide. The arthropods were first censused before the experiment and then on a regular basis approximately once every 3 weeks during the first year and again 2 years after defaunation. We restricted our analysis to the first census because it is the only one that is definitely at equilibrium. Piechnik *et al.* (2008) determined the trophic interactions among 250 arthropod taxa of the dataset using scientific literature and expert opinions. The regional food web is thus independent of local food webs, similar to the lake data. Each island comprised between 15 and 38 species, with 32–331 feeding links (Table 1). There are 13 068 feeding links in this regional food web.



**Figure 2** Predicted effect of island area on the equilibrium food web structure on islands. (a) Effect of the regional food web complexity on the species–area relationship where  $\alpha$  is the immigration-to-extinction ratio, which should increase monotonically with area. The regional connectance varies between 0.01 (red) and 0.1 (blue). The regional species pool contains 10 primary producers and 100 consumer species. All consumer species have the same diet breadth  $g$ . The black line corresponds to the classic TIB. (b) Heterogeneity in the distribution of consumers' diet breadth is introduced into the analytical model to show the predicted relationship between  $\alpha$  and the proportion of consumers in local food webs. The regional food web is taken from Havens (1992) (see Testing the Theory) and has 107 primary producers, 103 consumer species and 2010 links. (c) Predicted local connectance–area relationship assessed from stochastic simulations with Havens' regional food web. The local connectance ( $C_L$ ) asymptotes with the regional connectance (dotted line) in large communities. The dotted black line represents the prediction of the classic TIB.

The high number of sites for the lake data also allowed us to test if the connectance scales with lake size (volume). We controlled for lake pH because this variable is known to have a strong effect on the community structure in these lakes (Brose *et al.* 2004). Moreover, because the pH reduces population size, we hypothesise that this environmental variable could also control the extinction risk and thus community structure. We tested the relationship between connectance, pH and lake volume (also considering the interaction pH  $\times$  lake volume) with a linear model.

### Maximum likelihood comparison

We investigated through likelihood-based goodness-of-fit measures over the whole dataset the ability of the trophic TIB to predict species-specific occupancies and compared it with the null expectation of the classic TIB. The log-likelihood for the observation of a species' presence in a lake is simply the log of its predicted occupancy  $p_i$  and  $\log(1 - p_i)$  for its absence. Under the trophic TIB, the predicted occupancy of a species with diet breadth  $g$  is computed following the analytical approximation given in the online supporting information, while it is simply local species richness divided by the size of the regional species pool under the TIB. We also considered the predicted occupancies of stochastic simulations of the trophic TIB because the analytical solution did not explicitly consider the food web topology but only the distribution of diet breadths. We estimated the parameter  $\alpha$  for all 50 lakes and six islands for the three models (TIB, trophic TIB analytical approximation and stochastically simulated) by maximum likelihood. Note that for both the analytical prediction and the simulations, the likelihood function has a single peak.

### Simulation model

The analytical derivation of the occupancy assumes a random food web structure and does not consider the network topology. Previous metapopulation studies have established that persistence and occupancy of a consumer are influenced by its trophic position (Holt 1997; Holt *et al.* 1999; Calcagno *et al.* 2011; Gravel *et al.* 2011). Basically, for a predator to occupy a patch, it needs the herbivore it feeds on to be present, which also needs a primary producer to feed on, etc. This constraint has dramatic consequences for the occupancy of the highest trophic levels. We wondered if the assumption of a random food web structure could alter the predicted community composition in local communities and consequently compared the analytical derivation with results of a simulation model taking explicitly into account the topology of the regional food web. We simulated the dynamics of occupancy in local communities with a stochastic model. The regional food web we considered is based on the compilation of the regional food webs for both the lake and the island datasets. The model approximates the continuous dynamics described by equation by discretising it into small time steps ( $\Delta t$ ). At each time step, the probability that a consumer species absent from the local community colonises it is 0 if it has no prey already present (among the potential ones in the regional food web) and  $e\Delta t$  if there is at least one prey present. The probability that a primary producer colonises the local community is  $e\Delta t$ , irrespective of community composition. The probability that a consumer species present in the local community goes extinct is  $e\Delta t$  if it has at least one prey present and 1 if its last prey went extinct at the previous time step. The probability that a primary producer present goes extinct is  $e\Delta t$ , independent of



**Table 1** Comparison of food web properties between the regional food web and the observed food webs. Expectations from the classic TIB are based on random sampling of the regional pool for  $S_L$  species, yielding a constant fraction of non-trophically constrained species and connectance. Expectations of from the trophic TIB are based on simulations of the insular dynamics for each local community using the parameters estimated by maximum likelihood (see Table 2). Correlations are provided to indicate the goodness of fit of the parameter estimation for the trophic TIB

Statistics	Dataset	Regional food web	Observed food webs	Expectation from classic TIB	Expectation from trophic TIB	(r pred. vs. obs.)
			mean $\pm$ SD	mean $\pm$ SD	mean $\pm$ SD	
Species richness	Lakes	210	38.8 $\pm$ 14.8	38.8 $\pm$ 14.8	50.9 $\pm$ 18.2	(0.62)
	Islands	250	26.8 $\pm$ 7.4	26.8 $\pm$ 7.4	28.1 $\pm$ 11.3	(0.99)
Fraction of non-trophically constrained species*	Lakes	0.51	0.49 $\pm$ 0.10	0.51 $\pm$ 0	0.61 $\pm$ 0.03	(0.56)
	Islands	0.48	0.49 $\pm$ 0.07	0.48 $\pm$ 0	0.49 $\pm$ 0.005	(0.99)
Number of links L	Lakes	2020	168.5 $\pm$ 130.9	78.5 $\pm$ 58.3	152.4 $\pm$ 97.9	(0.64)
	Islands	13 068	192.0 $\pm$ 109.4	161.4 $\pm$ 90.8	199.8 $\pm$ 150.3	(0.96)
Connectance C	Lakes	0.09	0.2 $\pm$ 0.03	0.05 $\pm$ 0	0.14 $\pm$ 0.02	(0.33)
	Islands	0.21	0.25 $\pm$ 0.03	0.21 $\pm$ 0	0.23 $\pm$ 0.01	(-0.48)
Fraction of isolated consumer species†	Lakes	0	0 $\pm$ 0	0.36 $\pm$ 0.11	0 $\pm$ 0	(1)
	Islands	0	0.07 $\pm$ 0.05	0.20 $\pm$ 0.00	0 $\pm$ 0	(0)

\*Primary producers are not constrained to find their food in the lake dataset, while the herbivores feeding on mangrove trees and detritivores are not constrained in the islands dataset.

†For each of the lakes and islands of  $S_L$  species richness, we calculated the null expectation with 10 000 artificial communities of  $S_L$  randomly drawn species from the regional species pool.

community composition. We calculated the expected occupancy for each of the 210 species of lake data and of the 250 species of the island data for a wide range of values (at interval of 0.0001). We fixed  $e\Delta t$  at 0.1 and varied  $e\Delta t$  with the parameter  $\alpha$  following the relation  $e = c/\alpha$ . For each value, we started with a bare local community and ran the model 1000 time steps to reach equilibrium and then ran the model for another 250 000 time steps to record the average occupancy (number of time steps present/total number of time steps). We obtained a large table with the expected occupancy for all species from the regional pool in rows and the different  $\alpha$  values in columns. We used this table to estimate the parameter  $\alpha$  for each of the 50 lakes and the six islands by maximum likelihood.

## RESULTS

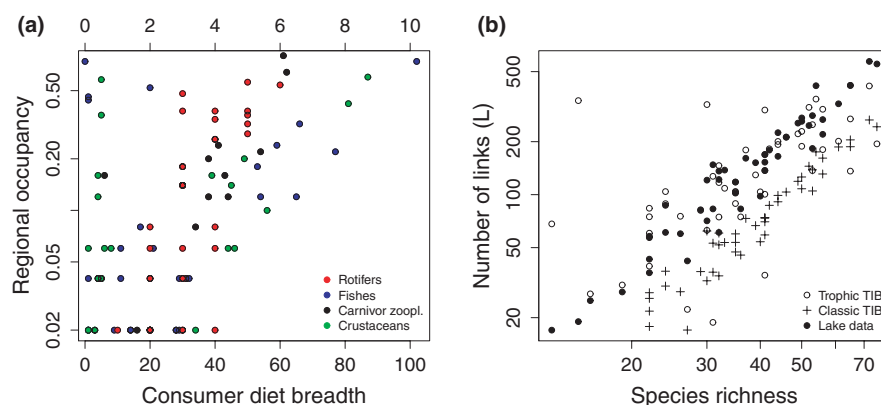
The classic TIB is a null model where local webs are random samples from the regional food web and thus predicts no association between diet breadth and island area. The trophic TIB instead predicts that, in small islands, species with larger diet breadth are more likely to occur than more specialised consumers. We found a much higher number of links per local food web for both the lakes and the islands, and a higher connectance than under the hypothesis of random sampling (Table 1). These results suggest a selection process in favour of consumers with larger diet breadths. Previous work has shown that the number of feeding links in the lake dataset scales with lake volume (Brose *et al.* 2004). We also found for this dataset (the island dataset does not have enough sites to test this hypothesis), with a multiple regression linear model, that once accounting for the interaction with pH, the number of trophic links significantly increases with lake volume and connectance significantly decreases with lake volume (Table 2), as predicted by our trophic TIB.

Connectance is a global descriptor of food web properties averaging the distribution of species' diet breadth (Dunne *et al.* 2002b). The fundamental prediction of the trophic TIB is, however, a species-specific relationship between diet breadth and occupancy. The positive relationship between diet breadth and regional occupancy is illustrated in Fig. 3a for the lake dataset. We thus investigated the

effect of trophic constraints on insular dynamics by comparing the ability of the classic and trophic TIB to predict species-specific occupancies. Our model is a likelihood function for occurrence probability that we used to estimate the parameter  $\alpha$  for each lake and island from the empirical diet breadth and occurrence data (details in the Supporting Information Data S1). This parameter was estimated for the classic and trophic TIB models and we compared their goodness-of-fit through maximum likelihood. We found a significantly larger log-likelihood for the trophic TIB in comparison to the classic TIB for the lakes and a similar one for the islands (Table 3; see also correlations between observed and predicted food web statistics in Table 1 for an assessment of the goodness-of-fit). The trophic TIB well predicts the link–species relationship, while the classic TIB underpredicts the number of trophic links (Fig. 3b). We also expected a better fit from the trophic TIB to the lake dataset than to the island dataset because of their differences in regional connectance and maximum food chain length (the island dataset contains fewer trophic levels among more connected species). The trophic TIB predicts that the effect of trophic constraints on occupancy should decrease with regional connectance to a point where occupancy is similar to the classic TIB (Fig. 1a). The occupancy for given immigration and extinction rates is predicted to reach an asymptote at  $c$ . 10–30 prey species, depending on the parameter  $\alpha$ , because at larger diet breadth consumers are no longer constrained to find their prey. The fraction of consumers having fewer than 10 prey species is indeed much higher in the lake dataset than for the islands (40% versus 8% respectively). This comparison between datasets suggests that the classic TIB could

**Table 2** Summary results for linear models between food web properties (species richness, link density and connectance) and lake characteristics (pH and volume)

Variable	Estimate ( <i>P</i> -value)			<i>R</i> <sup>2</sup>
	pH	log volume	pH $\times$ log volume	
Species richness	1.29 (<0.001)	-10.59 (0.793)	1.98 (0.068)	0.61
Link density	-83.15 (<0.001)	-158.86 (0.138)	31.43 (0.002)	0.59
Connectance	-0.06 (0.006)	-0.04 (0.590)	0.008 (0.003)	0.29



**Figure 3** Empirical investigation of the theory. (a) The relationship between diet breadth and regional occupancy across the 50 Adirondack lakes. Note the diet breadth for rotifers is given by the top axis. The linear regression between the occurrence probability, the log of the number of trophic links ( $g$ ) per consumer and the trophic rank (TR) is highly significant ( $P < 0.001$ ) for all four groups, but not significant when all species are considered together. The  $R^2$  for the carnivorous zooplankton is 0.52 ( $g$ ) and 0.59 ( $g + \text{TR}$ ); for rotifers is 0.56 ( $g$ ) and 0.77 ( $g + \text{TR}$ ); for fishes is 0.15 ( $g$ ) and 0.18 ( $g + \text{TR}$ ) and for crustacean zooplankton is 0.19 ( $g$ ) and 0.75 ( $g + \text{TR}$ ). (b) Scaling relationship between species richness and the number of trophic links for the lake dataset and predictions from the classic TIB and the trophic TIB (based on maximum likelihood parameter estimation).

**Table 3** Log-likelihood comparison for the different models and datasets

Dataset	Classic TIB	Trophic TIB (analytical)	Trophic TIB (simulations)
Adirondack lakes	-2428.2	-2416.8	-2392.4
Florida islands	-259.3	-259.9	-260.0

be a sufficient approximation to insular dynamics for less trophically constrained systems.

We also considered a simulation model because our analytical derivation of occupancy does not explicitly consider network topology. We found a significantly larger log-likelihood for the simulations with the trophic TIB for the lake dataset (Table 3), telling us that knowledge of food web topological details, such as trophic rank and food chain length, improves predictions on species-specific occupancy.

## CONCLUSION

MacArthur and Wilson were among the first to envision that species richness could be the result of processes occurring at a large scale, independent of the details of local ecological interactions. With no impinging on model parsimony, our model improves MacArthur and Wilson's TIB in two ways: (1) with the inclusion at a macroscopic level of the basics of ecological interactions through information on food web structure, (2) by providing richer predictions (species-specific occupancies and descriptors of community structure that can be derived from diet breadth-based occupancies). Remarkably, our model remains as simple to parameterise as the classic TIB, but it greatly improves its estimation. Our results suggest that trophic constraints contribute to the diversity of islands, nonetheless we might underestimate their importance to insular dynamics: indeed, we have considered neither the need for multiple preys, e.g. because of seasonality or to maintain nutrient homeostasis, nor top-down control of prey extinction rates by their predators (Ryberg & Chase 2007; Holt 2009; Calcagno *et al.* 2011; Gravel *et al.* 2011). Other concurrent processes related to generalist/specialist distinctions, such as increased colonisation rates, behavioural plasticity or the ability to feed on

allochthonous inputs (Polis & Hurd 1995; Massol *et al.* 2011), should also be considered further.

Ecologists need better models to understand the interplay of the environment and species interactions in the shaping of species distributions at macro-ecological scales (Araujo & Luoto 2007; Gotelli *et al.* 2010). An important challenge is to predict which species might become extinct and the functional consequences of their loss. A major issue remains the prediction of future species geographic distributions from which we may infer extinction rates (Thomas *et al.* 2004), changes in biodiversity patterns (Thuiller *et al.* 2011) and ultimately the loss of ecosystem services (Mooney *et al.* 2009). Such predictions classically rely on spatial modelling methods that only use environmental variables to predict species occupancy but that rarely include population dynamics (Keith *et al.* 2008) or species interactions (Araujo & Luoto 2007). However, there is growing evidence that the next generation of coarse-grained macro-ecological models will need to account for biological interactions and trophic relationships among species to reach accurate predictions of species distributions and biodiversity patterns (Schweiger *et al.* 2008; Gotelli *et al.* 2010; Lavergne *et al.* 2010). The ongoing challenge is thus to include information about species interactions while keeping the parsimony of macro-ecological models used to predict species occupancy on large scales, i.e. without complexifying the biogeographical background beyond our analysing and parameterisation abilities. Our trophic TIB provides such a simple theoretical framework to include interactions into species distribution models. Our model has focused on food webs, but it could be easily extended to apply to other interaction networks, e.g. plant-pollinator or plant-disperser networks. The integration of species interactions into distribution models, as exemplified in the present work, should improve our ability to predict the consequences of global change for communities with complex structures.

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## AUTHOR CONTRIBUTIONS

D.G., F.M., E.C., D.M. and N.M. designed research; D.G., F.M., E.C. conducted research and contributed to the model, analytical tools; D.G., F.M. and N.M. wrote the paper; D.G., F.M., E.C., D.M. and N.M. edited the paper.

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# Supplementary materials: Trophic theory of island biogeography

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## 1 Theoretical model

### 1.1 Reminder: MacArthur & Wilson’s island biogeography

MacArthur & Wilson [1] provided probably one of the first process-based explanation for the diversity of species observed on islands. The basis of their model is simple. Any species present on mainland near the focal island has a certain probability of being on the island at time  $t$ , noted  $p(t)$ . This probability changes through time according to two processes: first, the focal species can colonize the island if it was not present beforehand (with rate  $c$ ) ; second, the focal species can go extinct if it was present on the island (with rate  $e$ ). Hence, the equation controlling the dynamics of  $p$  reads as:

$$\frac{dp}{dt} = c(1 - p) - ep \quad (1)$$

Under the simplest assumptions, all species share the same colonization and extinction rates. At steady state, equation (1) yields

$$p = \frac{c}{c + e} \quad (2)$$

so that the ratio between the expected local richness ( $s_L = E[S_L]$ ; Table 1 summarizes notations used in the model) and potential richness (i.e. the total number of species present on mainland,  $P_T$ ) is given as:

$$\frac{s_L}{P_T} = \frac{\alpha}{1 + \alpha} \quad (3)$$

where  $\alpha = c/e$ . Based on equation (3), a number of interesting predictions can be made because, e.g.,  $c$  is bound to depend on the distance between mainland and the focal island and  $e$  will eventually depend on the number and diversity of available resources, and hence on island area.

### 1.2 Introducing trophic components into MacArthur & Wilson’s model

We now suppose that all species are not exactly similar in their colonization and extinction rates, generalizing an approach earlier developed by Holt and others (see review in ref [2]). More precisely, we make two assumptions:

1. a species can only invade the focal island if at least one species already present on the island is a natural prey of the focal species ;
2. a species that loses its last prey species on the island (because of extinction processes) also goes extinct.

Symbol	Relationship(s)	Meaning
$c$		colonization rate
$e$		extinction rate
$\alpha$	$\alpha = c/e$	diversity parameter
$X_i$		Random variable describing the occurrence of species $i$
$S_L$	$S_L = \sum_{k>0} S_k + S_B$	Total number of locally observed species
$S_k$		Number of locally observed species with $k$ prey species ( $ H  = k$ )
$S_B$		Number of locally observed basal species
$S_0$	$S_0 = \sum_{k>0} P_k - \sum_{k>0} S_k$	Number of locally unobserved consumer species
$P_T$	$P_T = \sum_{k>0} P_k + P_B$	Total number of potential species
$P_k$		Number of potential species with diet breadth $k$ ( $ G  = k$ )
$P_B$		Number of potential basal species
$p_i$		probability that species $i$ is present (species $i$ occupancy)
$p_g$		probability for any species with diet breadth $g$ to be present
$p_B$		probability for a basal species (primary producer) to be present
$q_i$	$q_i = 1 - \mathbb{E} \left[ \prod_{j \in G_i} (1 - X_j) \mid X_i = 0 \right]$	probability that the island is hospitable to consumer species $i$
$\epsilon_i$	$\epsilon_i = \mathbb{E} \left[ \sum_{j \in G_i} e_j X_j \prod_{\substack{k \in G_i \\ k \neq j}} (1 - X_k) \mid X_i = 1 \right]$	rate at which the last prey species of species $i$ gets extinct
$e_i$	$e_i = e + \epsilon_i$	extinction rate of species $i$
$G_i$		set of potential prey species for species $i$
$H_i$		set of observed prey species for species $i$ . When $ H_i  = 0$ , species $i$ is absent
$\beta$	$\beta = \langle \log(1 - p_g) \rangle_P$	logarithm of the geometric mean of species' absence probabilities

Table 1: Notations used in the model.

These assumptions imply that, on average, all species that have the same number of prey species share the same probability of presence on the island. Thus, we note  $p_g$  the probability that a species which has  $g$  potential prey species is present on the island. To account for the two above assumptions, we also introduce the quantities  $q_g$ , the probability that a species with  $g$  potential prey species (diet breadth  $g$ ) has one or more of its prey species present on the island when the focal species is absent from the island, and  $\epsilon_g$ , the rate at which a species with  $g$  potential prey species loses its last prey on the island. Note these quantities are not fixed parameters, but themselves variables emerging from the theory below. Equation (1) can be modified to account for new model assumptions and yields the following dynamics for  $p_g$ :

$$\frac{dp_g}{dt} = c(1 - p_g)q_g - (e + \epsilon_g)p_g \quad (4)$$

which yields the steady-state probability

$$p_g = \frac{cq_g}{cq_g + e + \epsilon_g} \quad (5)$$

For basal species (primary producers, index  $B$ ), occupancy still follows MacArthur and Wilson's model, i.e.:

$$p_B = \frac{c}{c + e} = \frac{\alpha}{1 + \alpha} \quad (6)$$

When the number of consumer species with diet breadth  $g$  is  $P_g$  and the number of basal species is  $P_B$  (with  $\sum P_g + P_B = P_T$ ), the predicted species richness is given as:

$$\frac{S_L}{P_T} = \sum_g \left( \frac{P_g}{P_T} \right) \left( \frac{\alpha q_g}{1 + \alpha q_g + (\epsilon_g/e)} \right) + \left( \frac{P_B}{P_T} \right) \left( \frac{\alpha}{1 + \alpha} \right) \quad (7)$$

### 1.3 Solving equation (5)

#### 1.3.1 Definitions

**Diet breadth** The set of prey species of species  $i$  is noted  $G_i$  (so that its cardinal  $|G_i|$  denotes the number of species preyed upon by species  $i$ , i.e. its diet breadth). The *observed* diet breadth of species  $i$  (i.e. the number of its prey species present in the observed food web) is noted  $|H_i|$  (corresponds to the set  $H_i$ ).

**Species richness** The number of consumer species with diet breadth  $g$  in the regional food web is noted  $P_g$ . The number of consumer species with observed diet breadth  $h$  in the local food web is noted  $S_h$ .  $S_0 = \sum_g P_g - \sum_h S_h$  represents the number of consumer species present in the regional food web but not observed in the local food web.



The number of basal species in the regional food web is noted  $P_B$ . The number of basal species observed in the local food web is noted  $S_B$ , so that  $P_B - S_B$  is the number of unobserved basal species.

The total number of species in the regional food web is noted  $P_T = \sum_g P_g + P_B$ . The total number of species observed in the local food web is noted  $S_L = \sum_h S_h + S_B$ .

**Expectations and averages** We will use two different sorts of expectations/averages:

1. **Expectation:** If  $U$  is a random variable (varying with food web realization), we note  $E[U]$  the *expectation* of  $U$  over food web realizations (submitted to the same conditions for community assembly) ;
2. **Regional average:** If  $u_g$  is a quantity that depends on the diet breadth  $g$ , we note  $\langle u \rangle_P = \frac{1}{P_T} \sum_g P_g u_g + \frac{P_B}{P_T} u_B$  the *average value* of  $u_g$  over all species in the regional food web ( $P$  is for “potential”).

**Random variables** To model food web assembly, we need to make use of random variables that vary in value between different food web realizations:

1. the indicator variable for species  $i$  occurrence,  $X_i$ :  $X_i = 0$  when species  $i$  is absent from the island food web and  $X_i = 1$  when it is present. We note that for a binary variable  $p_i = E[X_i]$ ;
2. for consumer species  $i$ , the indicator variable  $Y_i$  which equals 1 when at least one prey of species  $i$  is present. We note the expectation of species  $i$  having at least one prey present when it is absent is  $q_i = E[Y_i | X_i = 0]$  (as in equation [4]). Because it is impossible for a species to survive without any prey, we have the expectation a prey is present when species  $i$  is present is  $E[Y_i | X_i = 1] = 1$ , so that the expectation for the indicator variable is  $E[Y_i] = (1 - p_i) q_i + p_i$ , and  $E[Y_i X_i] = p_i$ .  $Y_i$  may be expressed in terms of the indicator variables for species  $j$  occurrence variables  $X_j$ ’s:

$$Y_i = 1 - \prod_{j \in G_i} (1 - X_j) \quad (8)$$

Based on equation (8), we can express the expectation  $q_i$  of species  $i$  having at least one prey when it is absent:

$$q_i = 1 - E \left[ \prod_{j \in G_i} (1 - X_j) | X_i = 0 \right] \quad (9)$$

Following the definition of species richness, the number of species present in the local food web ( $S_L$ ) can be simply obtained through variables  $X_i$ ’s:

$$S_L = \sum_{i=1}^{P_T} X_i \quad (10)$$

**Rates** As before, we note  $c$  and  $e$  the basic colonization and extinction rates. We note  $e_i = e + \epsilon_i$  to include the trophic constraint on the extinction rate for consumer species  $i$  resulting from intrinsic extinction ( $e$ ) and the extinction of its last prey species ( $\epsilon_i$ ). The expression for  $\epsilon_i$  is given by:

$$\epsilon_i = E \left[ \sum_{j \in G_i} e_j X_j \prod_{\substack{k \in G_i \\ k \neq j}} (1 - X_k) | X_i = 1 \right] \quad (11)$$

The equation (11) describes the rate at which a focal consumer species loses its last prey. Its meaning is the following: the increase in extinction rate ( $\epsilon_i$ ) for the focal species ( $i$ ) is obtained as the average over all prey species of their extinction rates (hence,  $\sum_{j \in G_i} e_j X_j$ ), taken when only one prey species is present (hence,  $X_j$ ) and all the other prey species are absent (hence,  $\prod_{\substack{k \in G_i \\ k \neq j}} (1 - X_k)$ ) and the focal species is assumed present (hence, the condition on the mean).

For basal species,  $e_i = e$ , as in MacArthur and Wilson’s model.

### 1.3.2 Solving the model

We now solve equations (5), (9) and (11) assuming that conditional expectations are equal to their unconditional counterparts, i.e.  $E[X_j | X_i = 0] = E[X_j | X_i = 1] = E[X_j] = p_j$ . This assumption implies that covariances between species that are part of the same prey set are null, i.e.  $E[X_i X_j] = E[X_i] E[X_j]$ .

Based on this assumption we have the following expectation for  $q_i$  :

$$1 - \mathbb{E} \left[ \prod_{j \in G_i} (1 - X_j) \mid X_i = 0 \right] \approx 1 - \mathbb{E} \left[ \prod_{j \in G_i} (1 - X_j) \right] \quad (12)$$

This approximation can be simplified even more:

$$1 - \mathbb{E} \left[ \prod_{j \in G_i} (1 - X_j) \right] \approx 1 - \prod_{j \in G_i} (1 - \mathbb{E}[X_j]) \quad (13)$$

so that solving for  $q_i$  yields (from equation [9]):

$$\begin{aligned} q_i &\approx 1 - \prod_{j \in G_i} (1 - p_j) \\ &= 1 - e^{|G_i| \langle \log(1-p_g) \rangle_P} \end{aligned} \quad (14)$$

In the same vein, we find the expectation for  $\epsilon_i$ :

$$\begin{aligned} \mathbb{E} \left[ \sum_{j \in G_i} e_j X_j \prod_{\substack{k \in G_i \\ k \neq j}} (1 - X_k) \mid X_i = 1 \right] &\approx \mathbb{E} \left[ \sum_{j \in G_i} e_j X_j \prod_{\substack{k \in G_i \\ k \neq j}} (1 - X_k) \right] \\ &\approx \sum_{j \in G_i} e_j \mathbb{E}[X_j] \prod_{\substack{k \in G_i \\ k \neq j}} (1 - \mathbb{E}[X_k]) \end{aligned} \quad (15)$$

and thus solving for  $e_i$  yields (from equation [11]):

$$\begin{aligned} e_i &\approx e + \sum_{j \in G_i} e_j p_j \prod_{\substack{k \in G_i \\ k \neq j}} (1 - p_k) \\ &= e + \sum_{j \in G_i} \frac{e_j p_j e^{|G_i| \langle \log(1-p_g) \rangle_P}}{1 - p_j} \\ &= e + \left( |G_i| \left\langle e_g \frac{p_g}{1 - p_g} \right\rangle_P \right) e^{|G_i| \langle \log(1-p_g) \rangle_P} \end{aligned} \quad (16)$$

From equations (5) and (14), we obtain the following expression:

$$\begin{aligned} e_i &= \frac{c q_i (1 - p_i)}{p_i} \\ &= \frac{c (1 - e^{|G_i| \langle \log(1-p_g) \rangle_P}) (1 - p_i)}{p_i} \end{aligned} \quad (17)$$

Plugging equation (17) into equation (16) yields the equation obeyed by  $p_i$  at equilibrium (using  $\alpha = c/e$ ):

$$\frac{p_i}{1 - p_i} = \frac{\alpha (1 - e^{|G_i| \langle \log(1-p_g) \rangle_P})}{1 + \alpha (1 - e^{|G_i| \langle \log(1-p_g) \rangle_P}) |G_i| e^{|G_i| \langle \log(1-p_g) \rangle_P}} \quad (18)$$

Taking expectations over the whole food web and replacing species indices by diet breadths, we obtain the following equation which yields the probability  $p_g$  that a species with diet breadth  $g$  is present on the island (with  $\beta = \langle \log(1 - p_g) \rangle_P$ ):

$$p_g = \frac{\alpha (1 - e^{\beta g})}{1 + \alpha (1 - e^{\beta g}) (1 + g e^{\beta g})} \quad (19)$$

The complete resolution of equation (19) involves rewriting  $\beta$ :

$$\begin{aligned} \beta &= \langle \log(1 - p_g) \rangle_P \\ &= \sum_g \left( \frac{P_g}{P_T} \right) \log(1 - p_g) + \left( \frac{P_B}{P_T} \right) \log \left( \frac{1}{1 + \alpha} \right) \\ &= \sum_g \left( \frac{P_g}{P_T} \right) \log \left( \frac{1 + \alpha (1 - e^{\beta g}) g e^{\beta g}}{1 + \alpha (1 - e^{\beta g}) (1 + g e^{\beta g})} \right) + \left( \frac{P_B}{P_T} \right) \log \left( \frac{1}{1 + \alpha} \right) \end{aligned} \quad (20)$$

Equation (20) cannot be solved in closed form, but a numerical solution for  $\beta$  can be found easily, given  $\alpha$  and the distribution of  $P_g$ .

## 2 Testing the theory

### 2.1 Empirical food web data

The complete methodology for the sampling of the 50 lakes could be found in ref [4]. The lakes were sampled once during the summer 1984. The potential predator-prey interactions among the 210 species of the regional food web were determined by Havens [2] from the literature, precluding the potential effect of regional abundance [5] and sampling effort on network structure [6]. A feeding link between two species found in the regional food web was automatically assumed to occur when both species were present in a given lake. Each of the 50 lakes comprised 13 to 75 species, with 17-577 feeding links (Table 1 in main text). There are 2020 feeding links in this regional food web.

The methodology for the sampling of the island data is described in refs [7, 8]. Six islands from the Florida keys, 11-25 in diameter, were defaunated with insecticide. The arthropods were first censused before the experiment and then on a regular basis approximately once every three weeks during the first year and again two years after defaunation. We restricted our analysis to the first census because it is the only one that is definitely at equilibrium. Piechnick et al.[9] determined the trophic interactions among 250 arthropod taxa of the dataset using scientific literature and expert opinions. The regional food web is thus independent of local food webs, similarly to the lake data. Each island comprised between 15 and 38 species, with 32-331 feeding links (Table 1 in main text). There are 13 068 feeding links in this regional food web.

We compared descriptors of the observed local food webs with the expectation of the classic TIB (random sampling of the regional pool). If species are randomly sampled from the regional species pool, then the fraction of primary producer species, of non-trophically constrained species and the connectance in local webs should be the same as the regional species pool. The number of links expected should then be the regional connectance multiplied by the number of potential links in the interaction matrix ( $S_L S_C$ ). We also considered the fraction of the consumer species that are isolated (i.e. they have no prey species in the local food web). For each local food web of  $S_L$  species, we calculated the expectation of this statistic under the classic TIB by randomly sampling  $S_L$  species from the regional food web 10 000 times. We compared the statistics for the observed food webs to their expectation under the classic TIB with a t-test for paired samples.

The high number of sites for the lake data also allowed us to test if the connectance scales with lake size (volume). We controlled for lake pH because this variable is known to have a strong effect on the community structure in these lakes. Moreover, because the pH reduces population size, we hypothesize this environmental variable could also control the extinction risk and thus community structure. We tested the relationship between connectance, pH and lake volume (also considering the interaction pH\*lake volume) with a linear model.

### 2.2 Maximum likelihood estimate of turnover rate

We investigated through likelihood-based goodness-of-fit measures over the whole dataset the ability of the trophic TIB to predict species-specific occupancies and compared it to the null expectation of the classic TIB. The log-likelihood for the observation of a species' presence in a lake is simply the log of its predicted occupancy  $p_i$  and  $\log(1 - p_i)$  for its absence. Under the trophic TIB, the predicted occupancy of a species with diet breadth  $g$  is computed following the analytical approximation given by equation (19), while it is simply local species richness divided by the size of the regional species pool under the TIB ( $S_L/P_T$ ). We also considered the predicted occupancies of stochastic simulations of the trophic TIB because the analytical solution did not explicitly consider the food web topology but only the distribution of diet breadths. We estimated the parameter  $\alpha$  for all 50 lakes and 6 islands for the three models (TIB, trophic TIB analytical approximation and stochastically simulated) by maximum likelihood. Note that for both the analytical prediction and the simulations, the likelihood function has a single peak.

### 2.3 Simulation model

The analytical derivation of the occupancy given by equation (19) assumes a random food web structure and does not consider the network topology. Previous metapopulation studies have established that persistence (and thus occupancy) of a consumer is influenced by its trophic position [10, 11]. Basically, for a predator to occupy a patch, it needs the herbivore it feeds on to be present, which also needs a primary producer to feed on, etc. This constraint has dramatic consequences for the occupancy of the highest trophic levels. We wondered if the assumption of a random food web structure could alter the predicted community composition in local communities and consequently compared the analytical derivation with results of a simulation model taking explicitly into account the topology of the regional food web.

We simulated the dynamics of occupancy in local communities with a stochastic model. The regional food web we considered is based on the compilation of the regional food webs for both the lake and the island datasets. The model approximates the continuous dynamics described by equation (4) by discretizing it into small time steps ( $\Delta t$ ). At each time step, the probability that a consumer species absent from the local community colonizes it is 0 if it has no prey already present (among the potential ones in the regional food web), and  $c\Delta t$  if there is at least one prey present. The probability that a primary producer colonizes the local community is  $c\Delta t$ , irrespective of community composition. The



probability that a consumer species present in the local community goes extinct is  $e\Delta t$  if it has at least one prey present and 1 if its last prey went extinct at the previous time step. The probability that a primary producer present goes extinct is  $e\Delta t$ , independently of community composition.

We calculated the expected occupancy for each of the 210 species of Havens' data for a wide range of values (at interval of 0.0001). We fixed  $c\Delta t$  at 0.1 and varied  $e\Delta t$  with the parameter  $\alpha$  following the relation  $e\Delta t = c\Delta t/\alpha$ . For each value, we started with a bare local community and ran the model 1000 time steps to reach equilibrium, and then ran the model for another 250,000 time steps to record the average occupancy (number of time steps present/total number of time steps). We obtained a large table with the expected occupancy for all species from the regional pool in rows, and the different  $\alpha$  values in columns. We used this table to estimate the parameter  $\alpha$  for each of the 50 lakes and the 6 islands by maximum likelihood.

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## Original Article

## A framework to compare theoretical predictions on trait evolution in temporally varying environments under different life cycles

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## ABSTRACT

Predicting the evolution of traits such as dispersal or local adaptation, in a variable environment is an important issue in theoretical evolutionary ecology. With concepts such as hard selection vs. soft selection or fine-grained vs. coarse-grained environmental variability, this issue has attracted much attention, and yet different models seldom agree on qualitative predictions about, e.g. the evolution of generalist or specialist strategies, or the occurrence of stabilizing or disruptive selection on studied traits.

Here, I investigate the effect of the order of events in the life cycle on trait evolution in a spatially heterogeneous, temporally varying landscape using a Wright–Fisher island model. I first develop a methodological framework allowing for different life cycles. Then I illustrate the importance of life cycles on selection regimes by looking more closely at the evolution of local adaptation.

Model results show that the occurrence of disruptive selection and bi- or tristability mainly depends on the life cycle, the convexity of the trade-off behind local adaptation, the immigration rate, and the autocorrelation in patch state. With the same forces driving the evolution of local adaptation, different life cycles induce different evolutionary outcomes. Model results highlight the importance of accounting for life cycle specificities when attempting to predict the effects of the environment on evolutionarily selected trait values, as well as the need to check the robustness of evolutionary model conclusions against modifications of the life cycle.

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## 1. Introduction

Predicting the evolution of traits in variable environments has been a classical issue in theoretical evolutionary ecology now for more than fifty years. This issue is central from a population genetics viewpoint because it underlies the whole argument on environmentally maintained polymorphism, *i.e.* the fact that genotypes specialized on different types of environments stably coexist due to frequency-dependent selection. It is also central from a more applied viewpoint since being able to make predictions on adaptation to changing environments is the key to understand how organisms might cope with future changes, *e.g.* climatic changes or habitat fragmentation. For both fundamental and applied reasons, models have been developed to understand how variability in environmental conditions might influence evolutionary trajectories.

Environmental variability can be conceived as both spatial and temporal. On the one hand, environmental variability can be found among sites (*e.g.* ponds with or without insecticide, at different

temperatures, with different levels of nutrients, *etc.*). On the other hand, variability in habitat conditions can be a function of time, so that a currently good patch can turn bad for the next generation. It is very tempting to think that different environmental conditions should select for different adaptations in organisms and, hence, should tend to create specialized sister “species” exploiting different environmental conditions regardless of whether variability in habitat conditions is temporal or spatial. However, some early works, such as Levins’ coarse-grained habitats vs. fine-grained habitats (Levins, 1968, 1979), have proved that the same level of habitat variability might select for two specialized genotypes or a single generalist one, depending on whether each individual experiences several or only one habitat for its entire life. In the 1950s, population geneticists also proposed models to assess the effect of spatial environmental variability on the evolution of traits. More specifically, they focussed on the study of local adaptation polymorphisms maintained by fixed spatial differences in habitat conditions (Christiansen, 1975; Dempster, 1955; Karlin and Campbell, 1981; Levene, 1953; Wallace, 1975). Their results, which have been part of every population genetics handbook ever since, prove that different models can lead to different predictions: whereas Levene’s soft selection model allows for protected polymorphisms, Dempster’s hard selection model only predicts

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the dominance of a single genotype, corresponding to the one more adapted to the most abundant habitat.

At some point came the realization that models by Levene, Dempster or others were not dealing with the same situations. For instance, population regulation (*i.e.* the process by which population abundances remain stable) operates in a very different fashion in soft and hard selection models (Christiansen, 1975; de Meeus and Goudet, 2000; de Meeus et al., 1993; Ravigné et al., 2004; Wallace, 1975): under hard selection, propagules are regulated at the landscape level, so that different habitats can emit different amounts of propagules; under soft selection, regulation is local and equally effective among habitats, so that there is no possibility for types specialized in using very productive habitats to overwhelm the whole system. However true these statements may be, it is much more enlightening to interpret differences in model assumptions from a more biological perspective. One such perspective was achieved by Ravigné et al. (2004) who proposed to interpret the models as representing different life cycles: essentially, what happens to individual organisms in these models can be summarized as reproduction, regulation, emigration, and immigration. When regulation occurs just after reproduction, the equations corresponding to the life cycle are those of Levene's model; when regulation occurs in-between emigration and immigration (*i.e.* in the propagule pool), then the life cycle yields Dempster's hard selection model. The last possible case (putting regulation after immigration) yields another different model that Ravigné et al. (2004) have studied at length. Interestingly, Ravigné's third type of model can be classified as either hard or soft depending on whether the model allows for habitat selection (Ravigné et al., 2004).

In spite of the various models that have been brought forth to study the effects of temporal or spatial sources of environmental conditions on evolution of traits such as local adaptation (de Meeus and Goudet, 2000; Dempster, 1955; Levene, 1953; Ravigné et al., 2004), habitat selection (Garcia-Dorado, 1987; Ravigné et al., 2009) or dispersal (Hastings, 1983; Holt, 1985; Kisdi, 2002; Massol et al., 2011), there have been only a few approaches actually tackling both temporal variability and spatial heterogeneity, and most of them focus on the evolution of dispersal (Blanquart and Gandon, 2011; Cheptou and Massol, 2009; Massol and Cheptou, 2011; Mathias et al., 2001; Parvinen, 2002). For traits such as dispersal, it is likely that habitat predictability (McNamara and Dall, 2011), or equivalently habitat temporal coarseness, and the spatial heterogeneity of habitats in the landscape (Hastings, 1983), should both have a say on evolutionary outcomes – and indeed they do (Massol and Cheptou, 2011). However, such results have yet to be extended to the evolution of other important traits affecting fitness, and it is still not clear that results obtained so far on the evolution of dispersal in spatio-temporally variable landscapes (Massol and Cheptou, 2011; McNamara and Dall, 2011) are general laws or depend on the specifics of the life cycle assumed. Results obtained on the evolution of local adaptation (Débarre and Gandon, 2011; Ravigné et al., 2004) suggest, on the contrary, that different life cycles may lead to different evolutionary outcomes. In this paper, I present a general methodological framework to predict the effects of spatio-temporal environmental variability and the order of events in the life cycle on the evolution of life-history traits. As an example, I illustrate present method for local adaptation. By way of studying this general problem, I also aim to show that much care should be taken when describing the assumptions made on life cycles in evolutionary ecology and population genetics model because such models can display much different predictions with a simple swap in life cycle events. Finally, I discuss results in the context of current research aimed at understanding evolutionary reasons for biological diversity.

## 2. Model

### 2.1. General principles

Consider the following problem: to predict evolutionary trajectories for a set of traits (vector  $\mathbf{X}$ ) that evolve in a given species, I want to predict whether a given mutant (trait values  $\mathbf{X}'$ ) can invade a landscape filled by a monomorphic resident type (trait values  $\mathbf{X}$ ), *à la* adaptive dynamics (Geritz et al., 1998; Hofbauer and Sigmund, 1990) with clonal reproduction. I assume that the demographics follow Wright–Fisher island model assumptions (discrete time, synchronous reproduction, constant density, dispersal is not distance-limited) with an infinite number of patches containing an infinity of individuals, and can be modeled as simple semelparous life cycles (Ravigné et al., 2004) consisting in four different events. These events are:

- reproduction, noted as event  $S$  (or diagonal matrix  $\mathbf{D}$  when needed, with entries  $S_{ij}$ ) whereby local individual densities in patch class  $i$  are multiplied by a local growth factor  $S_{ii}$ ;
- environmental change, noted as event  $E$  (or matrix  $\mathbf{E}$  with entries  $E_{ij}$ ), which is assumed to be a stochastic process, occurring independently for each patch, and which keeps the expected proportion of patches of each type constant while allowing for autocorrelation in patch type before and after environmental change. Element  $E_{ij}$  corresponds to the probability that a patch of class  $j$  becomes of class  $i$ ;
- dispersal, noted as event  $D$  (or matrix  $\mathbf{D}$  with entries  $D_{ij}$ ), which potentially accounts for conditional dispersal (different probabilities of emigrating based on current patch type), habitat selection (probabilities to land in patches of a given type may be different from its frequency), and the cost of dispersal. Element  $D_{ij}$  corresponds to the proportion of propagules originally in class  $j$  that is in class  $i$  after the dispersal event; and
- regulation, noted as event  $R$  (or diagonal matrix  $\mathbf{R}$  with entries  $R_{ij}$ ), which is assumed to occur independently in each patch. Because each patch contains an infinity of individuals, regulation consists in dividing the number of mutants obtained after all other life cycle events in a given patch by the number of residents obtained after the same steps.

Each event happens only once in the life cycles considered in this study. All individuals follow the same life cycle, *i.e.* the same series of events between birth and death. Because the model assumes non-overlapping generations, this reduces to the order of the four events. By convention, I assume that all life cycles finish with regulation – this convention allows for an easy enumeration of life cycles. Within a given generation, the demographics of the metapopulation are captured by the dynamics of individual mutant densities within each patch class relatively to individual mutant density taken after the last regulation episode. Patch classes are defined based on the level of detail necessary for the computation of regulation factors. In simple cases, patch classes equal patch types (2 classes); in complex cases, patch classes equal the recent history of a patch type, *i.e.* its current and former patch types (hence, 4 classes)

The general methodology developed here consists in finding the expressions for these event matrices. Once expressions for  $\mathbf{S}$ ,  $\mathbf{E}$ , ... have been found, these matrices are combined (*i.e.* multiplied) to obtain a next-generation matrix  $\mathbf{G}(\mathbf{X}', \mathbf{X})$  that defines the dynamics of the vector of mutant frequencies  $\mathbf{Y}_t$  in each patch type:

$$\mathbf{Y}_{t+1} = \mathbf{G}(\mathbf{X}', \mathbf{X}) \cdot \mathbf{Y}_t \quad (1)$$

Here, the expression for  $\mathbf{G}$  is a product  $\mathbf{R}(\mathbf{X}) \cdot \mathbf{C}(\mathbf{X}')$  where  $\mathbf{C}'$  is the cycle matrix corresponding to mutant demographics (hence the

prime) and  $\mathbf{R}$  is the regulation matrix corresponding to the matching resident demographics. The order of events in the life cycle determines how matrices are multiplied to obtain the next-generation matrix (this is not a trivial issue since matrix multiplication is not generally commutative). Assessing the outcome of evolutionary processes is then obtained through the expression for the mutant fitness  $W$ , computed as the dominant eigenvalue of the next generation matrix  $\mathbf{G}$ .

A first general step is to enumerate the possible life cycles. Both environmental change  $E$  and regulation  $R$  are local events, and happen independently in each patch. In addition, regulation does not depend on the type of patch: it only depends on the density of individuals present in the patch, when regulation occurs. For this reason, the events  $E$  and  $R$  commute, and the life cycles  $(E, X, Y, R)$  and  $(X, Y, E, R)$  (where  $X$  and  $Y$  are the two other events) are equivalent. We are left with four different life cycles, which are presented in Fig. 1: life cycle 1 ( $E, S, D, R$ ), life cycle 2 ( $E, D, S, R$ ), life cycle 3 ( $D, E, S, R$ ), and life cycle 4 ( $S, E, D, R$ ). Because life cycle events are listed from left to right, whereas matrix multiplication goes from right to left, this means that e.g. life cycle ( $E, S, D, R$ ) corresponds to  $\mathbf{Y}_{t+1} = \mathbf{R} \cdot \mathbf{D} \cdot \mathbf{S} \cdot \mathbf{E} \cdot \mathbf{Y}_t$ .

From a purely mathematical viewpoint, it is worth mentioning that life cycles 1 and 2 will allow for a simpler treatment than life cycles 3 and 4 because, in life cycles 3 and 4,  $E$  is embedded between at least one habitat-wise event and regulation, so that patch history has to be accounted for at the regulation step of these life cycles. By contrast, regulation only depends on current patch type in life cycles 1 and 2, and thus becomes equivalent to a habitat-wise process – habitats are just shuffled randomly at the beginning of each generation. In the following, I call life cycles 1 and 2 “simple life cycles” while life cycles 3 and 4 are noted as “complex life cycles” (Fig. 1).

Following Ravigné et al. (2004), I can describe these life cycles in terms of similarity with models of hard and soft selection regimes (Débarre and Gandon, 2011; Dempster, 1955; Karlin and Campbell, 1981; Levene, 1953) (Fig. 1). Since I assume that regulation is always local, i.e. does not affect propagules but established individuals, the life cycles can only correspond to Levene- or Ravigné-types of selection regimes (Dempster-type selection requires regulation in the propagule pool). Life cycles 2 and 3 are Levene-type selection regimes: reproduction is immediately followed by local regulation, so that propagule outputs are the same in all the patches. Conversely, life cycles 1 and 4 are arguably Ravigné-type selection regimes because dispersal is followed by local regulation. Another way to interpret these life cycles is to qualify the life stage at which individuals disperse: in life cycles 2

and 3, adults disperse; in life cycles 1 and 4, juveniles are the dispersing stage (Débarre and Gandon, 2011).

## 2.2. Two-patch type model specifics

In the following sections, I develop this framework for a simple landscape consisting in only two patch types, noted 1 and 2. The expected proportion of patches of type 1 is noted  $\rho$  and is assumed constant between generations. Local growth factors applied during reproduction are noted  $g_1$  in patches of type 1 and  $g_2$  in patches of type 2. The matrix of environmental change is completely described using only one autocorrelation parameter, noted  $\varphi$ .

To simplify notations, I will neglect the use of primes when describing the components of matrix  $\mathbf{C}'$  and there is no ambiguity in doing so, but one should remember that regulation is solely based on residents' trait values while reproduction and dispersal are described solely by mutants' traits. Important model notations are summarized in Table 1.

## 2.3. Formalization of simple life cycles

Environmental change can be described as the following  $2 \times 2$  matrix:

$$\mathbf{E} = \begin{pmatrix} 1 - \mu & \nu \\ \mu & 1 - \nu \end{pmatrix} \quad (2)$$

where  $\mu = (1 - \varphi)(1 - \rho)$  and  $\nu = (1 - \varphi)\rho$ . Because these probabilities in matrix  $\mathbf{E}$  are bound to remain between 0 and 1,  $\varphi$  must be greater than  $\max[-\rho/(1 - \rho), -(1 - \rho)/\rho]$ .

The reproduction matrix is given by:

$$\mathbf{S} = \begin{pmatrix} g_1 & 0 \\ 0 & g_2 \end{pmatrix} \quad (3)$$

With local adaptation to habitat of type 1 measured by trait  $s$ , I assume that the convexity of the trade-off between local adaptation to habitat 1 and habitat 2 is a power trade-off (Egas et al., 2004), which depends on parameter  $\beta$ , so that

$$g_1 = s^\beta \quad (4a)$$

and

$$g_2 = (1 - s)^\beta \quad (4b)$$

A trait value of  $s = 1$  is a patch type 1 specialist,  $s = 0$  describes a patch type 2 specialist, while  $s = 0.5$  corresponds to a perfect generalist with equal growth factors in both patch types.

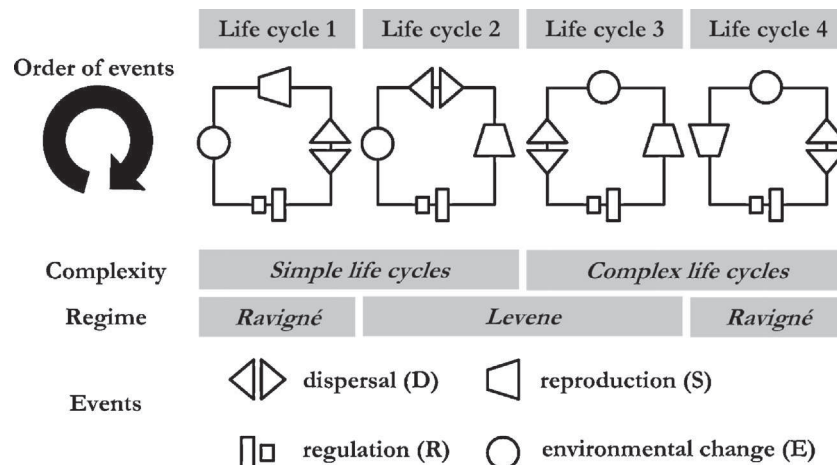


Fig. 1. Graphical summary of the four possible life cycles with four possible events.

**Table 1**  
Model notations.

Notation	Meaning	Value range
$d_i$	Dispersal rate out of type $i$ patches	$[0;1]$
$c$	Basic cost of dispersal	$[0;1]$
$\gamma$	Realized cost of dispersal	$[0;1]$
$I$	Immigration rate, immigrant-to-philopatric ratio $I=(1-c)d/(1-d)$	$[0;\infty[$
$g_i$	Fecundity in type $i$ patches	$[0;\infty[$
$\varphi$	Temporal autocorrelation in patch state	$\left[-\min\left(\frac{\rho}{1-\rho}, \frac{1-\rho}{\rho}\right); 1\right]$
$\rho$	Proportion of type 1 patches	$[0;1]$
$\varepsilon$	Uncertainty in patch state	$[0;1/2]$
$\bar{d}$	Average dispersal rate $\bar{d} = \rho d_1 + (1-\rho)d_2$	$[0;1]$
$\bar{g}$	Average fecundity $\bar{g} = \rho g_1 + (1-\rho)g_2$	$[0;\infty[$
$\overline{gd}$	Spatial average of fecundity times dispersal $\overline{gd} = \rho g_1 d_1 + (1-\rho)g_2 d_2$	$[0;\infty[$
$v_g$	Spatial variance of fecundity $v_g = \rho(1-\rho)(g_1 - g_2)^2$	$[0;\infty[$
$\mu$	Probability of transition from state 1 to state 2 $\mu = (1-\varphi)(1-\rho)$	$[0;1]$
$\nu$	Probability of transition from state 2 to state 1 $\nu = (1-\varphi)\rho$	$[0;1]$

Dispersal is assumed to be costly, *i.e.* a certain fraction of dispersed propagules is lost during dispersal. In the absence of habitat selection, this fraction is noted  $c$  and is assumed to be a parameter of the model (*i.e.* independent of dispersing genotype). If habitat selection occurs, organisms are assumed to have a separate acceptance probability for each habitat type, and have a certain probability to die before patch immigration trials. If I note  $h$  the fraction of propagules ending in patches of type 1, the realized dispersal cost  $\gamma$  with habitat selection is (Appendix A):

$$\gamma = \frac{c}{c + (1-c)\min[\rho/h, (1-\rho)/(1-h)]} \quad (5)$$

When organisms disperse from type  $i$  patches with probability  $d_i$ , the dispersal matrix  $\mathbf{D}$  is given as:

$$\mathbf{D} = \begin{pmatrix} 1-d_1 + (1-\gamma)hd_1 & (1-\gamma)hd_2 \\ (1-\gamma)(1-h)d_1 & 1-d_2 + (1-\gamma)(1-h)d_2 \end{pmatrix} \quad (6)$$

For simple life cycles, the regulation matrix can be computed as follows. If I note  $\mathbf{F}$  the life cycle matrix without the environmental change component, *i.e.* the product of matrices  $\mathbf{S}$  and  $\mathbf{D}$  that represents the order of life cycle events before regulation ( $\mathbf{F} \cdot \mathbf{E} = \mathbf{C}$  using residents' traits), the general shape of matrix  $\mathbf{R}$  is given by:

$$\mathbf{R} = \begin{pmatrix} r_1 & 0 \\ 0 & r_2 \end{pmatrix} \quad (7)$$

where the  $r_i$ s are regulation factors chosen so that:

$$\begin{pmatrix} \rho \\ 1-\rho \end{pmatrix} = \mathbf{R} \cdot \mathbf{F} \cdot \begin{pmatrix} \rho \\ 1-\rho \end{pmatrix} \quad (9)$$

For life cycle 1,  $\mathbf{F} = \mathbf{D} \cdot \mathbf{S}$  while for life cycle 2  $\mathbf{F} = \mathbf{S} \cdot \mathbf{D}$ . Regulation factors obtained through this direct computation are given in Table 2.

I then obtain the next generation matrix  $\mathbf{G}_i$  for life cycles 1 and 2 (Table 3). Because local adaptation and dispersal can be totally separated in the expression for  $\mathbf{G}_2$  (in Table 3, local adaptation appears in the leftmost matrix only, whereas dispersal and habitat selection traits are all in the middle matrix), selection gradients on dispersal and habitat selection traits will not depend on differences in patch types (these differences only appear when differentiating

**Table 2**  
Regulation factors computed for simple life cycles.

	life cycle 1	life cycle 2
$r_1^{-1}$	$g_1(1-d_1) + (1-\gamma)\frac{h}{\rho}\bar{g}\bar{d}$	$g_1[1-d_1 + (1-\gamma)\frac{h}{\rho}\bar{d}]$
$r_2^{-1}$	$g_2(1-d_2) + (1-\gamma)\frac{1-h}{1-\rho}\bar{g}\bar{d}$	$g_2[1-d_2 + (1-\gamma)\frac{1-h}{1-\rho}\bar{d}]$

the leftmost matrix, but this matrix does not contain dispersal and habitat selection traits), and thus the only effect of dispersal is to inflict a cost on offspring production. Hence, the evolution of dispersal and habitat selection under life cycle 2 will inevitably lead to zero dispersal and no habitat selection, in order to decrease dispersal cost to the minimum. From the viewpoint of the evolution of dispersal, this makes sense since soft selection regimes (like the one by life cycle 2) induce no spatio-temporal differences in local offspring production, and hence is unable to produce any selection pressure for more dispersal. This is the equivalent of what happens in self-fertilizing genotypes which do not perceive differences in pollination among patches, and thus evolve toward total philopatry (Cheptou and Massol, 2009).

#### 2.4. Formalization of complex life cycles

Complex life cycles can also be formalized using matrices for each life cycle event, but they require more details in the way patches are categorized and accounted for. The specificity of complex life cycles is that immediate patch history is relevant to the computation of regulation factors. Thus, two important points must be formalized:

- from regulation to environmental change, patches can be categorized in two classes (type 1 vs. type 2) whereas from environmental change to regulation, patches must be categorized using four classes (former type 1/current type 1, former type 1/current type 2, former type 2/current type 1, and former type 2/current type 2); and
- events occurring between  $R$  and  $E$  are represented as a  $2 \times 2$  matrix, events occurring between  $E$  and  $R$  are represented as a  $4 \times 4$  matrix, environmental change is represented as a  $4 \times 2$  matrix, and regulation is represented as the product of a  $2 \times 4$  matrix (noted  $\mathbf{K}$  and describing the process of “forgetting” immediate history of individual patch types) with a  $4 \times 4$  matrix (noted  $\mathbf{R}$ , describing class-wise regulation factors).

With this formalization, event  $E$  is described as the following matrix:

$$\mathbf{E}_4 = \begin{pmatrix} 1-\mu & 0 \\ \mu & 0 \\ 0 & \nu \\ 0 & 1-\nu \end{pmatrix} \quad (10)$$

Ecologically, the process associated with  $E$  turns a landscape initially consisting in proportions  $\rho$  and  $1-\rho$  of patches of types 1 and 2, respectively, into proportions  $\rho - (1-\varphi)\rho(1-\rho)$ ,



**Table 3**

Next generation matrices for all life cycles. For life cycle 4,  $\xi = \bar{g} \cdot \bar{d} + \rho(1 - \rho)\varphi(d_1 - d_2)(g_1 - g_2)$ ,  $\delta'_1 = (1 - \mu)d'_1 + \mu d'_2$ , and  $\delta'_2 = v d'_1 + (1 - v)d'_2$ .

Life cycle	Next generation matrix $\mathbf{G}_i$
1	$\begin{pmatrix} \frac{g'_1[1 - d'_1 + (1 - \gamma')h'd'_1]}{g_1(1 - d_1) + (1 - \gamma)(h/\rho)\bar{g}\bar{d}} & \frac{g'_2(1 - \gamma')h'd'_2}{g_1(1 - d_1) + (1 - \gamma)(h/\rho)\bar{g}\bar{d}} \\ \frac{g'_1(1 - \gamma')(1 - h')d'_1}{g_2(1 - d_2) + (1 - \gamma)(1 - h/1 - \rho)\bar{g}\bar{d}} & \frac{g'_2[1 - d'_2 + (1 - \gamma')(1 - h')d'_2]}{g_2(1 - d_2) + (1 - \gamma)(1 - h/1 - \rho)\bar{g}\bar{d}} \end{pmatrix} \cdot \mathbf{E}$
2	$\begin{pmatrix} g'_1 & 0 \\ g_1 & g'_2 \\ 0 & g_2 \end{pmatrix} \cdot \begin{pmatrix} \frac{1 - d'_1 + (1 - \gamma')h'd'_1}{1 - d_1 + (1 - \gamma)(h/\rho)\bar{d}} & \frac{(1 - \gamma')h'd'_2}{1 - d_1 + (1 - \gamma)(h/\rho)\bar{d}} \\ \frac{(1 - \gamma')(1 - h')d'_1}{1 - d_2 + (1 - \gamma)(1 - h/1 - \rho)\bar{d}} & \frac{1 - d'_2 + (1 - \gamma')(1 - h')d'_2}{1 - d_2 + (1 - \gamma)(1 - h/1 - \rho)\bar{d}} \end{pmatrix} \cdot \mathbf{E}$
3	$\begin{pmatrix} g'_1 & 0 \\ g_1 & g'_2 \\ 0 & g_2 \end{pmatrix} \cdot \mathbf{E} \cdot \begin{pmatrix} \frac{1 - d'_1 + (1 - \gamma')h'd'_1}{1 - d_1 + (1 - \gamma)(h/\rho)\bar{d}} & \frac{(1 - \gamma')h'd'_2}{1 - d_1 + (1 - \gamma)(h/\rho)\bar{d}} \\ \frac{(1 - \gamma')(1 - h')d'_1}{1 - d_2 + (1 - \gamma)(1 - h/1 - \rho)\bar{d}} & \frac{1 - d'_2 + (1 - \gamma')(1 - h')d'_2}{1 - d_2 + (1 - \gamma)(1 - h/1 - \rho)\bar{d}} \end{pmatrix}$
4	$\begin{pmatrix} \frac{(1 - \mu)(1 - d'_1) + (1 - \mu)(1 - \gamma')h'd'_1}{g_1(1 - d_1) + (1 - \gamma)(h/\rho)\bar{g}\bar{d}} + \frac{(1 - \gamma')\mu h'd'_1}{g_2(1 - d_1) + (1 - \gamma)(h/\rho)\bar{g}\bar{d}} & \frac{(1 - \gamma')(1 - \mu)h'd'_2}{g_1(1 - d_1) + (1 - \gamma)(h/\rho)\bar{g}\bar{d}} + \frac{v(1 - d'_1) + (1 - \gamma')\mu h'd'_2}{g_2(1 - d_1) + (1 - \gamma)(h/\rho)\bar{g}\bar{d}} \\ \frac{\mu(1 - d'_2) + (1 - \gamma')v(1 - h')d'_2}{g_1(1 - d_2) + (1 - \gamma)(1 - h/1 - \rho)\bar{g}\bar{d}} + \frac{(1 - \gamma')(1 - v)(1 - h')d'_2}{g_2(1 - d_2) + (1 - \gamma)(1 - h/1 - \rho)\bar{g}\bar{d}} & \frac{(1 - \gamma')v(1 - h')d'_2}{g_1(1 - d_2) + (1 - \gamma)(1 - h/1 - \rho)\bar{g}\bar{d}} + \frac{(1 - v)(1 - d'_2) + (1 - \gamma')(1 - v)(1 - h')d'_2}{g_2(1 - d_2) + (1 - \gamma)(1 - h/1 - \rho)\bar{g}\bar{d}} \end{pmatrix} \cdot \begin{pmatrix} g'_1 & 0 \\ 0 & g'_2 \end{pmatrix}$

$(1 - \varphi)\rho(1 - \rho)$ ,  $(1 - \varphi)\rho(1 - \rho)$  and  $1 - \rho - (1 - \varphi)\rho(1 - \rho)$  of patches of classes 1/1, 1/2, 2/1, and 2/2, respectively (where  $i/j$  stands for formerly of type  $i$ , currently of type  $j$ ).

Matrix  $\mathbf{K}$ , applied after regulation, converts back classes 1/1 and 2/1 into type 1 patches, and types 1/2 and 2/2 into type 2 patches:

$$\mathbf{K} = \begin{pmatrix} 1 & 0 & 1 & 0 \\ 0 & 1 & 0 & 1 \end{pmatrix} \quad (11)$$

A simple consistency check ensures that

$$\mathbf{K} \cdot \mathbf{E}_4 \cdot \begin{pmatrix} \rho \\ 1 - \rho \end{pmatrix} = \begin{pmatrix} \rho \\ 1 - \rho \end{pmatrix} \quad (12)$$

In fact,  $\mathbf{K} \cdot \mathbf{E}_4 = \mathbf{E}$ .

The  $4 \times 4$  versions of matrices  $\mathbf{S}$  and  $\mathbf{D}$  are easily guessed from their  $2 \times 2$  versions:

$$\mathbf{S}_4 = \begin{pmatrix} g_1 & 0 & 0 & 0 \\ 0 & g_2 & 0 & 0 \\ 0 & 0 & g_1 & 0 \\ 0 & 0 & 0 & g_2 \end{pmatrix} \quad (13)$$

$$\mathbf{D}_4 = \begin{pmatrix} 1 - d_1 & 0 & 0 & 0 \\ 0 & 1 - d_2 & 0 & 0 \\ 0 & 0 & 1 - d_1 & 0 \\ 0 & 0 & 0 & 1 - d_2 \end{pmatrix} + (1 - \gamma) \begin{pmatrix} (1 - \mu)hd_1 & (1 - \mu)hd_2 & (1 - \mu)hd_1 & (1 - \mu)hd_2 \\ v(1 - h)d_1 & v(1 - h)d_2 & v(1 - h)d_1 & v(1 - h)d_2 \\ \mu hd_1 & \mu hd_2 & \mu hd_1 & \mu hd_2 \\ (1 - v)(1 - h)d_1 & (1 - v)(1 - h)d_2 & (1 - v)(1 - h)d_1 & (1 - v)(1 - h)d_2 \end{pmatrix} \quad (14)$$

where  $\gamma$  is defined in Eq. (5).

With this formalism, next generation matrices of life cycles 3 and 4 are given as  $\mathbf{G}_3 = \mathbf{K} \cdot \mathbf{R}_4 \cdot \mathbf{S}_4 \cdot \mathbf{E}_4 \cdot \mathbf{D}$  and  $\mathbf{G}_4 = \mathbf{K} \cdot \mathbf{R}_4 \cdot \mathbf{D}_4 \cdot \mathbf{E}_4 \cdot \mathbf{S}$ . The analog of Eq. (9) for complex life cycles is:

$$\begin{pmatrix} \rho(1 - \mu) \\ (1 - \rho)v \\ \rho\mu \\ (1 - \rho)(1 - v) \end{pmatrix} = \mathbf{R}_4 \cdot \mathbf{C} \cdot \begin{pmatrix} \rho \\ 1 - \rho \end{pmatrix} \quad (15)$$

where  $\mathbf{C} = \mathbf{S}_4 \cdot \mathbf{E}_4 \cdot \mathbf{D}$  for life cycle 3 and  $\mathbf{C} = \mathbf{D}_4 \cdot \mathbf{E}_4 \cdot \mathbf{S}$  for life cycle 4, evaluated with residents' trait values. Regulation factors obtained through Eq. (15) are given in Table 4. Next generation matrices for life cycles 3 and 4 are given in Table 3. For reasons similar to those enounced for life cycle 2, the separation of reproduction and

dispersal in the expression for  $\mathbf{G}_3$  means that dispersal and habitat selection are expected to be inevitably selected against with life cycle 3.

## 2.5. Mutant fitness and adaptive dynamics

In general, mutant fitness corresponds to the dominant eigenvalue of matrix  $\mathbf{G}$ . For the life cycles considered in this study (i.e. because all  $\mathbf{G}$  matrices are  $2 \times 2$ ), mutant fitness is simply:

$$W(\mathbf{G}) = \frac{\text{Tr}(\mathbf{G}) + \sqrt{\text{Tr}(\mathbf{G})^2 - 4 \det(\mathbf{G})}}{2} \quad (16)$$

In Eq. (16),  $\text{Tr}$  and  $\det$  refer to the trace and the determinant of a matrix, respectively.

To assess the evolutionary outcomes associated with a certain fitness function, I use the following tools (Hofbauer and Sigmund, 1990).

First, to assess whether a particular strategy is singular, I compute selection gradients for all traits that evolve. Selection gradients are the partial derivatives of  $W$  with respect to mutant allele trait value when the mutant trait equals the resident's. A singular strategy is a strategy for which all selection gradients vanish. Adaptive dynamics theory predicts that monomorphic evolutionary dynamics first follow the dynamics driven by the selection gradient until they either reach a singular strategy (SS) or a limit of trait values. When the latter event occurs (boundary SS), then selection is said to be directional with respect to the trait that has reached its limit.

A monomorphic evolution can only reach an interior SS if it is convergence stable. Convergence stability (CS) occurs when the matrix of derivatives of the selection gradient has eigenvalues

**Table 4**

Regulation factors computed for complex life cycles.

	Life cycle 3	Life cycle 4
$r_{11}^{-1}$	$g_1 \left[ 1 - d_1 + (1 - \gamma) \frac{h}{\rho} \bar{d} \right]$	$g_1(1 - d_1) + (1 - \gamma) \frac{h}{\rho} [\bar{g} \cdot \bar{d} + \rho(1 - \rho)\varphi(d_1 - d_2)(g_1 - g_2)]$
$r_{12}^{-1}$	$g_2 \left[ 1 - d_1 + (1 - \gamma) \frac{h}{\rho} \bar{d} \right]$	$g_1(1 - d_2) + (1 - \gamma) \frac{1 - h}{1 - \rho} [\bar{g} \cdot \bar{d} + \rho(1 - \rho)\varphi(d_1 - d_2)(g_1 - g_2)]$
$r_{21}^{-1}$	$g_1 \left[ 1 - d_2 + (1 - \gamma) \frac{1 - h}{1 - \rho} \bar{d} \right]$	$g_2(1 - d_1) + (1 - \gamma) \frac{h}{\rho} [\bar{g} \cdot \bar{d} + \rho(1 - \rho)\varphi(d_1 - d_2)(g_1 - g_2)]$
$r_{22}^{-1}$	$g_2 \left[ 1 - d_2 + (1 - \gamma) \frac{1 - h}{1 - \rho} \bar{d} \right]$	$g_2(1 - d_2) + (1 - \gamma) \frac{1 - h}{1 - \rho} [\bar{g} \cdot \bar{d} + \rho(1 - \rho)\varphi(d_1 - d_2)(g_1 - g_2)]$

with negative real parts. Otherwise, the SS is an evolutionary repeller.

When monomorphic evolution reaches a CS strategy, this strategy is the final evolutionary outcome only if it is also evolutionarily stable (ESS), *i.e.* if no mutant can invade a resident population consisting only of individuals from the ESS (a case of stabilizing selection). Evolutionary stability of an interior SS is assessed through computing the Hessian matrix of the fitness function with respect to all evolving traits that have not reached a boundary. When the Hessian matrix has all its eigenvalues with negative real parts, the SS is an ESS, otherwise it is an evolutionary branching point (a case of disruptive selection). A SS that is both CS and an ESS is a continuously stable strategy (CSS) (Eshel, 1983).

## 2.6. General results

Expressions obtained for next generation matrices (Table 3) allow us to make the following general statements:

- (i) under life cycles 2 and 3, dispersal and habitat selection always evolve so as to diminish the actual cost, *i.e.* dispersal is selected against, and so is habitat selection, if it is costly;
- (ii) when local adaptation is the only trait to evolve and dispersal is unconditional, life cycles 2 and 3 yield the same fitness, and so do life cycles 1 and 4; and
- (iii) when dispersal is the only trait to evolve, dispersal is unconditional, and there is no habitat selection, life cycles 2 and 3 share the same fitness function, and so do life cycles 1 and 4.

Statement (i) is straightforward because next generation matrices for life cycles 2 and 3 can be written as a product of matrices in which one matrix determines selection on dispersal and habitat selection and another matrix determines selection on local adaptation traits. Statement (ii) is also quite intuitive, and developed in more details in Section 3. Statement (iii), though less intuitive, stems from the fact that when dispersal is unconditional and when there is no habitat selection, environmental change and dispersal matrices commute.

## 3. Application: evolution of local adaptation

In this section, I will focus on the evolution of local adaptation only, and thus assume that habitat selection and dispersal are fixed traits.

Traits representing habitat specialization and local adaptation have already been thoroughly studied from a theoretical viewpoint (Billiard and Lenormand, 2005; Débarre and Gandon, 2010, 2011; Débarre and Lenormand, 2011; Egas et al., 2004; Kirkpatrick and Barton, 1997; Kisdí, 2002; Pease et al., 1989; Ravigné et al., 2004, 2009). Here, this modeling framework can help tackle the joint effects of life cycle event order, autocorrelation in patch state, convexity of the trade-off between adaptation to habitat 1 and

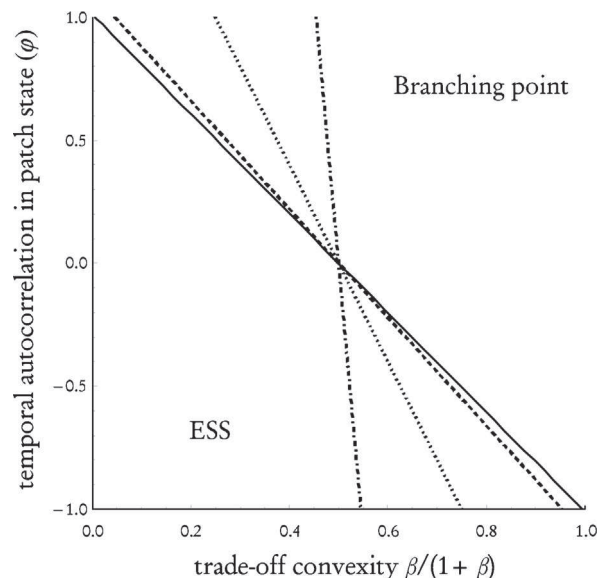
habitat 2 ( $\beta$  in Eq. (4)), and the unconditional dispersal rate ( $d = d_1 = d_2$ ). Because dispersal does not evolve, it is more convenient to use the immigration parameter  $I = (1 - c)d/(1 - d)$  as a means to characterize the intensity of migration.  $I$  varies between 0 (no dispersal or completely ruinous) and  $\infty$  (all offspring are dispersed). The quantity  $I/(1 + I)$  characterizes the proportion of surviving offspring that have actually emigrated.

First, I must note that unconditional dispersal and the absence of habitat selection simplify the problem of life cycles: life cycles 2 and 3 (Levene-type cycles) yield exactly the same fitness function, and life cycles 1 and 4 (Ravigné-type cycles) are equivalent. Second, studying the evolution of local adaptation in two habitats means that I am actually studying only one trait ( $s$  in Eq. (4)), and thus two convergence stable strategies, if they exist for the same parameter values, will be separated by an evolutionary repeller.

Because the formulation of the model is totally symmetrical with respect to local adaptation to habitat types, I will assume (when needed) that habitat type 1 is the rare habitat (*i.e.*  $\rho < 0.5$ ).

### 3.1. Levene-type life cycles

Under Levene-type life cycles, the selection gradient on  $s$  is tractable and reduces to  $\beta(\rho - s)/s(1 - s)$ . Thus, whatever the value of  $\beta$ ,  $\varphi$ ,  $I$  or  $\rho$ , there is always one convergence stable strategy  $s = \rho$ . The ESS condition at  $s = \rho$ , obtained using the second derivative of the fitness function with respect to the mutant trait, is (see also



**Fig. 2.** Evolution of local adaptation under life cycles 2 and 3: parameter values inducing ESS or branching points (respectively to the left/to the right of the line). Abscissa represents trade-off convexity,  $\beta/(1 + \beta)$ , while ordinates depict temporal autocorrelation in patch state,  $\varphi$ . Each line corresponds to a different value of parameter  $I$ :  $I = 0.01$  (solid line);  $I = 0.1$  (dashed line);  $I = 1$  (dotted line);  $I = 10$  (dash and dot line).



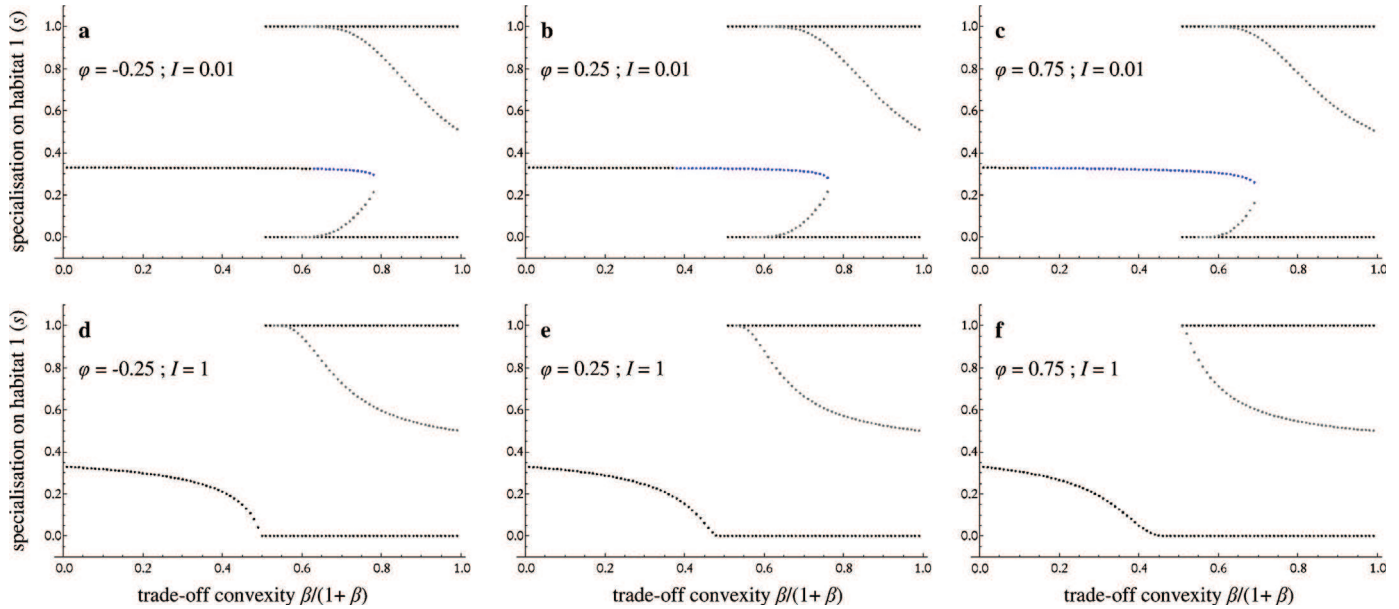
Débarre and Gandon, 2010 when variability is spatial only):

$$\beta < \beta_0 = \frac{1 - \varphi + I}{1 + \varphi + I} \quad (17)$$

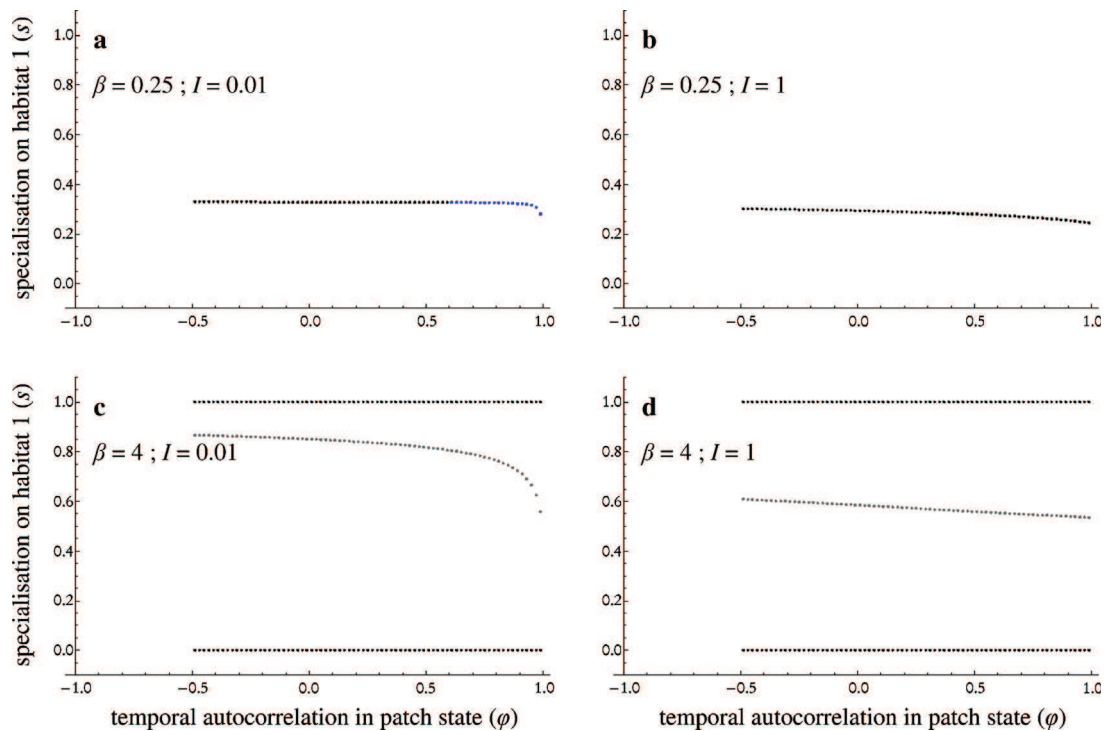
At low immigration, a weak trade-off and negative temporal autocorrelation in habitat type induce the existence of a unique generalist ESS, while a strong trade-off and positive temporal habitat autocorrelation favor the emergence of coexisting specialist strategies (Fig. 2). At high immigration, the question of

evolutionary stability approximately boils down to the classical  $\beta < 1$  (at high  $I$ ,  $\beta_0 \approx 1 - 2\varphi/I$ , i.e. the question of evolutionary stability becomes independent of temporal habitat autocorrelation (Fig. 2). This is because the mutant population tends to be submitted to an average environment at each generation, due to high migration.

The threshold value,  $\beta_0$ , equals 1 when dispersal is total (as predicted by models of local adaptation evolution under soft selection) or when patch type is random. The threshold value equals  $(1 - \varphi)/(1 + \varphi)$  when immigration vanishes – in the absence



**Fig. 3.** Evolution of local adaptation under life cycles 1 and 4: variation in singular specialization strategy (ordinates,  $s$ ) with convexity of the trade-off curve (abscissas,  $\beta/(1 + \beta)$ ). Black dots indicate ESS; blue dots indicate evolutionary branching points; and gray dots indicate evolutionary repellers. Parameters  $\varphi$  and  $I$  are indicated on panels. In all panels,  $\rho = 0.33$ .



**Fig. 4.** Evolution of local adaptation under life cycles 1 and 4: variation in singular specialization strategy (ordinates,  $s$ ) with temporal autocorrelation in patch state (abscissas,  $\varphi$ ). Black dots indicate ESS; blue dots indicate evolutionary branching points; gray dots indicate evolutionary repellers. Parameters  $\beta$  and  $I$  are indicated on panels. In all panels,  $\rho = 0.33$ . Note that this value of  $\rho$  implies  $\varphi > -0.5$ .

of migration, steadily alternating environments select for generalists while stable habitats allows the coexistence of two specialist types.

### 3.2. Ravigné-type life cycles

Under Ravigné-type life cycles, the number of CS strategies may vary from 1 to 3, and these strategies may be ESS or branching points. Boundary CS strategies are noted  $S_1$  ( $s = 1$ ) and  $S_2$  ( $s = 0$ ). If there is only one non-boundary CS strategy, it is noted G; if there are two, the one closest to  $s = 1$  is noted  $G_1$ , the other  $G_2$ . If a non-boundary CS strategy is a branching point, it is noted with an asterisk. For instance, an evolutionary outcome like “ $S_1G^*S_2$ ” would mean that there are three alternative CS strategies, two boundary ESS and one interior branching point. Sometimes, the difference between a  $G_1$  and a  $S_1$ , or a  $G_2$  and a  $S_2$ , is hardly perceptible because the CS is very close to the boundary. However, some analytical results (Appendix B) allow us to predict that only the nine following configurations are possible:

- when  $\beta < 1$ :  $G$ ,  $G^*$ ,  $G_1G_2$ ,  $G_1^*G_2$ ,  $G_1G_2^*$ ,  $G_1^*G_2^*$
- when  $\beta > 1$ :  $S_1S_2$ ,  $S_1GS_2$ ,  $S_1G^*S_2$

Configuration G occurs only for concave trade-offs ( $\beta < 1$ ). The value of the CSS is approximately equal to  $\rho$  at low immigration (Appendix B; Fig. 3). It decreases with increasing values of  $\beta$  (Fig. 3),  $\varphi$  (Fig. 4) and  $I$  (Fig. 5), and increases with  $\rho$  (Fig. 6). It occurs more likely when  $\varphi$  is low or even negative, and when  $I$  is large (Fig. 7).

Configuration  $G^*$  is the equivalent of the branching point under life cycles 2 and 3, i.e. it leads to the emergence of a stable polymorphism on  $s$ . It occurs only for concave trade-offs. The value of the branching point is approximately equal to  $\rho$  at low immigration (Appendix B; Fig. 3c). This configuration is favored when  $\varphi$  is high (i.e. in static environments) and when  $I$  is low (Fig. 7).

Configurations  $G_1G_2$ ,  $G_1^*G_2$ ,  $G_1G_2^*$  and  $G_1^*G_2^*$  are very “rare” in terms of parameter values necessary to obtain them. They occur mostly at intermediate  $I$  and very high  $\varphi$  (Fig. 7d and g).

Configuration  $G_1G_2$  is an extension of the configuration  $S_1S_2$  to the domain of concave trade-offs, and these two configurations are undistinguishable in practice. With  $\rho < 1/2$ , the most likely configurations among  $G_1^*G_2$ ,  $G_1G_2^*$  and  $G_1^*G_2^*$  is  $G_1^*G_2$ , depicted in green on Fig. 7g. With such a configuration, the evolutionary outcome is either evolutionary branching and coexistence of specialists of both type 1 and type 2 habitats or, with an initial  $s$  value sufficiently low, specialization on type 2 habitats only.

Configuration  $S_1S_2$  occurs only for convex trade-off ( $\beta > 1$ ). It is favored at high values of  $I$ ,  $\varphi$  and  $\beta$  (Fig. 7). Given the shape of the trade-off, one specialist ESS cannot exist without the other (Appendix B).

Configuration  $S_1GS_2$  represents a case of tri-ESS stability. It occurs only for convex trade-off, and is more likely when  $\beta$  is not very high,  $I$  is low and  $\varphi$  is negative (Fig. 7). The value of  $s$  at the G ESS follows the same dependences as in the G configuration, i.e. it decreases with  $\beta$ ,  $\varphi$  and  $I$ , and increases with  $\rho$  (Figs. 3–6).

Configuration  $S_1G^*S_2$  also represents a case of tristability, but one of the stable outcomes is actually an evolutionary branching point. This configuration occurs only with convex trade-offs, and is restricted to low immigration and high  $\varphi$  (Fig. 7).

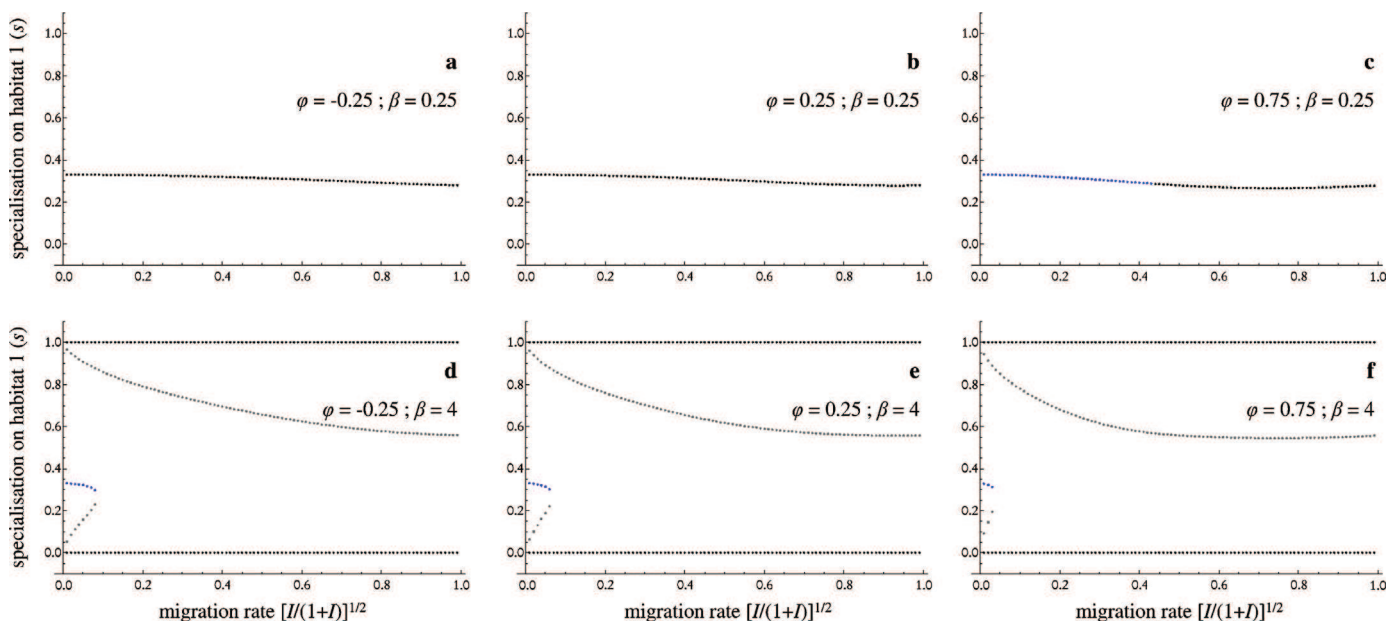
## 4. Discussion

### 4.1. Modeling framework and assumptions

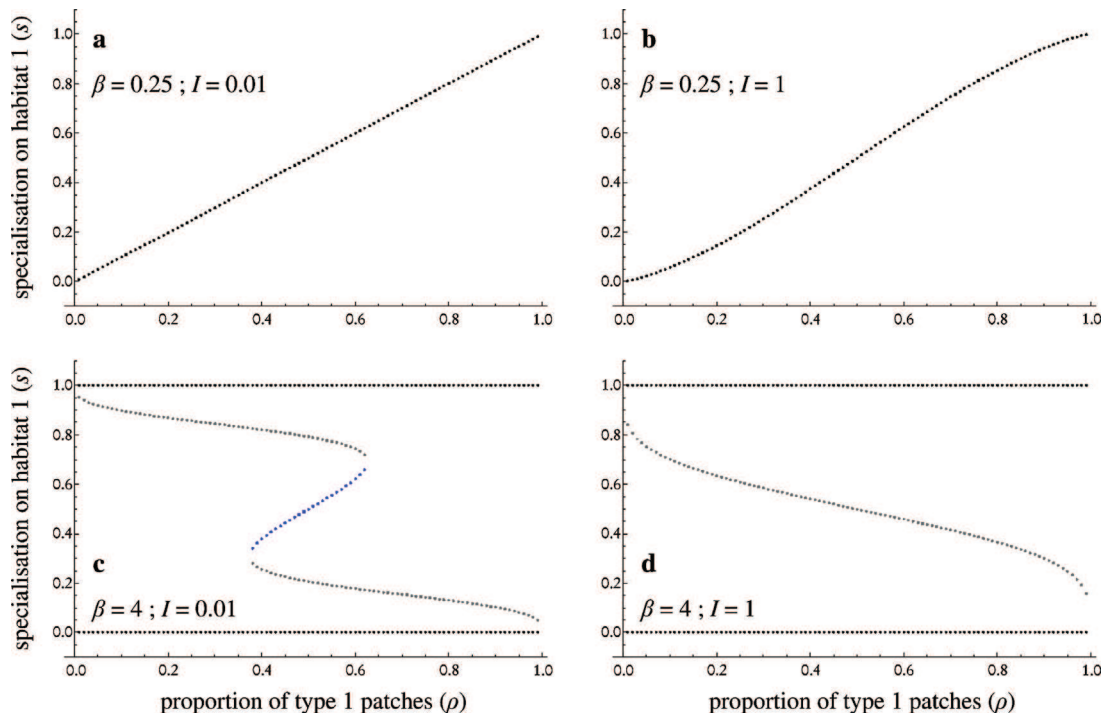
The modeling framework presented in this paper is based on a few key ingredients:

- generations are discrete, non-overlapping, and each generation has to go through a certain number of life cycle events;
- events always happen in the same order for a given life cycle;
- population sizes are large enough to neglect kin competition effects; and
- reproduction is clonal.

Based on assumptions (i) and (ii), it is possible to enumerate all possible life cycles (following Ravigné et al., 2004). Based on assumptions (iii) and (iv), it is possible to generate the fitness



**Fig. 5.** Evolution of local adaptation under life cycles 1 and 4; variation in singular specialization strategy (ordinates,  $s$ ) with migration rate (abscissas,  $[I/(1+I)]^{1/2}$ ). Black dots indicate ESS; blue dots indicate evolutionary branching points; and gray dots indicate evolutionary repellers. Parameters  $\varphi$  and  $\beta$  are indicated on panels. In all panels,  $\rho = 0.33$ .



**Fig. 6.** Evolution of local adaptation under life cycles 1 and 4: variation in singular specialization strategy (ordinates,  $s$ ) with the proportion of type 1 patches (abscissas,  $\rho$ ). Black dots indicate ESS; blue dots indicate evolutionary branching points; and gray dots indicate evolutionary repellers. Parameters  $I$  and  $\beta$  are indicated on panels. In all panels,  $\varphi = 0.25$ .

criteria corresponding to each life cycle in the enumeration. The present framework exploits the Markovian nature of environmental change and the fact that regulation is local to generate fitness functions. With a very general model, I am still able to obtain some general conclusions, e.g. based on the expression for next generation matrices (Table 3), it follows that life cycles 2 and 3 inevitably select for no dispersal and no habitat selection. The strength of this framework is that it is sufficiently simple and general to generate analytical predictions, without having to resort to massive simulations, and yet it can still generate quite complex patterns for evolutionary outcomes (see e.g. Fig. 7).

Assumption (i) could be somehow relaxed in the sense that non-overlapping generations are not a modeling necessity. With the same kind of expression for local fitness, Pen (2000) introduced adult survivorship in a model aimed at the evolution of dispersal. In the present framework, this complication would entail taking into account some age structure among individuals living in all types of patches, and thus at least double the size of the next generation matrix (if only the separation between adults and juveniles is relevant).

Relaxing assumption (ii) is quite a complex challenge. This would mean adding an element of stochasticity in the order of realization of life cycle events – for instance, the system could endure life cycle 1 for one generation and then life cycle 3 for the next generation. A potential approach could be to assign probabilities for the four basic life cycles, as if the chain of individual life cycles followed a Markov chain, and then to compute the resulting fitness as the dominant eigenvalue of the geometric average of all possible next generation matrices, weighted by the appropriate probabilities. Other possibilities include the study of complex life cycles in which the life cycle of the parents condition the choosing of the life cycle of their offspring.

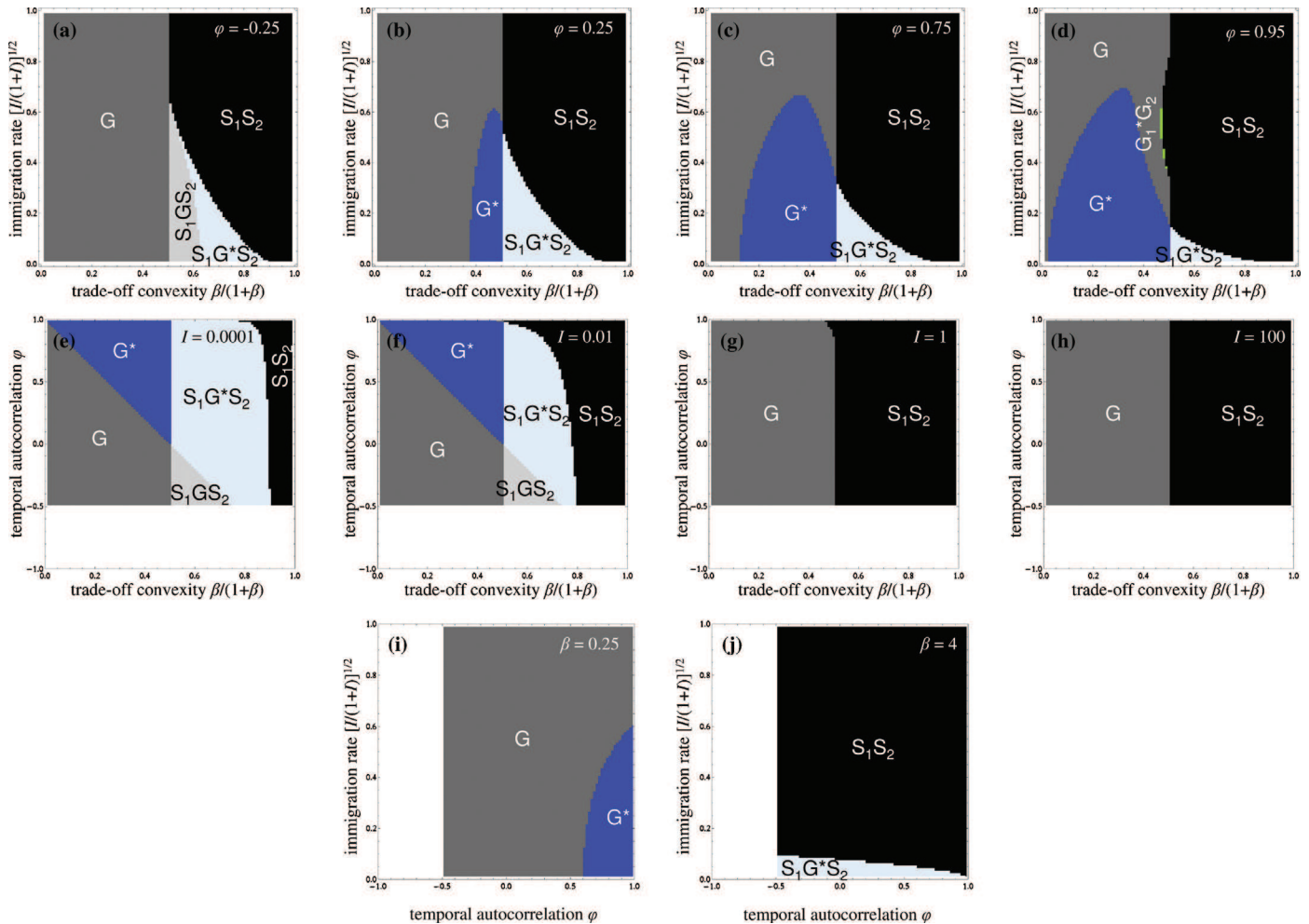
Another issue linked to assumption (ii) is the assumption of synchronicity of life cycle events among patches. If I would assume that only regulation events are synchronized among populations, it

would be possible to imagine that different patches could be submitted to different life cycles, especially if, e.g. the timing of environmental change would change among patches.

It is possible to conceive models where assumption (iii) is relaxed using the metapopulation fitness criterion in finite population systems (Ajar, 2003; Massol et al., 2009; Metz and Gyllenberg, 2001). The difficulty here is that existing computations for metapopulation fitness consider heterogeneous landscapes only, not temporally variable environments (Ajar, 2003; Massol et al., 2011). When the environment is both spatially and temporally variable, the expressions for matrices needed to describe the dynamics of proportions of patches containing  $n$  mutants become increasingly complex, and quite often intractable. Relaxing assumption (iv), i.e. tackling the evolution of traits in diploid organisms undergoing meiosis before reproduction, is also likely to complicate the expression of next generation matrices, though this issue has been recently theorized and explored (Metz and Leimar, 2011; Parvinen and Metz, 2008).

#### 4.2. The importance of life cycles

It has been already recommended by Ravigné et al. (2004, 2009) that paying attention to life cycles is important to assess the robustness of theoretical predictions on the evolution of traits. Here, I have shown that such differences among predictions can emerge in the context of spatio-temporal variability in environmental conditions among patches. Since the distinction between soft and hard selection models actually boils down to a difference in the timing of regulation in the life cycle (Ravigné et al., 2004), population geneticists are now well aware of this issue. However, models based on phenotypic descriptions, such as adaptive dynamics models, may not be so careful. For instance, it is often difficult to ascertain the precise order of events in life cycles in models dealing with the evolution of dispersal (McNamara and Dall, 2011).



**Fig. 7.** Evolution of local adaptation under life cycles 1 and 4: region plots depicting the occurrence of evolutionary scenarios along (a–d) the relative immigration rate (ordinates,  $I$ , scaled to relative units as  $\sqrt{I/(1+I)}$ ) and convexity of the trade-off curve (abscissas,  $\beta$ , scaled to relative units as  $\beta/(1+\beta)$ ) plane; (e–h) the temporal autocorrelation in patch state (ordinates,  $\varphi$ ) and convexity of the trade-off curve (abscissas,  $\beta$ , scaled to relative units as  $\beta/(1+\beta)$ ) plane; and (i and j) the relative immigration rate (ordinates,  $I$ , scaled to relative units as  $\sqrt{I/(1+I)}$ ) and the temporal autocorrelation in patch state (abscissas,  $\varphi$ ) plane. Parameter values: (a)  $\varphi = -0.25$ , (b)  $\varphi = 0.25$ , (c)  $\varphi = 0.75$ , (d)  $\varphi = 0.95$ , (e)  $I = 0.0001$ , (f)  $I = 0.01$ , (g)  $I = 1$ , (h)  $I = 100$ , (i)  $\beta = 0.25$ , and (j)  $\beta = 4$ . Other parameters:  $\rho = 0.33$ .

The example given by the evolution of local adaptation reveals some striking differences between predictions stemming from different life cycles. Most importantly, disruptive selection (branching points) occurs in a relatively “categorical” way under life cycles 2 and 3 (i.e. a simple criterion linking the trade-off convexity to  $\varphi$  and  $I$  actually predicts the nature of selection; Fig. 2), whereas life cycles 1 and 4 can generate wildly different evolutionary outcomes for very little differences in parameter values (e.g. Fig. 3). While  $\varphi$  and  $I$  are “equally” important in the criterion for evolutionary stability in life cycles 2 and 3, given by inequality (17),  $I$  seems to be much more important in determining evolutionary stability under life cycles 1 and 4 (Figs. 4, 5 and 7). In other words, parameter dependence of selection regimes actually depends on the life cycle.

#### 4.3. Evolution of local adaptation

The application of the framework to the evolution of local adaptation is a direct extension of the results given by Ravigné et al. (2004) and Débarre and Gandon (2011) to a system where dispersal can occur only once per life cycle and the environment does change between generations. Like Débarre and Gandon (2011), I find that immigration rate directly affects the evolutionary stability of convergence stable strategies and can provoke the

emergence of bi- or tristability. Like Ravigné et al. (2004), I find that differences in the order of events has a very strong effect on the predictions of the model.

As far as disruptive selection is concerned, I have found that this is more plausible at low immigration when the trade-off is convex, and more plausible at high autocorrelation in patch state when the trade-off is concave. Biologically, this means that I predict diversification in local adaptation strategies when (i) generalists are disadvantaged and migration is weak or (ii) generalists have an advantage (over a simple, linear model) and the environment is highly static. These two situations of disruptive selection represent two opposite scenarios. In case (i), it is simply the absence of mixing among populations that cause a clear spatial segregation between the two type of specialists and, hence, help them emerge and coexist at a large scale. In case (ii), generalists should have the upper hand and, thus, dominate the system, but disruptive selection takes place because the static nature of the environment creates two different kinds of habitats. Even though specialists can land in the “bad” type of habitat through migration, the existence of two static habitats allows the emergence and coexistence of two kinds of specialists because fitness differences between specialists and generalists increase with time in both habitats, and thus select against the generalist strategy (Levins, 1968).



In Massol and Cheptou (2011), it was suggested that autocorrelation in patch state only affected the emergence and evolution of specialist, dispersing strategies. However, the results presented here are not directly comparable with these predictions for two reasons: (i) here, I only looked at the evolution of local adaptation, not the evolution of dispersal; (ii) the trade-off imposed by Massol and Cheptou (2011) was linear, *i.e.* represents a critical situation in current model.

The model investigated here makes use of only two patch types. However, a more complex version with three or more types could also be of interest. No hard clue exists on what such a model would predict, but published models on the evolution of local adaptation (*e.g.* Egas *et al.*, 2004) and basic intuitions on the meaning of ecological niches would suggest that the more patch types there are, the more specialist strategies can emerge if branching happens. With three or more patch types, temporal correlation structures will involve more than just one autocorrelation parameter, and may be complex enough to mimic regular ecological succession, *e.g.* if changes from type 1 to 2, from type 2 to 3 and from type 3 to 1 are more likely than all other possible changes. Adaptation to certain patch types might also become “correlated” if the matrix describing environmental change contains strongly interacting “modules” *e.g.* if changes between patch types 1 and 2 happen very often, and so do changes between types 3 and 4, but changes between 1/2 and 3/4 almost never happen.

Overall, the results presented here show that depending on the life cycle (Levene-type vs. Ravigné-type), conditions favoring the existence of a stable polymorphism of local adaptation traits may differ: while conditions favoring polymorphisms under Levene-type cycles are fairly large, Ravigné-type cycles only promote polymorphisms under a subset of these conditions (compare Fig. 2 and Fig. 7, see also de Meeus *et al.*, 1993). While Levene-type cycles only lead to ESS or branching points, Ravigné-type cycles may lead to bi- or tristability (*i.e.* alternative stable states) and thus to a dependence between evolutionary outcomes and initial resident trait value (see also Débarre and Gandon, 2011).

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## Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.ecocom.2012.05.004>.

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## Appendix A: cost of habitat selection

Here, I justify the relation between realized and basic costs of dispersal, and habitat selection:

$$\gamma(h) = \frac{c}{c + (1-c) \min[\rho/h, (1-\rho)/(1-h)]} \quad (\text{A1})$$

I consider that, once dispersed, a propagule is submitted to a rapid cycle of events that occur with a certain probability:

1. the propagule has a probability  $m$  to die before reaching a patch;
2. if it survives, the propagule reaches a patch of type 1 with probability  $\rho$ , or type 2 with probability  $1-\rho$ ;
3. with probability  $a_i$ , the propagule accepts the patch of type  $i$  it is in and stays. With probability  $1-a_i$ , it returns to the propagule pool and begins anew at stage 1.

This rapid cycle happens until all propagules are either dead or assigned to a patch. After one cycle, a fraction  $\gamma_1 = m$  died, a fraction  $k_1 = (1-m)\rho a_1$  settled in type 1 patches, a fraction  $j_1 = (1-m)(1-\rho)a_2$  settled in type 2 patches, and the remaining fraction  $(1-m)(1-\bar{a})$  gets to the new cycle (with  $\bar{a} = \rho a_1 + (1-\rho)a_2$ ). After  $t$  cycles, these quantities become:  $\gamma_t = m(1-m)^{t-1}(1-\bar{a})^{t-1}$ ,  $k_t = \rho a_1(1-m)^t(1-\bar{a})^{t-1}$  and  $j_t = (1-\rho)a_2(1-m)^t(1-\bar{a})^{t-1}$ .

Simple calculations yield the fraction  $\gamma$  of propagules that died during dispersal and the fractions  $k$  and  $1-k$  of propagules that survived and settled in patches of type 1 and 2 respectively:

$$\gamma = \sum_{t=1}^{\infty} \gamma_t = \frac{m}{1-(1-m)(1-\bar{a})} \quad (\text{A2})$$

$$k = \sum_{t=1}^{\infty} k_t = \frac{\rho a_1(1-m)}{1-(1-m)(1-\bar{a})} \quad (\text{A3})$$

$$1-k = \frac{(1-\rho)a_2(1-m)}{1-(1-m)(1-\bar{a})} \quad (\text{A4})$$

Now, I observe that  $(1-\gamma)h = k$ , so that:

$$h = \frac{\rho a_1}{\bar{a}} \quad (\text{A5})$$

As  $c$  represents the cost of dispersal in the absence of habitat selection, *i.e.* when acceptance rates are both equal to 1, this entails (cf. equation [A2]) that  $m = c$ .

Finally, I observe that  $\gamma$  decreases with  $\bar{a}$ , and that  $h$  and  $1-h$  remains the same if acceptance rates are both divided by the same quantity (say  $\alpha$ ) while  $\bar{a}$  is divided by  $\alpha$  and thus  $\gamma$  increases as predicted by equation (A2). In order to optimize acceptance rates for a given  $h$ , one of the two acceptance rates must be equal to 1. If  $a_1 = 1$ , then (equation [A5])  $\bar{a} = \rho/h$  and necessarily  $(1-\rho)a_2 = \bar{a} - \rho = \rho(1-h)/h$ , so that  $(1-\rho)/(1-h) > \rho/h$ . Conversely, if  $a_2 = 1$ ,  $\bar{a} = (1-\rho)/(1-h) = \min[\rho/h, (1-\rho)/(1-h)]$ . Plugging these relations into equation (A2), I obtain equation (A1).  $\square$

## Appendix B: analytical results on the evolution of local adaptation under Ravigné-type life cycles

Here, I give several analytical results obtained for life cycles 1 and 4 on the evolution of local adaptation.

### Selection gradient, CS and ESS criteria for interior SS

The expression for the selection gradient can be given using  $x = s / (1 - s)$  and  $y = \rho / (1 - \rho)$ :

$$\left. \frac{\partial W}{\partial x'} \right|_{x'=x} = \frac{\beta}{s} \frac{Iy[1+y(1+I)]x^{2\beta} - I(1+I+y)x + [yI^2(1-x) + (y-x)(1+I)(1+y)(1-\phi)]x^\beta}{Iy[1+y(1+I)]x^{2\beta} + I(1+I+y) + [2I^2y + (1+I)(1+y)^2(1-\phi)]x^\beta} \quad (B1)$$

Interior singular strategies (*i.e.* those that make the right-hand side of equation [B1] vanish) are CS when:

$$\frac{\beta(y-x)[(1+I+y)x + (1+y+Iy)yx^{2\beta}]}{xy(1-x^\beta)[1+I+y+(1+y+Iy)x^\beta]} < 1 \quad (B2)$$

Interior SS are ESS when:

$$\beta[(1-x)y - 2x] - (1+x)y + \frac{2\beta(1+y)x^\beta(y-x)(1+y+I[1+y+I+(1+y+Iy)x^\beta])}{I(1-x^\beta)[1+y+I+(1+y+Iy)x^\beta]} < 0 \quad (B3)$$

### Selection gradient at the boundaries

At the boundaries for  $s$ , the selection gradient takes the following values:

- when  $\beta > 1$ :

$$\left. \frac{\partial W}{\partial s'} \right|_{s'=s=0} = -\beta \text{ and } \left. \frac{\partial W}{\partial s'} \right|_{s'=s=1} = \beta \quad (B4)$$

- when  $\beta < 1$ :

$$\left. \frac{\partial W}{\partial s'} \right|_{s'=s=0} \rightarrow +\infty \text{ and } \left. \frac{\partial W}{\partial s'} \right|_{s'=s=1} \rightarrow -\infty \quad (B5)$$

- when  $\beta = 1$ :

$$\left. \frac{\partial W}{\partial s'} \right|_{s'=s=0} = \frac{\rho[(1+I)(1-\phi) + (1-\rho)I^2]}{[1+(1-\rho)I](1-\rho)I} - 1 \text{ and } \left. \frac{\partial W}{\partial s'} \right|_{s'=s=1} = 1 - \frac{(1-\rho)[(1+I)(1-\phi) + \rho I^2]}{(1+\rho I)\rho I} \quad (B6)$$

### Low immigration approximations

When  $I = 0$ , the selection gradient is indistinguishable from the one obtained under life cycles 2 and 3:

$$\left. \frac{\partial W}{\partial s'} \right|_{s'=s} = \frac{\beta(\rho - s)}{s(1-s)} \quad (B7)$$

The CS strategy  $s = \rho$  is then an ESS when  $\beta < (1-\phi)/(1+\phi)$ , or else it is a branching point.

When  $I \approx 0$ , first-order Taylor series for the selection gradient yields:

$$\left. \frac{\partial W}{\partial s'} \right|_{s'=s} \approx \frac{\beta}{s} \left\{ \frac{\rho - s}{1-s} + \frac{\rho(1-\rho)[s^{2\beta} - (1-s)^{2\beta}]}{(1-\phi)s^\beta(1-s)^\beta} I + o(I) \right\} \quad (B8)$$

The selection gradient thus vanishes for the following singular strategy:

$$s \approx \rho + \frac{\rho^{1-\beta} (1-\rho)^{1-\beta} [\rho^{2\beta} - (1-\rho)^{2\beta}]}{1-\varphi} I + o(I) \quad (\text{B9})$$

The CS criterion for this SS is:

$$\frac{I \left\{ \beta [\rho^{2\beta} + (1-\rho)^{2\beta}] - (1-2\rho) [(1-\rho)^{2\beta} - \rho^{2\beta}] \right\}}{\rho^\beta (1-\rho)^\beta (1-\varphi)} + o(I) < 1 \quad (\text{B10})$$

The ESS criterion for this SS is:

$$\begin{aligned} & 1 - \frac{\beta}{1-\varphi} \left\{ 1 + \varphi + I \left[ 1 - \frac{(1-2\rho) [(1-\rho)^\beta - \rho^\beta]}{\rho^\beta + (1-\rho)^\beta} \right] \right\} \\ & + \frac{I}{1-\varphi} \left( 1 - \frac{2\beta}{1-\varphi} \right) \frac{\left\{ (1-2\rho) [(1-\rho)^{2\beta} - \rho^{2\beta}] - \beta (\rho^{2\beta} + (1-\rho)^{2\beta}) \right\}}{(1-\rho)^\beta \rho^\beta} + o(I) > 0 \end{aligned} \quad (\text{B11})$$

## High immigration approximations

When  $I \rightarrow \infty$

$$\left. \frac{\partial W}{\partial s'} \right|_{s'=s} \approx \frac{\beta}{s} \left[ 1 - \frac{1}{(1-s) \left[ 1 + \frac{\rho}{1-\rho} \left( \frac{s}{1-s} \right)^\beta \right]} \right] - \frac{\beta(1-\rho)\rho\varphi(1-s)^{\beta-1} s^{\beta-1} [(1-s)^\beta - s^\beta]}{I [\rho s^\beta + (1-\rho)(1-s)^\beta]^3} + o\left(\frac{1}{I}\right) \quad (\text{B12})$$

The selection gradient thus vanishes for the following singular strategy:

$$s = s_0 \left( \frac{1}{I} \right) = \frac{(1-\rho)^{\frac{1}{\beta-1}}}{\rho^{\frac{1}{\beta-1}} + (1-\rho)^{\frac{1}{\beta-1}}} \left\{ 1 + \frac{\varphi(1-\rho)^{\frac{1}{\beta-1}} \rho^{\frac{2}{\beta-1}} [(1-\rho)^{\frac{\beta}{\beta-1}} - \rho^{\frac{\beta}{\beta-1}}]}{(\beta-1)I [\rho^{\frac{1}{\beta-1}} + (1-\rho)^{\frac{1}{\beta-1}}]^2} \right\} + o\left(\frac{1}{I}\right) \quad (\text{B13})$$

i.e.  $x \approx y^{-1/(\beta-1)}$  using notations from equation (B1).

The CS criterion at this SS is:

$$y^{-\frac{1}{\beta-1}} \left( 1 + y^{\frac{1}{\beta-1}} \right)^2 (\beta-1) + \frac{(1+y) \left[ (1+y)(1+\beta) - y^{\frac{1}{\beta-1}} - y^{\frac{\beta}{\beta-1}} \right] \varphi}{Iy} + o\left(\frac{1}{I}\right) < 0 \quad (\text{B14})$$

The ESS criterion at this SS is:

$$\left( 1 + y^{\frac{1}{\beta-1}} \right)^2 \left( \beta-1 - \frac{(1+y)^2 \varphi}{Iy} \right) - \frac{(1+y) \varphi \left[ 1 - y^{\frac{2}{\beta-1}} - (1+y) \left( 1 + (2\beta+3)y^{\frac{1}{\beta-1}} \right) \right]}{Iy} + o\left(\frac{1}{I}\right) < 0 \quad (\text{B15})$$

When  $I$  is effectively infinite (order 0 in  $1/I$  in above equations),  $s_0$  is a CSS for  $\beta < 1$  and a repeller for  $\beta > 1$ . When  $\beta < 1$  and  $\rho < 1/2$ ,  $s_0(0) < \rho$ . When  $\beta > 1$  and  $\rho < 1/2$ ,  $s_0(0) > 1/2$ .



**Selection gradient at  $s = 1/2$** 

The selection gradient at  $s = 1/2$  is:

$$\left. \frac{\partial W}{\partial s'} \right|_{s'=s=1/2} = 2\beta(2\rho - 1) \quad (\text{B16})$$

Together with equation (B5), in the case  $\rho < 1/2$ , this shows that when  $\beta < 1$ , there is a CS strategy between 0 and  $1/2$ . With equations (B4) and (B16), it can also be shown that  $\rho < 1/2$  and  $\beta > 1$  imply the existence of an evolutionary repeller between  $1/2$  and 1.

**Selection gradient at  $s = s_0(0)$** 

At  $s = s_0(0)$  (as defined by equation [B11]), the selection gradient has the sign of:

$$\left. \frac{\partial W}{\partial s'} \right|_{s'=s=s_0} \propto (1 - y^{\beta/(1-\beta)}) [1 - (1+I)\varphi] \quad (\text{B17})$$

using notations from equation (B1). Hence, when  $\rho < 1/2$ , the selection gradient is positive at  $s = s_0(0)$  only when one of the following two conditions is met:

$$(i) \quad \varphi < 1/(1+I) \text{ and } \beta < 1 \quad (\text{B18})$$

$$(ii) \quad \varphi > 1/(1+I) \text{ and } \beta > 1 \quad (\text{B19})$$





## Review

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# An empiricist's guide to theoretical predictions on the evolution of dispersal

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Dispersal, the tendency for organisms to reproduce away from their parents, influences many evolutionary and ecological processes, from speciation and extinction events, to the coexistence of genotypes within species or biological invasions. Understanding how dispersal evolves is crucial to predict how global changes might affect species persistence and geographical distribution. The factors driving the evolution of dispersal have been well characterized from a theoretical standpoint, and predictions have been made about their respective influence on, for example, dispersal polymorphism or the emergence of dispersal syndromes. However, the experimental tests of some theories remain scarce partly because a synthetic view of theoretical advances is still lacking. Here, we review the different ingredients of models of dispersal evolution, from selective pressures and types of predictions, through mathematical and ecological assumptions, to the methods used to obtain predictions. We provide perspectives as to which predictions are easiest to test, how theories could be better exploited to provide testable predictions, what theoretical developments are needed to tackle this topic, and we place the question of the evolution of dispersal within the larger interdisciplinary framework of eco-evolutionary dynamics.

## 1. Introduction

Understanding why organisms from all species have a tendency to disperse away from their parents is a key question in evolutionary ecology [1–5]. From a fundamental perspective, dispersal propensity is intertwined with speciation and species extinction in a complex fashion [6]. On the one hand, dispersal may help species escape local catastrophes [7]; on the other hand, dispersal of common species may endanger rarer ones by 'stepping over' their geographical distributions, and limited dispersal favours divergence among allopatric populations. From a more applied viewpoint, understanding why certain species or genotypes disperse more than others might help to understand shifts in species distributions because of global change [8], to understand constraints on the adaptation of species to changing environmental conditions [9], to plan conservation strategies for threatened species or communities [10,11] and to design strategies for the management of invasive species [12] that build upon our knowledge of their evolutionary histories.

*Dispersal*, i.e. the tendency for an organism to reproduce away from its birth-place [3] (see glossary for definitions of words in italics), has been the subject of many theoretical studies, because (i) both population geneticists and ecologists have had hypothetical answers to the question of why organisms disperse and (ii) this topic has been linked to other important discoveries and theories in both fields of research. Historically, theoreticians have tried to understand why species disperse at all [13–15]; research questions have then focused on predicting (i) the proportion of dispersed offspring or (ii) the distribution of dispersal distances. Theoretical population geneticists have long been interested in the evolution of dispersal, because it is a good example of the effect of *kin competition* [13,16], and because inter-population *migration* tends to coevolve with inbreeding and recombination [17–20]. Ecologists have also proposed arguments on the evolution of dispersal based on emergent theories in ecology.

For example, perturbations have been proposed to be selective pressures acting on dispersal [7,21]. Another example is the link between the evolution of dispersal, source–sink dynamics and the ideal free distribution of organisms [14,22,23]: indeed, dispersal re-distributes individuals among patches with different growth rates.

Empirical studies on the evolution of dispersal have always lagged behind theoretical ones [5,24]. Several reasons account for this: (i) dispersal is rarely defined in an unequivocal fashion—and while this poses no problem for a self-contained theory, it impedes dialogue between theory and empirics; (ii) direct measures of dispersal, when they are possible, are difficult at best; (iii) proxies or indirect measures of dispersal—which are less costly—have received far less theoretical treatment than dispersal *per se*, and hence are prone to fewer empirical tests of any theory; (iv) experimental evolution studies can be lengthy and can only be applied to a restricted range of taxa; and (v) field data bring only information about correlation, not causation. As a result, empirical refutations of theories on the evolution of dispersal are scarce, despite the need to understand how and why differences in dispersal rates arise, e.g. to predict the potential invasiveness of a given species or genotype [25–27].

As theoretical approaches to the evolution of dispersal have considerably widened their scope, methods and assumptions, it is now time to lay out their various predictions and the assumptions they are based upon. Here, we review the different aspects of theories on the evolution of dispersal and propose a synthetic outlook on fruitful theoretical approaches that could lead to more easily testable predictions.

## 2. Selective pressures

After five decades of theoretical models, consensus among evolutionary ecologists has it that the evolution of dispersal has multiple causes [5,28–30]. This occurs because dispersal serves different functions: (i) spreading risk among offspring, through increasing variance in expected fitness among offspring; (ii) reducing competition or mating with relatives; and (iii) escaping locally bad conditions, such as crowded patches [30]. Selective pressures tending to increase dispersal thus include (i) spatio-temporal variation in local conditions, (ii) kin competition and inbreeding depression; and (iii) characteristics of population dynamics. Dispersal is, however, costly and its costs tend to reduce the propensity to disperse.

### 2.1. Dispersal costs

Dispersal may incur costs of different natures [31]. First, dispersal incurs an energetic cost. In animals, there is both a metabolic cost to move to a new place, and a cost to produce and maintain dispersal structures (muscles, wings, etc.). In contrast to animals, in plants the energetic cost of producing dispersal structures (fleshy fruits, pappus, samara, etc.) is borne by the mother. Second, dispersing takes time: this time is not used to feed or to mate. Third, dispersal may be risky: dispersed individuals may suffer predation. Last, dispersing means leaving a patch where reproduction was possible, to an unknown place where conditions may be worse. Dispersal costs may also arise due to imprecision of cues on patch quality in temporally variable environments [32] or be linked to the process of gaining information [33]. The propensity of organisms to disperse usually decreases

as dispersal becomes more costly [31], but this link is rarely linear [13,34]. Some models have investigated the role of distance-dependent costs [35], or of asymmetric dispersal costs [36], on the evolution of dispersal strategies.

### 2.2. Temporal variability of the environment

Variability in environmental characteristics is predicted to select for dispersal. In particular, random, extremely severe variations (i.e. catastrophic perturbations) select for dispersal as a means to evade large-scale extinction [7,21]. The frequency [37], magnitude [34], variability in magnitude [38], spatial correlation [39] and predictability [32,34,40] of environmental changes all have a say on the strength of this selective pressure. By contrast, perturbations aimed at habitats, rather than at populations, are expected to select against dispersal [41,42].

### 2.3. Spatial heterogeneity

When carrying capacities differ among patches, mean-field theory predicts that dispersal is disfavoured, because migrants will on average go from large patches with high associated fitness to smaller patches with lower fitness [14,22]. However, this prediction does not hold when demographic stochasticity, drift or other means of environmental heterogeneity are taken into account [38,41,43,44], mostly because lowering carrying capacity also means increasing kin competition, thus selecting for dispersal [41,43]. Spatial heterogeneity in population extinction rates also favours polymorphisms of dispersal rates [44].

### 2.4. Kin competition

When patch sizes are finite, a proportion of offspring are expected to disperse, even when dispersal costs are high, to avoid competing with local relatives [13]. The kin competition argument has been refined through focusing on spatial heterogeneity [43], conditional dispersal [45], overlapping generations [46], ploidy [47] or on maternal versus offspring control of dispersal [47,48].

### 2.5. Inbreeding depression and genetic incompatibilities

For sexual species, staying home means being likely to mate with relatives, which may incur a cost: inbreeding depression. Selection for dispersal depends on the balance between the costs of dispersal and of inbreeding depression [19,20,49,50]. When the cost of dispersal differs among sexes, this tendency to avoid inbreeding leads to the emergence of sexual dimorphisms in dispersal [18].

### 2.6. Demographic dynamics

The interplay between demographic dynamics and the evolution of dispersal has mostly been addressed through simulations. Non-equilibrium *metapopulation* dynamics select for some level of dispersal, possibly with various coexisting strategies [51], even when corresponding stable models predict zero dispersal [14]. This is because chaotic population dynamics generate spatio-temporal variability in population densities, which favour dispersal [15]. In turn, the evolution of dispersal sometimes tends to stabilize otherwise complex population dynamics [52] (but see [51]). Complex, non-equilibrium population dynamics can also select for

condition-dependent dispersal (e.g. in predators responding to spatio-temporal variability in prey availability [53]). Stochasticity in population dynamics affects dispersal evolution in ways similar to non-equilibrium dynamics, i.e. generally selects for dispersal [54] and can drive the evolution of density-dependent dispersal [55,56].

## 2.7. Life cycles and the timing of dispersal

In *semelparous* species (reproducing once in their lifetime), dispersal is most often assumed to occur at birth or during the juvenile stage. Both *iteroparity* and overlapping generations lead to increased level of dispersal, because they increase local relatedness, hence kin competition and potential inbreeding [46,57]. The timing of dispersal—whether occurring at juvenile or adult stage—also leads to different selective regimes for the evolution of local adaptation [58,59], and, hence, to different predictions on the evolution of dispersal in spatio-temporally variable environments [60,61].

## 2.8. Reproductive system

Mating systems may promote or impede the maintenance of dispersal polymorphisms: assortative mating tends to impede their emergence [62], yet the evolution of assortative mating in turn depends on the degree of spatial structuring among populations, hence on dispersal [63]. More generally, reproductive system and dispersal tend to coevolve, because they feedback on one another, and share selective pressures [63–65]. While different variances in reproductive success between sexes does not select for sex-biased dispersal, among-site variance in reproductive success does. Thus, mating system has a strong influence on the evolution of sex-biased dispersal [66].

# 3. Assumptions and predictions

One of the difficulties of interpreting theoretical models on dispersal evolution lies with understanding assumptions made and predictions given. Here, we review the main assumptions and predictions as they are tackled in theoretical models.

## 3.1. What dispersal?

Here, we review the various characteristics defining the dispersal trait in theoretical studies. These different axes mainly refer to (i) the recurrence of dispersal; (ii) the ploidy of the dispersed life stage; (iii) the representation of dispersal; and (iv) the viewpoint on dispersal; (v) the genetic architecture (or lack thereof) underlying dispersal; and (vi) the plasticity of dispersal.

### 3.1.1. The recurrence of dispersal

Dispersal is defined by gene flow among populations [5], thus the temporal scale of dispersal is intrinsically linked to the recurrence of reproductive events within an organism's lifetime—as opposed to non-dispersal movements. In mobile and iteroparous organisms, dispersal can occur between birth and the first reproduction, but can also occur between two successive reproductions: natal dispersal may differ from breeding dispersal.

### 3.1.2. Propagule dispersal versus gamete dispersal

In most sessile organisms, both gametes and propagules disperse away (e.g. pollen and seeds in angiosperms). Thus, dispersal might be coined for both gamete and propagule

dispersal. However, because of their different ploidy, gamete and propagule dispersal differ in sensitivity with respect to relatedness-based selective pressures (kin competition and inbreeding avoidance; [67]).

### 3.1.3. Representation of dispersal

One of the most divisive aspects of the literature on the evolution of dispersal is about whether dispersal refers to the propensity for individuals to disperse, or to parent–offspring distance. On the one hand, classic patch models focus on the propensity to disperse at a global scale (i.e. to any other patch). More sophisticated patch models can have non-global dispersal, e.g. when modelling metapopulations on graphs [68,69]. On the other hand, continuous space models characterize the distribution of dispersal distances by the statistical moments of the dispersal kernel. Continuous space representations may have trouble characterizing multiple-modes dispersal kernels based just on a few statistical moments. Dispersal propensity, although not an explicit variable, can emerge from the distributions of evolutionarily stable dispersal distances in explicit space models (e.g. [35]). Sometimes, dispersal distances and dispersal rates are explicitly modelled jointly [70].

Predictions of dispersal propensity and distance generally agree in the intuitive way, i.e. both are predicted to increase under the same conditions (e.g. compare [41] with [42]). For instance, kin competition can be thought of as increasing the propensity to disperse [13], or as increasing the average dispersal distance [71]. The only well-documented reason for a disagreement between these two measures of dispersal can be observed along a gradient of spatial autocorrelation of habitat quality [72].

While the spatial scale at which individuals disperse is meaningless in the absence of a comparative scale (figure 1), dispersal propensity—although a rough measure of dispersal—is a non-dimensional measure of dispersal, not prone to scale-related misinterpretations. In patch models, the different ecological processes (competition for resources, environmental perturbations, etc.) are assumed to be homogeneous at the scale of the patch. Dispersal propensity thus corresponds to the propensity for an individual to disperse further than the typical distance at which all of these processes can be considered homogeneous. Dispersal distance thus needs to be compared to the spatial scale of perturbation, competition and other metapopulation processes [74] (figure 1).

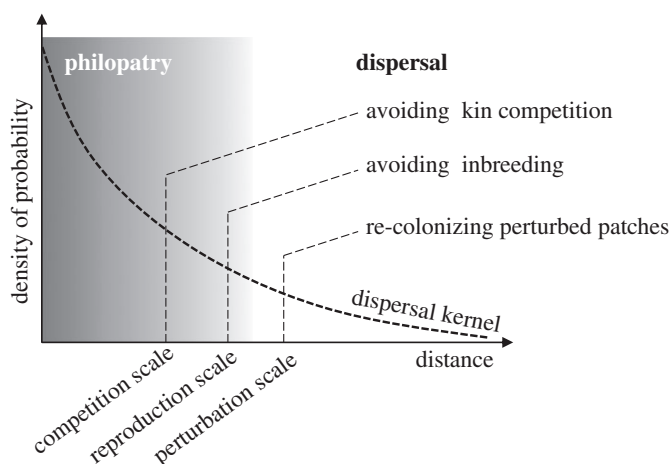
### 3.1.4. Viewpoints on dispersal

In patch models, dispersal may be defined by dispersal propensity,  $d$ , or by two other related quantities, the population genetics migration parameter,  $m$ , and the metapopulation colonization rate,  $c$ .

Population geneticists often treat gene flow as a cause, rather than as a consequence, of evolutionary processes. Dispersal has thus been quantified by the proportion of immigrant propagules: the migration parameter  $m$ . Here  $m$  and  $d$  are naturally related given sufficient knowledge about carrying capacities and dispersal cost, e.g. in the case of death–birth models [43]; yet the evolution of  $m$  is misleading, except in very simple ecological scenarios [75], because it overlooks constraints owing to dispersal cost.

In metapopulation models [76], dispersal is considered as a rare and costly process counteracting local extinction. As such,





**Figure 1.** Relationship between the dispersal kernel (i.e. the probability distribution function of the dispersal distance, thick dashed line) and the typical scales of processes involved in metapopulation dynamics, here competition, reproduction and perturbation (thin dashed lines). In this example, competition is assumed to be more localized than reproduction which, in turn, is more localized than perturbation, but other hierarchies of process scales are possible. Depending on the main ‘function’ assigned to dispersal (i.e. avoiding kin competition, avoiding inbreeding or helping re-colonize perturbed patches), a propagule is said to be dispersed if it disperses farther than the typical competition, reproduction or perturbation scale, respectively. These typical scales can change due to dispersal evolution. For instance, when dispersal increases, population density is expected to become more uniform, and hence competition scale is bound to decrease (e.g. [72,73]). Similarly, gamete dispersal influences reproduction scale, and thus gamete dispersal and propagule dispersal are bound to interfere with one another [67].

dispersal is studied through the colonization rate,  $c$ , which integrates the propensity to disperse and the probability that a single propagule might generate a viable population. Again, given sufficient information,  $c$  can be related to  $d$  [77]. In most situations however, the link between dispersal cost and the trade-offs between extinction, colonization and takeover rates is not clear [27].

### 3.1.5. Genetic determinism of dispersal

Two main approaches are commonly used to describe the evolution of life-history traits such as dispersal:

- (i) Describing the dynamics of alleles at certain loci that determine the value of the trait. This corresponds to the population genetics approach to evolutionary dynamics.
- (ii) Directly describing the dynamics of the trait under study. This is what has been dubbed by Grafen [78] the ‘phenotypic gambit’: as long as it allows understanding otherwise complex phenomena, it may be preferable to abstract from the intricacies of genetic architecture.

While most models on dispersal evolution have openly embraced Grafen’s phenotypic gambit, some models have treated this question using alleles at one or several loci as coding for dispersal value [79,80]. One good reason for explicitly accounting for genetic architecture is when dispersal coevolves with inbreeding depression or heterosis, so that recombination between dispersal and deleterious mutation alleles has to be accounted for [20,80]. Epistasis, dominance, genetic incompatibilities, variable ploidy are but a few potential elements that require taking genetic architecture into account because *adaptive dynamics* and *quantitative genetics* are not adapted to their modelling (but see [81]). One particular instance of genetic determinism that has garnered much attention is the question of maternal versus offspring control of dispersal [47,48,71].

### 3.1.6. Condition-dependent dispersal

While early models on the evolution of dispersal focused on the evolution of fixed, unconditional dispersal, more recent

approaches have explored the evolution of condition-dependent dispersal—i.e. plastic dispersal, which is informed by external conditions or by the organism’s internal state [82–84]. Classically, dispersal is assumed to be informed by within-patch density [55,56,85–88], carrying capacity [86], maternal age [89], body condition [90] or by expected local fitness [87,91], which can rely on the density of predators or prey [92], on the distance to inhospitable habitats [70] and/or on the distribution of local phenotypes. Age-, stage-specific [89,93] and sex-biased dispersal [18,66] have also been investigated. Theoretically, in the absence of information costs, informed dispersal evolves quite easily, e.g. when demography is stochastic [55]. Assessing how plastic dispersal evolves when information is costly or imprecise is a still poorly explored area (but see [32,33]).

## 3.2. Demographical assumptions and predictions

Model assumptions that are linked to the demographics of studied species mainly concern two characteristics: the timing and synchrony of life cycles, and the importance of stochasticity in demography.

### 3.2.1. Timing, synchrony and life cycles

Models on the evolution of dispersal treat the passing of time either as discrete [2,13] or continuous [43,44]. Discrete-time models are synchronized: reproduction, regulation and dispersal happen at the same time for all individuals. By contrast, continuous-time models consider populations where birth and death events happen at random—generally, following Poisson processes with constant rates. Because they describe life stages separately, discrete-time models often lend themselves to more detailed descriptions of the life cycle than continuous-time models.

Differences among life cycles that may impact dispersal traits include:

- (i) whether modelled organisms are semelparous or iteroparous. In the latter case, adult survival [46,57] and possibly age-structure [89,93] have to be modelled;

- (ii) the sequence of stages (reproduction, emigration, immigration and regulation) within a reproductive season [58,59,61].

### 3.2.2. Stochasticity and determinism

Stochastic population dynamics can affect different processes with a potential side effect on dispersal:

- (i) stochastic recruitment (or genetic drift) occurs when the numbers of offspring selected for the next generation are not equal to their expectations for each of the genotypes present, but rather represent a statistical sample drawn from a finite population. This form of stochasticity is at the heart of kin competition models on the evolution of dispersal;
- (ii) stochastic demographics arise when fecundity and mortality vary in time, leading to variable and unpredictable population sizes. Many models have looked at the effect of demographical stochasticity on the evolution of dispersal, mostly contrasting situations in which population sizes are assumed constant versus situations in which they are not [54–56]; and
- (iii) stochastic environments (where conditions cannot be predicted with 100% accuracy) usually select for dispersal. The most extreme case of environmental stochasticity is local population extinction. Environmental stochasticity can be studied independently from genetic drift and demographical stochasticity [38,64].

It is important to realize that stochastic recruitment and stochastic demographics are two separate forms of stochasticity: recruitment can be stochastic in the absence of demographic stochasticity—the reverse case is less plausible.

Well-known simple population dynamics models (such as the Lotka–Volterra equations for community dynamics) tend to use a mean-field description of the abundance of a given species, with no stochasticity in demography or in recruitment. The mean-field dynamics assumption implies that the coefficient of variation of abundance is expected to be very low, which, in turn, can be realized when mean abundance is sufficiently high (note though that this is not a strict requirement, but rather a loosely defined assumption common to most mean-field models). Hence, mean-field models implicitly have zero intra-population relatedness and, hence, do not take kin competition into account when modelling the evolution of dispersal. To capture the effect of kin competition, one can either describe population dynamics in a stochastic context (e.g. [94]), or explicitly compute the inclusive fitness version of the selection gradient and the average within-population relatedness coefficient [77].

### 3.2.3. Eco-evolutionary feedbacks

Exploring the feedback of the evolution of traits on population dynamics is a road seldom trodden [95,96]. Few models link dispersal traits to resulting population dynamics [51,52,97], even though this feedback naturally arises when dispersal evolves as a result of predator–prey dynamics [53]. Understanding in what instances higher dispersal triggers higher or lower complexity of population dynamics [98] is a topic worthy of interest, but still not really explored. For example, dispersal rate is expected to decrease as patches age [99]. An instance of extreme feedback

of dispersal evolution on population dynamics arises when dispersal evolves in metapopulations subjected to local Allee effects and to environmental stochasticity: the evolution of higher dispersal rates then tends to increase extinction risk [100].

## 3.3. More sophisticated predictions

Besides predicting whether evolutionary forces select for or against dispersal, less crude predictions can be obtained (figure 2), mainly (i) whether selection is stabilizing or disruptive at evolutionary equilibria, (ii) how different traits might coevolve with dispersal; and (iii) how evolutionarily selected dispersal values become spatially structured.

### 3.3.1. Dispersal polymorphism

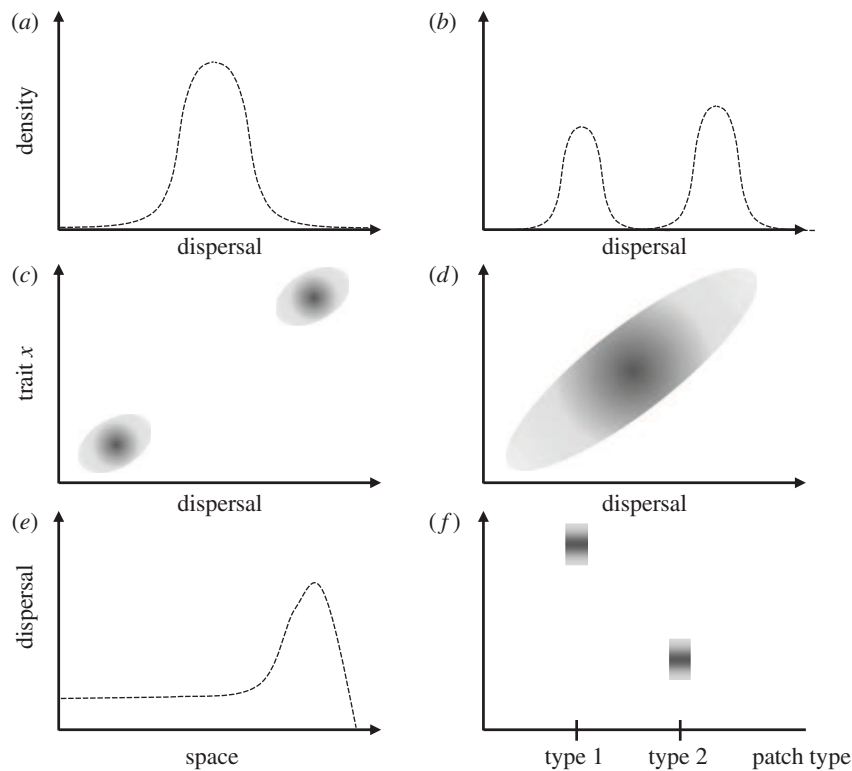
One type of prediction that has garnered much attention from evolutionary ecologists is whether selection on dispersal is stabilizing or disruptive (figure 2*a,b*). In game theory or adaptive dynamics parlance, the former is characterized by an evolutionarily stable strategy (ESS) for dispersal [101,102]; by contrast, disruptive selection is associated with evolutionary branching [103] or with an increase in the standing variance of the trait studied. Early papers on the evolution of dispersal had difficulties in teasing apart ESS from evolutionary branching—at least analytically—because the theory of inclusive fitness focuses on the derivation of the selection gradient, not on the higher order derivatives of the mutant fitness function that are needed to evaluate evolutionary stability [16,104]. However, novel methods (and resurrection of old ones) now allow for the computation of ESS criteria, in particular, the metapopulation fitness criterion  $R_m$  [81,88,94,105,106]. The connection between predictions of polymorphism and of condition-dependence is still not clear [107], especially in the case of dispersal evolution [82]. Besides, since many models dealing with the evolution of trait polymorphisms are based on the adaptive dynamics framework, they describe only eco-evolutionary dynamics under a restricted subset of mutation distribution and frequency [108,109]. Individual-based models have also tackled and predicted the evolution of dispersal polymorphisms [72].

### 3.3.2. Dispersal syndromes

While a number of studies concentrate on predicting the evolution of dispersal only, others have tackled the evolution of dispersal *syndromes*, i.e. of the set of traits coevolving with dispersal—or of values of other traits associated with high dispersal [110] (figure 2*c*). Natural candidate traits that are bound to be associated with dispersal are survival to dispersal [79,111] and habitat selection [112,113]. Other less intuitive candidates include traits that determine adaptation to local conditions (local adaptation *per se* [114] or self-fertilization rates [34,64,65]), and traits resulting in either the same kin competition aversion (altruism and cooperation [115,116]) or in the same bet-hedging strategy as dispersal (e.g. dormancy [117–119]).

### 3.3.3. Spatial structure

One fruitful aspect of research on the evolution of dispersal comes from the study of the spatial structure of dispersal abilities, for example, when the environment varies along a qualitative gradient, or when the focal species is invading



**Figure 2.** Classes of predictions about the evolution of dispersal. (a) The density of dispersal trait values within a metapopulation following an ESS, with residual variance corresponding to the result of mutation and local genetic drift (i.e. stochastic effects). (b) The density of dispersal trait values in a polymorphic population (here, with two modes). (c) Prediction of a positive association syndrome between dispersal and trait  $x$ . (d) Prediction of a genetic covariance between dispersal and trait  $x$  within a given population or metapopulation. (e) Spatial structure of average dispersal value along a one-dimensional space—here, dispersal is higher on the right, possibly because of an invasion wave into a new environment. (f) Structuring of dispersal trait values among two types of patches—here, dispersal is selected for in patches of type 1 and disfavoured in patches of type 2.

a novel environment [120–124] (figure 2*e,f*). Such studies aim at describing the spatial variation of dispersal traits along invasion waves or in response to habitat structure, and thus predict ecologically meaningful quantities such as invasion speed [125,126] or the latitudinal range of a species' distribution. In heterogeneous environments, dispersal evolution has mostly been studied through simulations while, by contrast, analytical approaches to diffusion–advection models have been used to study the evolution of dispersal in homogeneous environments or when invasion is considered at the landscape scale [113,127,128].

It is important to note that predictions of the spatial structure of dispersal will depend on the ecological scenario underlying the spatial structure of habitat. Three broad scenarios are distinguished in the literature [65]:

- (i) metapopulations in which migration among patches is bidirectional;
- (ii) mainland–island systems in which migration goes only from mainland to islands; and
- (iii) waves of advance where dispersal is expected to evolve as habitat becomes filled with more and more individuals or range shifts under changing conditions.

Between cases (i) and (ii), there is a continuum of scenarios that account for partially biased migration patterns [36]. Case (iii) can refer both to invasive species spreading onto new grounds [120,129], or to species evolving in response to environmental quality shifting in time (e.g. to mimic climate change [130–133]).

### 3.4. Evolutionary dynamics of dispersal

Theoretical work on the evolution of dispersal mostly proceeds through two main methods: analyses and simulations. While simulation work is bounded only by a modeller's proficiency with code writing, computer power and their ability to subsequently analyse the obtained simulations, analytical approaches are constrained by the state-of-the-art on the assessment of mutant invasibility analyses. Here, we briefly describe the different 'roads to analytical predictions' that have been used to understand the evolution of dispersal, with a clear articulation between how these methods handle evolutionary dynamics and spatial structure, and how their approximations impair or improve the study of certain selective pressures. This section ends with a short discussion on the pros and cons of analyses versus simulation models of the evolution of dispersal.

#### 3.4.1. Fitness and spatial structure

When modelling the evolution of a trait-like dispersal, three elements are needed to be able to compute evolutionary trajectories and outcomes:

- (i) How is the trait under study inherited?
- (ii) How do mutant trait values arise?
- (iii) How does the trait affect individual fitness?

Regardless of the trait and of its genetic architecture, the processes of inheritance and mutation are bound to trade-off at some point—genetic transmission cannot be both



perfectly accurate and innovative. How dispersal is described in terms of genetic architecture, and hence of transmission, has already been reviewed above (section ‘Genetic determinism of dispersal’). Thus, only remains the issue of describing the fitness effects of dispersal.

In well-mixed populations, mutant fitness corresponds to the growth rate of a population of initially scarce mutants [134]. What needs to be understood is that mutant invasion fitness is not a growth rate *per se*, but rather a criterion for the instability of the system in the absence of mutants. This can be seen when looking at populations with age- or size-structure, in which fitness is described by the dominant eigenvalue of the corresponding demographic transition matrix [135]. The idea behind this is that the typical ‘scarcity’ of an initial mutant population may be biased towards, e.g. young life stages when mortality accelerates with age. This typical scarcity is given by the eigenvector associated with the dominant eigenvalue of the demographic transition matrix, because all deviations from the structure defined by this eigenvector will inevitably decrease as they are associated with lesser eigenvalues of the matrix.

The crux of defining fitness thus resides in understanding the ‘typical scarcity’ and associated growth rate of a mutant for the dispersal trait. In patch models with global dispersal, one fruitful approach is to exploit the formulation of the metapopulation state in terms of classes of mutant abundance (with a metapopulation transition matrix between mutant abundant classes) and use the  $R_m$  criterion, derived in a fashion similar to the fitness of stage-structured population described above [88,94,105,106]. In patch models with local dispersal (i.e. graph models where nodes are patches), this approach becomes restricted to the case of regular graphs [68], as heterogeneity in node degrees will lead to correlations between local mutant abundance and patch location within the network. In diffusion–advection models, dominant eigenvalue-based methods have been developed using a decomposition of potential solutions in a series of waves with different speeds and frequencies [136]. In stochastic differential equation point-process models, the use of perturbation theory at the limit of large dispersal scale allows for the computation of a dominant eigenvalue representing the fitness of a rare mutant in a resident population at steady state [41,137]. This last method is promising as a general recipe to model the evolution of dispersal kernels, and in particular performs better than classical moment closure methods (e.g. [138]). However, the approximations underlying this approach restrict its use to the case of large-scale dispersal (i.e. when the effective degree of ‘patches’ as nodes on a graph amounts to 10 or higher).

### 3.4.2. Selective pressures and mathematical approximations

Because all models are wrong at least concerning one (or more) of their underlying assumptions, it is important to remember that each of the methods developed to obtain analytical results on the evolution of dispersal, described above, may be inadequate to account for certain selective pressures:

- (i) mean-field approaches (e.g. [14,22]) are particularly ill-suited to account for kin competition effects. Even worse fitted to this job are models that assume infinite population size, or continuous space models with localized competition (such as diffusion–advection models in which competition happens only between ‘individuals’ occurring at exactly the same location [139]);
- (ii) continuous-time models can hardly tackle questions about the effect of semelparity, life cycles or other characteristics linked to the precise life history of the species under study [46,57–59,61];
- (iii) as soon as competition for resources or space is introduced into the model, the calculation of fitness becomes complicated (as highlighted in the previous subsection) and gives rise to frequency-dependent or density-dependent selection. Thus, trying to ‘bluntly optimize fitness’ is not a good modelling strategy under such assumptions [65,140];
- (iv) when dispersal costs or carrying capacities are spatially heterogeneous and/or temporally variable, attempting to model the evolution of the migration parameter (measuring the proportion of immigrants among recruited offspring) is an ill-suited approach, because migration will be differentially constrained in patches with different carrying capacities or dispersal costs (e.g. [43,44]); and
- (v) when modelling the effects of environmental variability or heterogeneity on the evolution of dispersal, it is worth keeping in mind that natural settings are rarely separated in clearly different types of patches with different habitat quality. Instead, nature is more blurry. Changing the classic theoretical formulation of environmental heterogeneity from discrete to continuous would be much more useful to the empiricist.

### 3.4.3. Relative merits of simulations and analyses

While we have mainly discussed the different ways to obtain analytical results on the evolution of dispersal so far, using simulations has to be reckoned as a helpful exploratory approach as well. Many individual-based models on the evolution of dispersal have been able to pinpoint interesting phenomena in contexts that are too complex for analytical methods, e.g. on the link between accelerating invasion waves and selection for dispersal [141], on the evolution of dispersal during range expansion [142–145] or on the evolution of movement rules in patchy landscapes [91,146]. Simulation studies are also capable of disentangling more subtle effects of multiple selective pressures on dispersal, e.g. teasing apart the roles of kin versus individual selection in the evolution of dispersal [147].

It should be noted that both analytical and simulation approaches have their own merits and that, for sufficiently complex questions, e.g. arising from the combination of different selective pressures or in non-equilibrium conditions, striving to use both approaches is the best path to answering them. The advantage of simulation methods is that they can address complex questions ‘by brute force’, i.e. as long as the modeller is clear as to what ingredients to put in the model, simulations can be run and results can be obtained. However, the attached drawback is that simulations have intrinsically poor predictive power, insofar as one cannot extrapolate results obtained with some parameter values to other parameter values without running new simulations. Statistical analyses of large simulation data are sometimes difficult, especially when simulations run with the same parameter values show high inter-replicate variability. Analytical methods, on the other hand, are predictive by essence, i.e. results are predictable from a given equation, and hold as long as assumptions underlying that equation are not violated. However, analytical

methods can be constrained by the sheer complexity of a question, and even rough approximations might not help. As a rule of thumb to empiricists, complementing analytical approximations with simulations is always a wise move, as simulations may help confirming or infirming the validity of approximations, and, hence, help question the nature of approximations that can be made to obtain predictions in different situations.

## 4. Perspectives

### 4.1. Empirical considerations

Connecting theoretical models to data in evolutionary ecology is a difficult endeavour for several reasons, mainly because experimental manipulations involving evolutionary processes are often lengthy, and because field data bring only information about correlation, not causation. Yet, models on the evolution of dispersal need empirical testing.

Experimental evolution of dispersal traits needs to design a spatially structured device, where organisms can express different dispersal abilities. Artificial selection for dispersal traits may focus on a proxy of dispersal, like mobility (e.g. using wind tunnels [148]), the proportion of winged morphs (e.g. in aphids, planthoppers, crickets, etc. [149–151]), the proportion of seeds with explicit dispersal traits (e.g. pappus [152]), etc. Dispersal among populations can also be measured through capture–mark–recapture experiments. When directly measuring dispersal, experimental studies have mainly used two-patch settings—either small patches in Petri dishes [29,153], or larger ones [154]. More complex settings have also been set up for small organisms (e.g. linear stepping-stone habitats [155,156], or a set of connected patches for beetles and their parasitoids [157]). In the past decade, large-scale experiments aiming at measuring dispersal of middle-sized organisms were set up in artificially fragmented landscapes (e.g. measures of bird dispersal at the Savannah River Site, [158]). Another example is the Metatron, a structure of 48 patches of 100 m<sup>2</sup> arranged on a grid and connected by corridors, which allows to study dispersal behaviours of small animals over months to years [159].

Field data provide weaker tests of theories than do experimental tests, since causes and consequences may not really be disentangled in the absence of manipulation, and since diverse factors may interact to select for or against dispersal. If field data cannot be used to prove a particular theory, they may help disprove it [43,160,161], provided adequate proxies of dispersal and selective pressures are available. For example, if one were to assess the selective pressures driving the evolution of dispersal in a planthopper species, one could assess the possible influence of kin competition using joint measures of population size and relatedness. However, to assess whether spatio-temporal variability in reproductive success is sufficient to drive the evolution of dispersal is a lot harder. Notably, spatial heterogeneity and temporal variability ought to be quantified on a scale related to that of the studied organism [160].

Ideally, field data-based assessment of theories on the evolution of dispersal should be based on strong statistical tools, e.g. goodness-of-fit indices like the Akaike information criterion [162]. For empiricists to be able to test among different models, theories need to move from general to precise predictions, e.g. by providing a sampling theory [163] of

realized dispersal distance within landscapes. In practice, such a theory could be tested using information on local and landscape characteristics of interest (perturbation frequency, grain of spatial heterogeneity, etc.) and on dispersal of samples of individuals. Because dispersal distances might not always be readily measurable, proxies may be used, such as genetic indicators of spatial structure (measures of relatedness [164] or assignment tests [165]). When competing theories on the evolution of dispersal are able to provide unique predictions on the expected realizations of such samples, a strong test of the theory will be at hand.

In order to become testable, models on the evolution of dispersal need to derive sufficiently cleaving predictions on, e.g. trait associations, age-trait, population age-trait and spatial trait correlations, which can be used to disentangle the influence of selective pressures on the evolution of dispersal. When field data on the dispersal of species are associated with data on the co-occurrence of focal species and their natural enemies, they could be exploited to obtain weak tests for or against the effect of natural enemies as an incentive for higher dispersal rates. In short, modellers need to rethink the way they formulate predictions on the evolution of dispersal, to (i) emphasize differences with existing predictions, (ii) yield directly testable predictions.

An important effort to be made in order to connect models and data on the evolution of dispersal lies with uncovering the existing mismatches between areas which have been heavily studied on one side and very little on the other. For example, empiricists have shown great interest in testing whether and why dispersal could be sex-biased [31,166,167], condition-dependent (depending on food level [168], on the local density of conspecifics [155], on brood size [169], on parasite load [156] or on temperature [170]) or in testing whether habitat persistence [153], kin competition [155,171,172] or habitat fragmentation [154,173] actually affect the evolution of dispersal. Other related issues with potential immediate applications, e.g. the existence of accelerating invasion fronts due to the evolution of dispersal [148,174], have also been investigated more heavily from the empirical side than from the theoretical one. Yet, many theoretical predictions remain scarcely tested, e.g. those linked with dispersal as a mechanism to avoid inbreeding or outbreeding depression, or predictions linking population dynamics to the evolution of dispersal. This occurs despite some models yielding ready-to-be-tested predictions, e.g. ‘In a metapopulation in which the dispersal rate is at its evolutionary endpoint the unrelatedness approximately equals the reciprocal of the dispersal rate minus twice the characteristic return time of the local population divided by the average lifetime of a patch.’ [77, p. 2394]. Other readily testable predictions include relating carrying capacities in a metapopulation with the occurrence (or not) of polymorphisms in dispersal, and with the levels of dispersal observed in differently sized patches [43], or checking whether species submitted to strong Allee effects are less likely to evolve higher dispersal and, thus, to become invasive [175,176].

To caricature the existing imbalance between the states of theories and empirics on the evolution of dispersal, empirical studies have been quite focused on highlighting costs of dispersal and their effects on limiting the evolution of high dispersal rates, while theoretical models have explored many different selective pressures, but rarely provided precise predictions on eco-evolutionary feedbacks between population dynamics

and the evolution of dispersal [97]. Few models link dispersal with population dynamics (but see [51,52,97]) or with local adaptation (but see [64,114,169]). Advancing these two avenues of theoretical research will probably bring some testable predictions that are still lacking. Moreover, these could also bridge the gap between theory on the evolution of dispersal and data on differences in range size among species with different dispersal rates [177] or different abilities to track climate change [178] and will also help in understanding differences in mobility among species at different trophic levels or in different functional groups [179,180].

## 4.2. Five emergent issues about the evolution of dispersal

Arguing that empirical studies need to feed on current theoretical results and vice versa is not sufficient to make a scientific field move forward. Having reviewed the literature on the question of dispersal evolution, we want to propose, as an ending to this review, a list of five key issues that might be addressed in the near future, provided that experimentalists and theorists collaborate more than they used to:

- (i) How do transient or non-equilibrium population dynamics affect the evolution of dispersal? Though some theoretical papers have tackled part of this issue [51,52], this topic has never really caught evolutionary ecologists' interest enough to be developed, both theoretically and experimentally. From what is now known about rapid evolution, especially in short-lived organisms (e.g. [181]), tackling how population cycles or the replenishment of resource pool might impact the evolution of dispersal in bacteria may be useful for disease treatments.
- (ii) What are the links between the evolution of dispersal and the ability of a species to invade a new environment? Theoretical models and empirical data seem to indicate that selection for dispersal accelerates invasion waves [8,141]. However, there is still much to be developed on this subject, in particular, regarding the different ways in which we could exploit knowledge on the evolution of dispersal to compare different schemes aimed at curbing invasions, similarly to the framework proposed to compare vaccination targets using knowledge on the evolution of virulence in pathogens [182]. Likewise, answers to this question could help predict the effects of climate change on species extinctions through the understanding of how dispersal evolution could effectively serve as 'evolutionary rescue' for polewards moving species. Indeed, the probability of evolutionary rescue in metapopulations strongly depends upon dispersal [183].

- (iii) Can we relate movement patterns to dispersal in animals or, more generally, how do we make a connection between micro- and macro-scale considerations on the evolution of dispersal? This is clearly an emerging topic for theoreticians [91,145,146], but it would successfully feed on tracking data collected by field ecologists on, e.g. marine birds, turtles, large mammals, etc. This question would need to delve into the costs associated with information gained about the environment [33], and the impacts of these cues and their costs on the evolution of condition-dependent dispersal.
- (iv) How do habitat spatial structure and connectivity affect the evolution of dispersal? Even though some theoretical works have been studying the effect of patchy landscape structure and spatial autocorrelation on the evolution of dispersal [41,42], we still need the equivalent of Ohtsuki and Nowak's framework [68] to study the evolution of traits affecting population structures on irregular graphs. This would allow for the identification of 'sources' and 'sinks' due to the combined effects of habitat heterogeneity and local dispersal evolution [184]. Because the new wave of experimental facilities designed to study dispersal evolution can be thought of as 'small-size networks' of patches (see, e.g., the Metatron facility [159]), such a theory would help in predicting and interpreting the results of experiments run in such facilities.
- (v) How can we apply knowledge on the evolution of dispersal to biological conservation issues? When models predict the emergence of a polymorphism in dispersal, high- and low-dispersal types tend to segregate across the landscapes [184], e.g. when carrying capacity varies across space, highly dispersing types tend to be associated with small patches [43]. Thus, it seems straightforward to ask whether we can make use of such models to predict the effect of landscape alterations on the polymorphism of dispersal within a given endemic species, and whether these alterations will indirectly fuel the extinction of this species or not through dispersal evolution. More generally, when human impacts on the environment affect the carrying capacity, fecundity or mortality rates of a given species, knowledge of how dispersal tends to evolve in response to these changes can help predict migrational melt-downs [185], and ways to prevent them.

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## Glossary

**Adaptive dynamics:** a mathematical framework aimed at studying the evolutionary dynamics of phenotypic traits [102]. Adaptive dynamics relies on two main assumptions: (i) mutations are rare and (ii) of weak effect. Based on these two assumptions, analyses are performed so that, at any moment, the population consists of a given number of resident strategies (initially, one) and one mutant strategy equipped with a trait value infinitesimally

close to one of the residents'. Evolutionary trajectories are obtained through the computation of the mutant fitness, the ensuing selection gradient (first-order derivative of the mutant fitness with respect to mutant trait value) which determines evolutionary trajectories through the 'canonical equation' [186], and second-order derivatives defining the convergence and evolutionary stability of the coalition of phenotypes [103].

**Colonization:** a process by which a species or genotype invades a patch still devoid of the focal species or genotype. The 'colonization rate' has been popularized by R. Levins' metapopulation model [76] in which species are alternately present or absent from patches, following extinction and colonization processes. The metapopulation paradigm can be related to more detailed descriptions of within-patch demographics [187–189], with a natural interpretation of colonization as the result of dispersal, survival and successful build-up of a new population [77].

**Dispersal:** dispersal can be defined in different ways. The most commonly admitted definition of dispersal is 'any movement of individuals or propagules with potential consequences for gene flow across space' [5, p. 232]. On the one hand, for zoologists, dispersal involves the movement of individuals, at any life stage, between the birth place (or a former breeding site) towards a new breeding site [83]. Botanists, and zoologists interested in sessile organisms, on the other hand, tend to consider dispersal as a two-sided process, with gamete dispersal and zygote dispersal being two sides of the same coin [190,191]. While the mode of dispersal in animals is almost always straightforward (but see [36]), plants can use many different modes of gamete and zygote dispersal (see, e.g., [192] for a good glossary of terms). One difficulty linked to defining dispersal without any explicit relation to gene flow is that many animal species move all the time in search of food (foraging movements), so that definitions of dispersal based on spatial or temporal scales of movements are more difficult to formulate [74].

**Iteroparity:** a species is iteroparous if it can reproduce more than once in a lifetime. Botanists sometimes refer to iteroparity as polycarpy.

**Kin competition:** the process by which related individuals tend to compete with one another. Strong kin competition selects for dispersal following Hamilton's rule [193,194]. It should be noted that relatedness is influenced by both dispersal and local population size, so that dispersal and relatedness feedback on one another [16].

**Metapopulation:** a population of populations, i.e. a collection of populations subjected to the processes of colonization and extinction [76,195]. By extension, in the context of dispersal evolution, subdivided populations (i.e. collections of

populations subjected to dispersal but not to extinctions) have been termed metapopulations (e.g. [43]).

**Migration:** in population genetics, migration is often used as an equivalent for dispersal. Migration rates specifically relate to the proportion of the next-generation gene pool that is contributed by reproduction events outside of the focal patch (e.g. [196]). As argued in the main text, substituting migration for dispersal in models of phenotypic evolution can lead to confusion because dispersal cost and differences in population sizes among patches are implicit in the migration formulation, while they are explicit in the dispersal formulation.

**Quantitative genetics:** a mathematical framework aimed at studying the evolutionary dynamics of traits. Quantitative genetics relies on the conceptualization of phenotypes as the sum of a genetic and an environmental effects [197, eqn. 8.11] and assume by default that all traits follow Gaussian distributions given a proper transformation (because of the assumed large number of loci underlying the trait). The central analytical tenet of quantitative genetics is the 'breeder's equation' which predicts the response to selection based on the value of a trait's heritability [197, eqn. 11.2].

**Semelparity:** a species is semelparous if it can reproduce only once in a lifetime, usually at the very end of its life. Annual plants, some fish (e.g. salmon), some arachnids, insects and squids are some of the best-known examples of semelparous organisms. Botanists sometimes refer to semelparity as monocarpy.

**Syndrome:** an association of values of different phenotypic traits due to selection (figure 2c). For a syndrome to exist, there should be at least one reason for divergent selection of different trait values across habitats. Syndromes should not be confused with standing genetic variances and covariances, which specify how traits co-vary (within a population or metapopulation) as a consequence of mutation (with potentially pleiotropic mutations affecting more than one trait at once), recombination (linked loci would statistically co-vary), selection, drift and migration (figure 2d). A syndrome does not emerge as a result of a trade-off either (i.e. a constraint on trait values due to physical or chemical constraints).



# A Neutral Theory for Interpreting Correlations between Species and Genetic Diversity in Communities

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**ABSTRACT:** Spatial patterns of biological diversity have been extensively studied in ecology and population genetics, because they reflect the forces acting on biodiversity. A growing number of studies have found that genetic (within-species) and species diversity can be correlated in space (the so-called species–gene diversity correlation [SGDC]), which suggests that they are controlled by nonindependent processes. Positive SGDCs are generally assumed to arise from parallel responses of genetic and species diversity to variation in site size and connectivity. However, this argument implicitly assumes a neutral model that has yet to be developed. Here, we build such a model to predict SGDC in a metacommunity. We describe how SGDC emerges from competition within sites and variation in connectivity and carrying capacity among sites. We then introduce the formerly ignored mutation process, which affects genetic but not species diversity. When mutation rate is low, our model confirms that variation in the number of migrants among sites creates positive SGDCs. However, when considering high mutation rates, interactions between mutation, migration, and competition can produce negative SGDCs. Neutral processes thus do not always contribute positively to SGDCs. Our approach provides empirical guidelines for interpreting these novel patterns in natura with respect to evolutionary and ecological forces shaping metacommunities.

**Keywords:** neutral theory, SGDC, coalescence, community genetics, diversity pattern, mainland–island model.

## Introduction

It has been recognized for several decades that the diversity patterns of genes within species and those of species within communities are not independent. Understanding their interactions is the main goal of “community genetics” (Antonovics 1976), an interdisciplinary field that has recently seen a burst of interest (Wares 2002; Agrawal 2003; Neu-

hauser et al. 2003; Bernhardsson et al. 2013). The rise of environmental genomics and long-term surveys of populations and communities has enhanced the opportunity to confront these two organizational levels (Gugerli et al. 2013). In particular, it is becoming common practice to compute “species–genes diversity correlation” (SGDC; Vellend 2003), which consists in quantifying the link between the genetic diversity in several populations of a species (the focal species) and the species diversity of the local communities within which these populations are embedded. This has been done in more than 40 studies since the seminal work of Vellend and coworkers (see Vellend et al. 2014 for a review).

SGDCs provide information on both fundamental and applied issues with regard to biodiversity. From a fundamental perspective, investigating the generality of SGDC patterns can help to uncover determinants of ecological processes shaping diversity at different levels. For example, several empirical studies have shown that site area (Vellend 2003), which often constitutes a proxy for carrying capacity in community ecology, and site connectivity (Lamy et al. 2013) contribute markedly to positive SGDCs. This suggests that drift and migration might have a strong impact on both species and genetic diversity. From a more applied perspective, detecting positive SGDCs might be useful, in conservation studies, to infer diversity from one level to the other (e.g., predicting species diversity based on genetic data; Papadopoulou et al. 2011).

The growing number of empirical studies on SGDCs constitute a strong incentive to build a quantitative theoretical basis that would help interpreting observed patterns. Vellend and Geber (2005) made a conceptual advance on this issue by envisioning three types of relationships between diversity levels that may generate interpretable signals in community genetics: causal effects of genetic diversity on species diversity, causal effects of

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species diversity on genetic diversity, and simultaneously parallel effects of external factors on both levels. Neutral theories of molecular evolution (Kimura 1984) and of biodiversity (Hubbell 2001) provide some conceptual elements regarding these potential parallel effects. Indeed, both theories consider limited dispersal and drift to be the main drivers of diversity patterns, and they both predict that carrying capacities and immigration rates should be positively related to diversity (Wright 1931; Hubbell 2001). A positive SGDC should then arise from any external factor generating variation in carrying capacity and connectivity across sites, as has been supported by simulation work (Vellend 2005).

However, even under a neutral framework, the interpretation of positive SGDCs may not be as straightforward as suggested above, because of interactions between the focal species (i.e., the one studied for genetic variation) and other species of the community within sites. In particular, the local abundance of a species may be positively linked to its genetic diversity but also negatively linked to the abundance of other species, and thus to species diversity, as a consequence of competition for limited space. This might produce a negative SGDC (Vellend 2005; Wehenkel et al. 2006; Odat et al. 2010) under specific circumstances that remain to be characterized quantitatively. To our knowledge, no analytical model predicts the sign and magnitude of SGDCs when accounting for the two effects mentioned above, namely, (i) local competition dynamics and (ii) variation in carrying capacity and connectivity among sites. A first objective here is to propose such a model.

A complete quantitative theory of SGDCs also has to include the forces generating diversity, namely, mutation and speciation. These processes have indeed been neglected when discussing SGDC on the grounds that they are often too slow compared with ecological processes (Vellend and Geber 2005). This is true when these rates are negligible with respect to migration. For speciation, this assumption may be challenged when considering archipelagoes (Losos and Schluter 2000) but remains correct when studying metacommunities at limited spatial scale (e.g., a pond network in a single island; Lamy et al. 2013). Here we focus on situations where speciation can be neglected. However, even in this context, assuming that mutation has a negligible impact on genetic diversity is still questionable, especially when using highly mutable markers such as microsatellites (Jarne and Lagoda 1996; Ellegren 2002). Such markers are commonly used in studies reporting SGDCs (Cleary et al. 2006; He et al. 2008; Struebig et al. 2011; Blum et al. 2012; Lamy et al. 2013). Our second objective is thus to provide insights on how mutation may affect SGDCs, even at rather limited spatial and temporal scales.

We build a spatially implicit model of a metacommunity using a unifying neutral framework for both genetic and species dynamics to generate theoretical expectations on SGDCs. Our approach takes into account drift and migration at both diversity levels, as well as mutation, while speciation is neglected. We consider a set of local communities receiving migrants from a larger regional community (Hubbell 2001). This model allows distinguishing within- and among-site effects on SGDCs and thus disentangling the effects of competition within local sites from those of drift and migration among sites. When mutation is neglected, the SGDC turns out to be positive. However, high mutation rates, compared with immigration rates, can produce negative SGDCs. Even under neutral assumptions, the sign of SGDCs can be labile, and understanding SGDCs is therefore not straightforward. On the basis of our framework, we provide some empirical guidelines for interpreting SGDCs.

## Material and Methods

### *Modeling the Dynamics of Species and Gene Diversity in a Site*

Our work is based on an individual-based model derived from the classical neutral model of ecological communities (Hubbell 2001). We describe it hereafter following the standardized “overview, design concepts, and details” protocol (Grimm et al. 2010).

*Purpose.* The model aims at simultaneously providing the species composition of a sample taken from a community and the genotypes of the individuals that belong to the focal species in this sample. Model predictions are based on two features of the sampled site: the carrying capacity ( $K$ ) and the immigration rate from the regional pool ( $m$ ). The symbols used are summarized in table 1.

*Entities, State Variables, and Scale.* The model contains three types of entities: a site, its individuals, and a regional pool serving as a source of migrants. Individuals are described using two state variables: the species they belong to and, for individuals that belong to the focal species, their allelic state at a given locus (under the assumption of haploidy). The latter variable is ignored for individuals that do not belong to the focal species. The site is described by parameters  $K$  and  $m$  (which are permanent characteristics) and the list of individuals that it contains (which varies in time). The regional pool of individuals is characterized by a set of constant state variables, including the relative abundances of  $B$  species  $\mathbf{f} = (f_1, f_2, \dots, f_B)$  and a parameter  $\theta$  which quantifies the mutation-drift ratio in the regional population of the focal species (app. A; apps.

**Table 1:** Symbols used in model to predict species-gene diversity correlation (SGDC) in a metacommunity

Symbol	Definition
$K$	Carrying capacity of a local site (variable across sites)
$m$	Probability of immigration in a local site (variable across sites)
$I$	Effective number of migrants in a local site (variable across sites)
$\sigma_K, \sigma_m$	Mean values of $\log(K-1)$ and $\log(m/(1-m))$ over local sites
$\sigma_K^2, \sigma_m^2, \sigma_I^2$	Variance in $\log(K-1)$ , $\log(m/(1-m))$ , and $\log(I)$ across local sites
$\rho_{Km}$	Correlation between $\log(K-1)$ and $\log(m/(1-m))$ across local sites
$C_{Im}$	Covariance between $\log(I)$ and $\log(m/(1-m))$ across local sites
$B$	Number of species in the regional pool
$\mathbf{f}$	Relative abundances of species in the regional pool
$f_e$	Relative abundance of the focal species in the regional pool
$\theta$	Drift-mutation parameter of the regional population of the focal species (weak mutation)
$\mu$	Probability of mutation at the genetic locus ( $\mu = 0$ under weak mutation)
$S$	Number of individuals sampled per site (constant across sites)
$\mathbf{s}$	Composition of species sample
$k$	Number of individuals in the genetic sample (constant across sites)
$\mathbf{u}$	Composition of genetic sample
$R_{\text{spe}}$	Number of species in the species sample ( $\mathbf{s}$ )
$R_{\text{all}}$	Number of alleles in the genetic sample ( $\mathbf{u}$ )
$C_{\text{sg}}$	Expected covariance between $R_{\text{all}}$ and $R_{\text{spe}}$
$C_{\text{within}}$	Contribution of stochastic competition for space within sites to the expected covariance
$C_{\text{among}}$	Contribution of variation in $K$ and $m$ among sites to the expected covariance
SGDC	Expected correlation between $R_{\text{all}}$ and $R_{\text{spe}}$

Note: Boldface type indicates vectors.

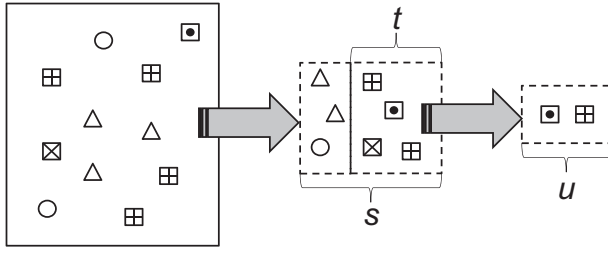
A–C available online). When not neglected, mutation is characterized by a per-birth mutation rate  $\mu$  in the focal species.

*Process Overview.* The model is characterized by discrete death-birth cycles in the site. At the beginning of each cycle, the site contains exactly  $K$  individuals (i.e., is saturated). An individual is then randomly chosen, discarded, and replaced by the offspring of a reproducer which either belongs to the site, with probability  $1 - m$ , or to the regional pool, with probability  $m$ . When the reproducer belongs to the site, the offspring inherits its species identity. Its genotype (focal species) is either the same as the reproducer's genotype (with probability  $1 - \mu$ ) or a mutated allele not already present in the species (with probability  $\mu$ ; see below for additional discussion of the mutation regime). When the reproducer belongs to the regional pool, the species identity of the immigrant offspring is randomly drawn from the distribution of the species relative abundances in the regional pool ( $\mathbf{f}$ ). When the offspring belongs to the focal species (with probability  $f_e$ ), its genotype is determined as explained below. Note that, in our model, competition among genotypes and species occurs during these cycles, when dead individuals are replaced by offspring of either migrant or local origin (i.e., a lottery competition for space).

Two scenarios are considered with respect to mutation.

The first scenario corresponds to a weak mutation regime ( $\mu \ll m$ ; in practice,  $\mu$  is set to zero) in which mutation is neglected in the local community dynamics. At the regional scale, the allelic frequencies of the focal species are assumed to be at mutation-drift equilibrium and follow a Ewens distribution with parameter  $\theta$  (Ewens and Tavaré 2006). The second scenario corresponds to a strong mutation regime where mutation at the focal locus cannot be neglected when compared to migration ( $\mu \approx m$ ). Mutation process follows an infinite-allele model: any mutation event generates an allele that never occurred before in the site. As a consequence of high mutation rate, the regional allelic pool is assumed to be infinitely diverse (app. A): immigrants always harbor alleles that did not occur before in the site.

*Outputs.* Species diversity and allelic diversity are determined through a sampling process designed to mimic a typical SGDC study.  $S$  individuals are randomly sampled from the site (the species sample; fig. 1). The species composition of this sample is described by  $\mathbf{s} = (s_1, s_2, \dots, s_B)$ , where  $s_i$  individuals belong to species  $i$ , and  $\sum_i s_i = S$ . Species diversity is computed as species richness ( $R_{\text{spe}}$ ; i.e., as the number of distinct species occurring in  $\mathbf{s}$ ). In the species sample, the allelic states of the individuals belonging to the focal species  $e$  are described by  $\mathbf{t} = (t_1, t_2, \dots, t_n)$ , where  $t_j$  individuals carry allele  $j$ , and



**Figure 1:** Sampling protocol of a site in the model. The large rectangle on the left depicts a site. Arrows represent random sampling. Dashed rectangles represent samples, and pictograms represent species. The focal species (squares) harbors alleles that are depicted with different graphical patterns (crosses and points). The genetic sample  $\mathbf{u}$  is obtained by subsampling  $k$  individuals among individuals of the focal species ( $\mathbf{t}$ ) included in the species sample ( $\mathbf{s}$ ). Here  $S = 7$  and  $k = 2$ .

$\sum_j t_j = s_e$ . A random subset,  $\mathbf{u}$ , of  $\mathbf{t}$  containing  $k$  individuals is genotyped and constitutes the “genetic sample” within sites. The genetic diversity is estimated using allelic richness ( $R_{\text{all}}$ ), computed as the number of distinct alleles occurring in  $\mathbf{u}$ . Note that with this sampling procedure, allelic and species richness can be computed only for sites containing more than  $S$  individuals ( $K > S$ ) and yielding a sample  $\mathbf{s}$  containing more than  $k$  individuals of species  $e$  ( $s_e > k$ ).

#### *Modeling and Decomposing Species-Genetic Diversity Relationships across Sites*

The influence of variation in carrying capacity ( $K$ ) and immigration rate ( $m$ ) among sites on SGDC is modeled by considering a set of sites created by independently drawing values of  $K$  and  $m$  from a bivariate distribution with given variance and covariance (app. B). All the sites are connected to the same regional pool and follow the same mutation dynamics (i.e., weak or strong).  $R_{\text{all}}$  and  $R_{\text{spe}}$  are computed using our model in all the sites where  $K > S$  and  $s_e > k$  (see above). Note that our sampling protocol controls for sample size at both species (through  $S$ ) and genetic levels (through  $k$ ), which allows comparing diversity measures among sites. We provide below theoretical expectations about the sign of the expected covariance between  $R_{\text{all}}$  and  $R_{\text{spe}}$  computed across sites ( $C_{\text{sg}}$ ). Although  $C_{\text{sg}}$  is not the SGDC classically estimated in empirical studies (i.e., authors generally use Pearson’s correlation coefficient), it provides qualitative information about the sign of the expected relationship between genetic and species diversity. Besides,  $C_{\text{sg}}$  can be decomposed into two effects. The first one occurs within sites as the result of local competition. The second effect stems from the variation in carrying capacity ( $K$ ) and migration ( $m$ ) among

sites. Technically speaking, this can be expressed as the decomposition of  $C_{\text{sg}}$  as the sum of two covariances,  $C_{\text{within}}$  and  $C_{\text{among}}$  (app. C), with

$$\begin{cases} C_{\text{sg}} = C_{\text{within}} + C_{\text{among}} \\ C_{\text{within}} = \mathbb{E}[\text{Cov}_{K,m}[R_{\text{spe}}, R_{\text{all}}]] \\ C_{\text{among}} = \text{Cov}[\overline{R_{\text{spe}}}(K, m), \overline{R_{\text{all}}}(K, m)] \end{cases}, \quad (1)$$

where  $\text{Cov}_{K,m}[R_{\text{spe}}, R_{\text{all}}]$  is the covariance between specific and allelic richness (considered as random variables) within a site with given  $K$  and  $m$  values,  $\mathbb{E}$ , and  $\text{Cov}$  are the expectation and covariance over  $(K, m)$  distribution, respectively, and overlined quantities are expectations within sites with given  $K$  and  $m$  values.  $C_{\text{among}}$  reflects the effect of  $(K, m)$  variation among sites. Importantly,  $C_{\text{among}}$  is null when  $K$  and  $m$  do not vary among sites, in which case only local competition ( $C_{\text{within}}$ ) determines  $C_{\text{sg}}$  and thus the sign of SGDC. From a statistical point of view, this decomposition of  $C_{\text{sg}}$  can be interpreted as in an analysis of variance framework,  $C_{\text{among}}$  being the part of covariance explained by  $K$  and  $m$  and  $C_{\text{within}}$  being the residual covariance.

#### *Simulating $R_{\text{all}}$ and $R_{\text{spe}}$ in a Set of Local Sites*

Simulations illustrate our theoretical predictions about the sign of SGDC and provide more quantitative information about SGDC (i.e., Pearson’s correlation coefficient) variation with respect to  $K$  and  $m$  distribution among sites. An efficient sampling approach in our model is to simulate the genealogy of the  $S$  individuals per sample backward in time (coalescence approach; Rosindell et al. 2008). This simulation strategy is used here to generate  $\mathbf{s}$  and  $\mathbf{u}$  samples within local sites, from which  $R_{\text{all}}$  and  $R_{\text{spe}}$  are computed. More details about the simulation algorithm are provided in supporting material.

In all the simulations, the regional community contains 20 species, the relative abundances of which are derived from a truncated geometric distribution with parameter 0.2 (i.e.,  $f_i = (1 - 0.2) \times 0.2^{i-1} / (1 - 0.2^{20})$ ). The most abundant species in the regional pool is chosen as the focal one ( $f_e \approx 0.8$ ) to avoid discarding many sites because of unsuccessful sampling; this is a reasonable assumption with regard to empirical studies reporting SGDCs, which generally analyze genetic diversity in common species. Under weak mutation,  $\theta$  is set to 10. Under strong mutation,  $\mu$  is set to  $10^{-3}$ , in line with what is known for microsatellite markers (Jarne and Lagoda 1996; Ellegren 2002). Landscapes considered here are sets of 100 sites.  $K$  and  $m$  per site are determined by sampling ( $\log(K - 1)$ ,  $\log[m/(1 - m)]$ ) in a “discretized” bivariate Gaussian distribution with mean  $(\alpha_K, \alpha_m)$ , marginal variances



( $\sigma_K^2, \sigma_m^2$ ), and covariance  $\rho_{Km}\sigma_K\sigma_m$  (app. B). The size of the species sample  $\mathbf{s}$  is set to  $S = 50$  individuals, and that of the genetic sample  $\mathbf{u}$  is set to  $k = 5$  individuals. In each site,  $R_{\text{all}}$  and  $R_{\text{spe}}$  values are obtained by simulating the above-mentioned coalescent process (pseudo code available online) with an algorithm implemented in Java (Jdk 7u17, Oracle; code available from the authors upon request). SGDC is computed from the values of  $R_{\text{all}}$  and  $R_{\text{spe}}$  across sites, using Pearson's correlation coefficient.

### Results

An important outcome of our work is to provide a decomposition of the covariance between diversity levels ( $C_{\text{sg}}$ ) into effects occurring within ( $C_{\text{within}}$ ) and among sites ( $C_{\text{among}}$ ) and derive predictions about each of them. We separately analyzed each type of effects in our model and generated conclusions about the overall sign and value of SGDC. Because the mutation-to-migration ratio strongly affects both  $C_{\text{within}}$  and  $C_{\text{among}}$ , we considered the weak mutation regime and the strong mutation regime separately.

#### Weak Mutation Regime

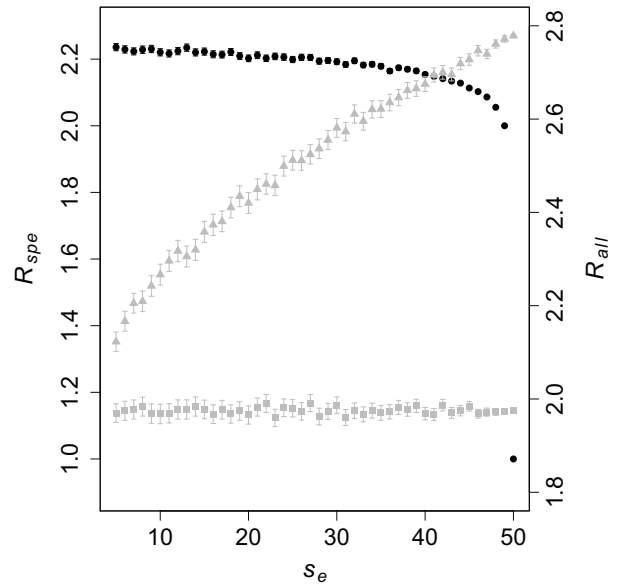
The behavior of the within- and among-site components of  $C_{\text{sg}}$  can be analyzed by considering the joint probability of  $\mathbf{s}$  and  $\mathbf{u}$ . Under the weak mutation regime, we established that the compositions of  $\mathbf{s}$  and  $\mathbf{u}$  are probabilistically independent within a site (app. A), so that  $C_{\text{within}}$  is null. This result is a consequence of controlling for genetic sample size (through the parameter  $k$  here) when estimating genetic diversity, thus dampening any effect of local population size on  $R_{\text{all}}$ . We performed repeated simulations of a single site with given  $K$  and  $m$  values to estimate the relation between genetic and species diversity and the abundance of the focal species in the site. Because  $s_e$  provides a proxy for the abundance of the focal species within sites, species and genetic diversity were actually sorted as a function of  $s_e$  (fig. 2). As predicted by our theoretical analysis (see app. A),  $R_{\text{spe}}$  decreases with  $s_e$ , but  $R_{\text{all}}$  does not show any trend with respect to  $s_e$ .

As the within-site component is null, the covariance between species and genetic diversity under the weak mutation regime reduces to the  $C_{\text{among}}$  component, which depends on the variation in  $(K, m)$  among sites. It turns out that the latter influences  $\mathbf{s}$  and  $\mathbf{u}$  compositions only through the variation in  $I = (K - 1)m/(1 - m)$ , the so-called effective number of migrants (app. A; Etienne and Olff 2004; Etienne and Alonso 2005), which quantifies the relative strength of drift and immigration within sites. The expression of  $C_{\text{among}}$  in equation (1) can therefore be rewritten as

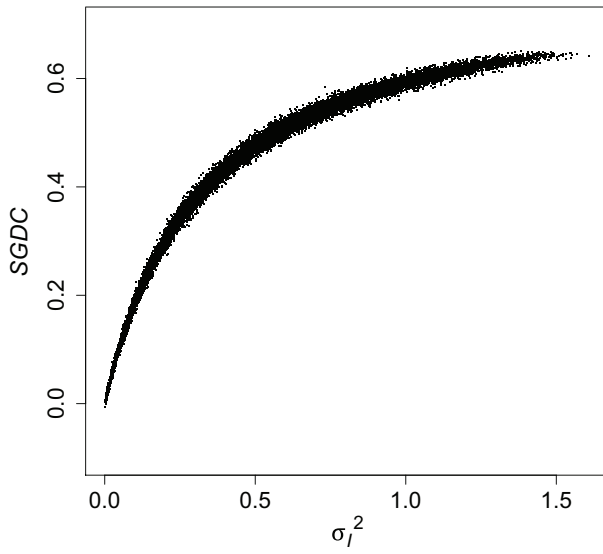
$$C_{\text{among}} = \text{Cov}[\overline{R_{\text{spe}}}(I), \overline{R_{\text{all}}}(I)], \quad (2)$$

where overlined quantities are expectations in sites with parameter  $I$ . It can be shown (app. A) that both  $\overline{R_{\text{spe}}}(I)$  and  $\overline{R_{\text{all}}}(I)$  increase with  $I$ , so that  $C_{\text{among}}$  is expected to be positive.

From these results,  $C_{\text{sg}}$  (equal to  $C_{\text{among}}$ ) always takes positive values. Simulations (fig. 3) illustrate these theoretical expectations: simulated SGDCs are always positive. Moreover, SGDCs increase with the variance in  $I$  and, for a given variance in  $I$ , they show very little variation. These results are consistent with our theoretical prediction: both  $R_{\text{spe}}$  and  $R_{\text{all}}$  depend on site parameters through the value of  $I$  only and increase with  $I$ . The variance in  $I$  is positively related to the variances in both  $K$  and  $m$  as well as to the covariance between  $K$  and  $m$ . Note, however, that a large variance in both  $K$  and  $m$ , associated to a strong negative covariance between these two parameters, generates a low variance in  $I$ , leading to weak values of  $C_{\text{sg}}$  and SGDCs (app. B).



**Figure 2:** Variation in mean  $R_{\text{spe}}$  and  $R_{\text{all}}$  as a function of  $s_e$  (sampling size of the focal species) in a site with given carrying capacity ( $K$ ) and connectivity ( $m$ ). A total of 10,000 simulations were performed under each mutation regime. Simulation outputs were sorted according to  $s_e$  value, and for each  $s_e$  value, the mean values of observed  $R_{\text{spe}}$  (black circles),  $R_{\text{all}}$  under weak mutation (gray squares), and  $R_{\text{all}}$  under strong mutation (gray triangles) are reported. For  $R_{\text{spe}}$ , the output of the 20,000 simulations are considered together to compute mean values for each  $s_e$  (because  $R_{\text{spe}}$  does not depend on the mutation regime). A 95% confidence interval (1.96 times the standard error) is given with the  $R_{\text{spe}}$  and  $R_{\text{all}}$  mean values. Other parameters are set to  $K = 1,000$ ,  $m = 0.001$ ,  $B = 20$ ,  $f_i = (1 - 0.2) \times 0.2^{i-1}/(1 - 0.2^{20})$ ,  $e = 1$ ,  $f_e \approx 0.8$ ,  $\theta = 10$  (for weak mutation),  $\mu = 10^{-3}$  (for strong mutation),  $S = 50$ , and  $k = 5$ .



**Figure 3:** Mean species-gene diversity correlation (SGDC) as a function of  $\sigma_I^2$  (the variance in  $\log_{10} I$  across sites) under the weak mutation regime for a set of simulated landscape. Each point corresponds to a landscape. For each landscape,  $(K, m)$  follows a bivariate discretized lognormal distribution (see “Material and Methods”). The mean of SGDCs obtained in 500 independent simulations is represented as a function of  $\sigma_I^2$ , recalling that  $\sigma_I^2 = \sigma_K^2 + \sigma_m^2 + 2\rho_{Km}\sigma_K\sigma_m$  (see app. B).  $\sigma_m^2$  and  $\rho_{Km}$  are numerically explored over the  $[0, 1] \times [-1, 1]$  space by steps of 0.01, leading to 19,900 combinations. Other parameters are set to  $\alpha_K = 3, \alpha_m = -3, \sigma_K^2 = 3, B = 20, f_i = (1 - 0.2) \times 0.2^{i-1}/(1 - 0.2^{20}), e = 1, f_c \approx 0.8, \theta = 10, S = 50$ , and  $k = 5$ .

#### Strong Mutation Regime

Under the strong mutation regime,  $C_{\text{within}}$  is not necessarily zero anymore. Indeed,  $R_{\text{all}}$  increases with  $s_e$ , whereas  $R_{\text{spe}}$  tends to decrease (fig. 2), generating negative expectations for  $C_{\text{within}}$ . This clearly appears when simulating homogeneous landscapes, with the same  $(K, m)$  values in all sites (i.e.,  $C_{\text{among}} = 0$ ; fig. 4). The SGDC is negative, especially when the carrying capacity  $K$  of sites is large and their immigration rate  $m$  is small. A delta method to order 0 on  $C_{\text{within}}$  in equation (1) yields the following approximation:

$$C_{\text{within}} \approx \text{Cov}_{\text{floor}(\bar{K}), \bar{m}} [R_{\text{spe}}, R_{\text{all}}], \quad (3)$$

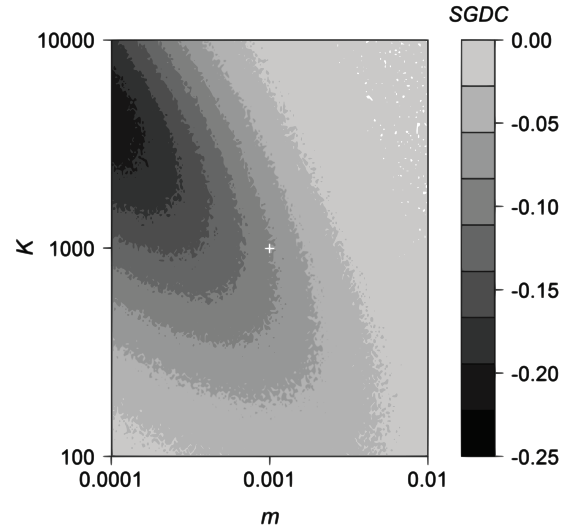
where  $\bar{K}, \bar{m}$  are means of  $K$  and  $m$  across the landscape and  $\text{floor}()$  is the integer part operator. Other notations are similar to equation (1). We expect  $C_{\text{within}}$  to depend mostly on mean carrying capacity and immigration in the set of sites and not on variance and covariance of  $K$  and  $m$  across sites. Thus the negative impact observed in the homogeneous landscapes ( $K$  and  $m$  constant across sites) detailed in figure 4 should also occur in more complex landscapes that share the same  $(\bar{K}, \bar{m})$  values. However,

the total covariance will result from the addition of  $C_{\text{within}}$  and  $C_{\text{among}}$ , which may have different signs.

Mutation also has an impact on  $C_{\text{among}}$ . As under the weak mutation regime,  $C_{\text{among}}$  is affected by variation in  $I$ , but also by variation in migration alone ( $m$ ), independently from  $I$ . This is because, when migration is high, mutation events have less impact on within-site diversity, which depends mainly on new alleles brought by immigrants (app. A). The expression of  $C_{\text{among}}$  is more complex than under the weak mutation regime (eq. [2]), because genetic diversity depends on both  $I$  and  $m$  as follows:

$$\begin{aligned} C_{\text{among}} &= \text{Cov} [\bar{R}_{\text{spe}}(I), \bar{R}_{\text{all}}(I, m)] \\ &\approx \frac{\partial \bar{R}_{\text{spe}}}{\partial I} \times \frac{\partial \bar{R}_{\text{all}}}{\partial I} \text{Var}(I) \\ &\quad + \frac{\partial \bar{R}_{\text{spe}}}{\partial I} \times \frac{\partial \bar{R}_{\text{all}}}{\partial m} \text{Cov}[I, m], \end{aligned} \quad (4)$$

where the notation is identical to that in equation (2),  $\partial$  is the symbol for partial derivative, and the approximation



**Figure 4:** Values of species-gene diversity correlations (SGDCs) with respect to carrying capacity ( $K$ ) and immigration rate ( $m$ ) of sites for simulated homogeneous landscapes (i.e.,  $\sigma_K^2$  and  $\sigma_m^2$  are set to zero) under strong mutation. For each landscape, 500 simulations were performed, and the average SGDC was reported as a dot in the  $(m, K)$  space, with a shade of gray indicating the magnitude of the associated value. The white dots on the upper-right corner represent simulations for which a positive SGDC was obtained because of numerical noise. The white cross indicates the points used as a mean in site distributions of figures 5 and 6.  $K$  and  $m$  were numerically explored on logarithmic scales, leading to 40,401 sets of parameters (landscapes). Other parameters were set to  $B = 20, f_i = (1 - 0.2) \times 0.2^{i-1}/(1 - 0.2^{20}), e = 1, f_c \approx 0.8, \mu = 10^{-3}, S = 50$ , and  $k = 5$ .

is based on the delta method. Equation (4) shows that  $C_{\text{among}}$  is influenced by  $I$  at both organizational levels (first term in the approximation) but also by the spatial covariation between  $I$  and  $m$  (second term in the approximation). As mentioned in the section on weak mutation,  $\overline{R_{\text{spe}}}(I)$  is an increasing function of  $I$ .  $\overline{R_{\text{all}}}(I, m)$  is an increasing function of  $I$  ( $m$  being constant; app. A) and a decreasing function of  $m$  ( $I$  being constant; app. A). The variation in  $I$  (first term) therefore contributes positively to  $C_{\text{among}}$  (first term), whereas a positive correlation between  $I$  and  $m$  among sites has a negative impact on  $C_{\text{among}}$  (second term).

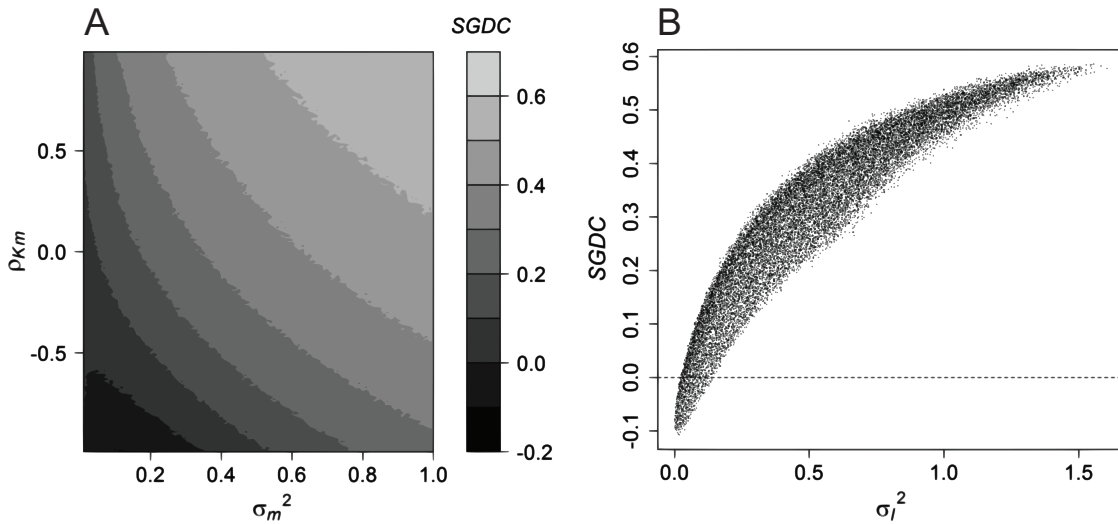
The sign of  $C_{\text{sg}}$  depends on the relative values and sign of  $C_{\text{within}}$  and  $C_{\text{among}}$  (eq. [1]). When the variance in  $I$  across sites is very low, equation (4) implies that  $C_{\text{among}}$  is close to 0, and  $C_{\text{within}}$  is the dominant term in equation (1).  $C_{\text{sg}}$  is then expected to be negative. Our simulations confirm this prediction: figure 5A illustrates that negative SGDCs occur when the variance in  $m$  is low and the correlation between  $K$  and  $m$  negative; this corresponds to the region where the variance in  $I$  is the lowest in figure 5B. When the variance in  $I$  increases, equation (4) suggests that  $C_{\text{among}}$  increases, whereas equation (3) suggests that  $C_{\text{within}}$  remains unchanged as it is mostly determined by the means of  $K$  and  $m$  over sites and not by variance or covariance of  $K$  and  $m$  (or equivalently  $I$  and  $m$ ) across sites. Therefore, theory predicts that  $C_{\text{sg}}$  increases and becomes positive when the effect of  $C_{\text{among}}$  exceeds that of

$C_{\text{within}}$ . We retrieve these results through simulations when considering the SGDC rather than  $C_{\text{sg}}$ : the SGDC increases with the variance in  $I$  and eventually becomes positive (fig. 5B).

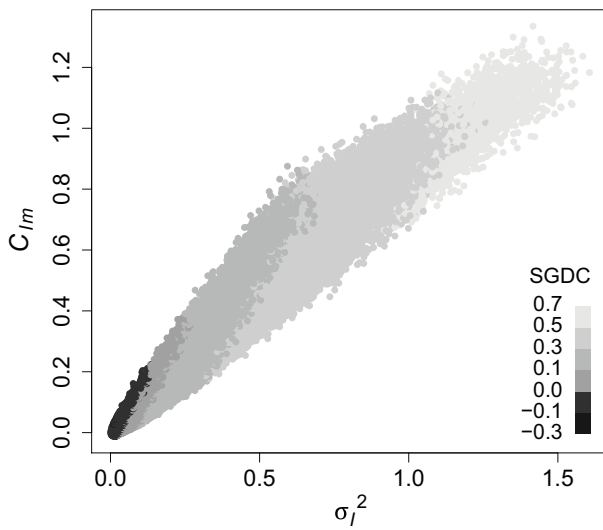
A comparison of figure 3 (weak mutation) with figure 5B (strong mutation) indicates that the variance in  $I$  is not as good a predictor of the value of SGDC in the latter as in the former case. Equation (4) shows a negative effect of the covariance between  $I$  and  $m$  on  $C_{\text{among}}$  under strong mutation, in addition to variance in  $I$ . Representing the SGDC as a function of both the variance in  $I$  and the covariance between  $m$  and  $I$  (or equivalently between  $\log[m/(1-m)]$  and  $\log(I)$ ,  $C_{\text{Im}}$ ; fig. 6) corroborates that, for constant  $\sigma_I^2$ , the SGDC consistently decreases with  $C_{\text{Im}}$ , as predicted by equation (4). Although the parameterization in  $(I, m)$  makes computation simpler, the initial parameterization in  $(K, m)$  is more accessible to intuition. In terms of  $(K, m)$  distribution, increasing  $C_{\text{Im}}$  value for a constant  $\sigma_I^2$  value can be achieved, for instance, by increasing the variance in  $m$ , keeping variance in  $K$  constant, and making  $\rho_{Km}$  more negative (app. A). This effect of  $C_{\text{Im}}$  explains the wider spread of the values of SGDC for a given  $\sigma_I^2$  in figure 5B than in figure 3.

### Discussion

Community genetics is a rising field of research that has developed along several lines, such as studying relation-



**Figure 5:** Values of expected species-gene diversity correlation (SGDCs) with respect to the variation (and covariation) in  $K$ ,  $m$  and  $I$  across sites for simulated landscapes under the strong mutation regime. A total of 500 simulations were performed for each of the sets of parameters, and the mean SGDC was computed. Panel A depicts the mean value of SGDC as a function of  $\sigma_m^2$  and  $\rho_{Km}$ . Panel B depicts the mean value of SGDC as a function of  $\sigma_I^2$ .  $\sigma_m^2$  and  $\rho_{Km}$  were numerically explored over the  $[0, 1] \times [-1, 1]$  space by steps of 0.01, leading to 19,900 combinations. Other parameters were set to  $\alpha_K = 3$ ,  $\alpha_m = -3$ ,  $\sigma_K^2 = 3$ ,  $B = 20$ ,  $f_i = (1 - 0.2) \times 0.2^{i-1}/(1 - 0.2^{20})$ ,  $e = 1$ ,  $f_e \approx 0.8$ ,  $\mu = 10^{-3}$ ,  $S = 50$ , and  $k = 5$ .



**Figure 6:** Values of expected species-gene diversity correlations (SGDCs) with respect to the variation in  $I$  and the covariation between  $m$  and  $I$  across sites (i.e., the  $[\sigma_I^2, C_{lm}]$  space) for simulated landscapes under the strong mutation regime. A total of 500 simulations were performed for each landscape, and mean SGDC was represented here by a dot, with shades of gray indicating the associated value. The parameters were set to  $\alpha_K = 3$ ,  $\alpha_m = -3$ ,  $\sigma_K^2 = 3$ .  $\sigma_m^2$  and  $\rho_{Km}$  were numerically explored in  $[0, 1] \times [-1, 1]$  by step of 0.01, leading to 19,900 combinations. Other parameters were set to  $B = 20$ ,  $f_i = (1 - 0.2) \times 0.2^{i-1} / (1 - 0.2^{20})$ ,  $e = 1$ ,  $f_e \approx 0.8$ ,  $\mu = 10^{-3}$ ,  $S = 50$ , and  $k = 5$ .

ships between herbivore communities and the genetics of plants supporting these communities at small geographic scale (Bernhardsson et al. 2013; McArt and Thaler 2013) or using phylogeography to better understand past processes that have shaped present communities at larger scale (Wares 2002; Webb et al. 2002). The study of correlations between genetic diversity at the species level and species diversity at the community level (SGDCs; Vellend and Geber 2005) is one of these offshoots. Up to now, predictions on SGDCs have essentially been formalized on the basis of verbal models. We propose here a theoretical framework encompassing both species and genetic levels to more fully analyze and interpret SGDCs. We based our work on genealogical approaches and sampling formulae that are now commonly used in both population genetics (Wakeley 2008) and community ecology (Etienne and Olff 2004) to infer processes from patterns. Those techniques proved very useful, for instance, when searching for selective processes (Fu and Li 1993; Etienne 2005, 2007). Although sampling formulae are available for modeling both genetic and species dynamics (Etienne and Alonso 2005), we know of no previous work generating simultaneous predictions at both levels on the basis of a generalized coalescent of genes and species.

An important result of our work is that the covariance between species richness and allelic richness ( $C_{sg}$ ) can be additively decomposed into (i) the effect of competition between the focal species and other species within local sites (the  $C_{within}$  term) and (ii) the parallel effect of variation in carrying capacity and immigration rate of sites on allelic and species richness (the  $C_{among}$  term; eq. [1]). Both effects had previously been identified in the literature. Local competition was thought to negatively affect SGDCs (i.e.,  $C_{within} < 0$  in our framework; Vellend 2005; Wehenkel et al. 2006), while variation in area and isolation among sites was thought to generate positive SGDCs (i.e.,  $C_{among} > 0$ ; Vellend 2003). The dominant effect could, in principle, be inferred from the SGDC sign without further need of a quantitative framework. However, our predictions are partially at variance with these intuitions. When the mutation rate is much lower than the immigration rate,  $C_{among}$  is positive, as expected, but  $C_{within}$  is always zero. When the mutation rate is comparable to or higher than the immigration rate,  $C_{within}$  is negative, which corresponds to expectations, but  $C_{among}$  can take both signs, which does not.

Because mutation drastically changes the predictions on SGDC patterns, an important aspect in empirical studies should be to determine the mutation-to-migration ratio before interpreting SGDCs. In particular, many estimates of SGDCs are based on microsatellites when evaluating the genetic diversity (Cleary et al. 2006; He et al. 2008; Struebig et al. 2011; Blum et al. 2012; Lamy et al. 2013). These markers may have high mutation rates (Jarne and Lagoda 1996; Ellegren 2002) that are potentially high enough to compare with immigration rates, especially in isolated sites. Insights on the mutation-to-migration ratio can be obtained by computing the relationships between a proxy of the number of migrants in a site ( $I$ ), a proxy of the local carrying capacity ( $K$ ), and the allelic richness of the focal species. If allelic richness increases with carrying capacity when controlling for the number of migrants (which can be assessed with a partial correlation analysis for instance), this suggests that mutation contributes strongly to the build-up of variation in these sites. Alternatively, one can also directly use the genetic polymorphism of the focal species to assess the relative strength of mutation and migration processes. For instance, when considering microsatellites, testing for a significant difference between  $R_{ST}$  and  $F_{ST}$  estimators of genetic structure in the focal species could help in evaluating whether mutation could be neglected (Hardy et al. 2003). We note that speciation may have an impact on SGDC patterns similar to that of mutation. Speciation was not considered in our model, because we focused on a temporal/spatial scale at which it is unlikely to generate species variation to a significant extent. When the immigration and speciation rates are of



similar magnitude (e.g., in isolated metacommunities, such as archipelagoes), a larger number of endemic species should be generated in sites with lower immigration rates (Rosindell and Phillimore 2011). Interactions between the effects of speciation and connectivity on SGDC should then be similar to those detected in our model about mutation.

When mutation is weak compared with immigration, our model predicts that local competition should not affect the SGDC pattern. We emphasize here the importance of the sampling protocol. Earlier studies predicted a negative  $C_{\text{within}}$ , because genetic diversity of the focal species is expected to increase with its population size (Vellend 2005; Wehenkel et al. 2006). The sampling protocol of our model (fig. 3) did not allow this positive relationship to occur, because a fixed number of individuals of the focal species were genotyped ( $k$  individuals in sample  $u$ ; smaller samples were disregarded). Other sampling protocols can generate the same disconnection between the allelic richness and the population size of the focal species as long as they incorporate a control of the genetic sample size. For instance, the same disconnection occurs when genetic diversity is measured by genotyping all individuals belonging to the focal species ( $t$ ) and computing a rarefied richness indicator (Petit et al. 1998), as most empiricists do. Under weak mutation, controlling for the size of species and genetic samples filters out the influence of local competition, which facilitates the interpretation of observed patterns.

As the among-sites effect is always positive under weak mutation, our neutral theory yields the simple prediction that SGDC should always be positive and reflects the variance of the effective number of migrants among sites (fig. 3). Empirical studies that (i) demonstrated that mutation is weak, (ii) controlled for sample size in the sampling protocol, and (iii) observed strong variation in size and connectivity among sites should then expect a positive SGDC. When this prediction is not verified, it may mean one of three things. First, variation in size and connectivity may be negatively correlated among sites in such a way that the overall variation in the number of immigrants among sites is low (app. B). Second, there may be a non-neutral process at work. For instance, Derry et al. (2009) illustrated how species-sorting along an environmental gradient may contribute to cancel the positive parallel effects of variation in size and connectivity on SGDC. Finally, some other assumptions of our model may be violated. The last explanation may apply when considering spatially continuous systems (e.g., alpine forest; Taberlet et al. 2012) for which our implicit description of space may prove insufficient to describe the spatial autocorrelation in the system.

Under strong mutation, the analysis of SGDC patterns is different, because the correlation sign predicted by the

neutral theory developed here is more labile than under the weak mutation regime. On the one hand, local competition ( $C_{\text{within}}$  term) has a negative impact on SGDC. Indeed, the positive relationship between the population size of the focal species and the allelic richness of the genetic sample is maintained, and this occurs even when controlling for genetic sample size (fig. 3). On the other hand,  $C_{\text{among}}$  can take either sign depending on the co-distribution of carrying capacities and immigration rates among sites. In particular, a negative  $C_{\text{among}}$  value emerges when sites tend to receive the same effective number of immigrants per generation irrespective of their carrying capacity (i.e., low variance in  $I$ ). Such a situation could occur, for example, in fragmented landscapes with patches of different sizes connected by corridors; the effective number of immigrants would primarily depend on the presence of corridors and may be uncorrelated to patch size (which determines its carrying capacity). On the whole, any sign of the SGDC is compatible with the neutral framework when mutation is strong, so that, contrary to the weak mutation regime, neutrality cannot be rejected on the basis of the sign of the correlation only. Note, however, that using markers that show different levels of polymorphism (using polymorphism as a proxy of mutation rate) may provide further tests. If the correlation is positive when using poorly variable markers and negative when considering highly variable ones, the overall observation is compatible with the neutral framework. By contrast, a consistently negative SGDC, whatever the level of polymorphism of the considered marker, may be interpreted as a rejection of our neutral model. When our framework applies, interpreting the SGDC sign under strong mutation is not straightforward. A significantly positive SGDC indicates a strong positive  $C_{\text{among}}$  and can be interpreted as an effect of high variance in the number of migrants among sites. However, nonsignificant and negative SGDCs lead to ambiguous interpretation. In particular, negative correlations can indicate an effect of local competition but can also result from a negative  $C_{\text{among}}$ .

One way to progress in the interpretation of SGDCs is to decompose the covariance between species and genetic diversity ( $C_{\text{sg}}$ ) into the  $C_{\text{within}}$  and  $C_{\text{among}}$  effects. Some authors suggested statistical methods to analyze the contribution of size and connectivity of sites to the overall SGDC (Vellend 2003; Lamy et al. 2013). Both studies detected significantly positive SGDCs along with a strong contribution of area and connectivity, respectively, to these correlations, which may indicate a strong positive  $C_{\text{among}}$ . Our model provides a theoretical basis for going one step further in this analysis by allowing a covariance decomposition based on mechanisms (instead of environmental factors) to be performed in empirical studies. One approach could be to estimate  $I$  in sites and to directly per-

form covariance decomposition along those estimates instead of using proxies of size and connectivity, as done in former studies. This should provide a more direct assessment of  $C_{\text{among}}$ . However, estimating  $I$  is not straightforward. One solution could be to use loci different from those used to compute SGDCs and to independently assess the migration-drift ratio in populations of the focal species through  $Nm$  ( $N$  and  $m$  are the population size and immigration rate, respectively, in, for example, island models of population structure; Rousset 2004), which should provide a relevant proxy for  $I_f$ . Separate estimates of  $f_c$  could be obtained by other approaches, such as by pooling all the local species samples to generate a regional sample (Jabot et al. 2008) so that  $I$  could be isolated. Ultimately, decomposing SGDC patterns should contribute to a deeper understanding than the sign of SGDC alone. Beyond helping to interpret ambiguous cases such as negative SGDCs under strong mutation, disentangling  $C_{\text{within}}$  and  $C_{\text{among}}$  may also provide new tests of our framework: for instance, under low mutation, observing a large positive SGDC but no significant  $C_{\text{among}}$  may indicate other non-neutral processes, such as positive interactions between the focal species and the rest of the community within sites (e.g., facilitation in plant communities; Brooker et al. 2008).

With the building of an adequate theory, SGDC patterns may be used to study the processes, such as dispersal and drift, acting in metacommunities. Certainly, a further step is the development of neutral models, including a full sampling theory to provide useful null hypotheses to detect selective processes, based on both species count data and genomic sequencing. The spectacular increase in the availability of genomic data opens interesting perspectives. It seems unlikely, however, that comparison of local diversity across levels provides enough information to unravel the complex processes acting in metacommunities, such as niche structure and environmental filtering among sites. Interestingly enough, empirical studies have started to report other patterns, such as correlations between species and genetic  $\beta$ -diversity (Papadopoulou et al. 2011; Baselga et al. 2013). Theoretical analyses, along the line followed here, are certainly required to evaluate their inferential power and to incorporate them in a spatially explicit neutral theory of SGDCs.

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## Appendix A from F. Laroche et al., “A Neutral Theory for Interpreting Correlations between Species and Genetic Diversity in Communities” (Am. Nat., vol. 185, no. 1, p. 000)

### Mathematical Analysis of the Neutral Model of SGDC

#### Timescale Assumptions about Speciation and Mutation in the Neutral Model of the SGDC

We first define the local timescale in the model. We then provide conditions on model parameters that allow us to assume constant relative abundances of species in the regional pool at the local timescale as well as those under which mutation can be neglected.

##### *Definition and Duration of Local Timescale*

The whole theoretical treatment of the model is done considering the associated coalescent process. In other words, we focus on lineages of a given sample of individuals going from the present toward the past. Backward in time, lineages within local sites can either merge (a coalescence event) or go back in the regional pool (an immigration event). The number of lineages within sites decreases because of coalescence and immigration events until reaching zero. The event that leads to this state is necessarily an immigration event, because the last lineage in the site has no other lineage to merge with. We refer to this event as “first immigration.” We define the local timescale as the time span that goes from the first immigration to the present.

In a local site with parameters  $K$  and  $m$ , a lineage has a probability  $m/K$  of undergoing a death-birth event and reaching immigration at each time step. Then, assuming that  $S$  individuals have been sampled at the present time, one gets a rough upper bound of local timescale  $T_{\text{loc}}$

$$\mathbb{E}[T_{\text{loc}}] \leq \frac{SK}{m} \delta_{\text{loc}} = \frac{S}{m} \Lambda, \quad (\text{A1})$$

where  $\delta_{\text{loc}}$  is the expected duration of a time step in the site and  $\Lambda$  is the life expectancy of an individual. In the following, we assume that  $S$  is not very high ( $S = 50$ ).

##### *Condition for Getting a Constant Composition of the Regional Species Pool at the Local Timescale*

Making the assumptions that (i) the regional pool of individuals undergoes a death-replacement dynamic, (ii)  $K_{\text{reg}} \gg 1$ , and (iii) speciation can be neglected ensures that the stochastic dynamics of species  $i$  relative abundance ( $f_i$ ) verifies

$$\begin{cases} \mathbb{P}(f_i(t+1) = f_i(t) + df | f_i(t)) = (1 - f_i(t))f_i(t) \\ \mathbb{P}(f_i(t+1) = f_i(t) | f_i(t)) = (1 - f_i(t))^2 + f_i(t)^2 \\ \mathbb{P}(f_i(t+1) = f_i(t) - df | f_i(t)) = f_i(t)(1 - f_i(t)) \end{cases}, \quad (\text{A2})$$

where  $df = 1/K_{\text{reg}}$  and time is measured in regional death replacement cycles (i.e., on the scale of  $\Lambda/K_{\text{reg}}$ ).

Equation (A2) yields  $f_i$  conditional variance through time

$$\mathbb{V}[f_i(t+z)|f_i(t)] = (1 - f_i(t))f_i(t) \left\{ 1 - \left[ 1 - 2 \left( \frac{K_{\text{reg}}}{K_{\text{reg}} - 1} \right) df^2 \right]^{K_{\text{reg}}(z/\Lambda)} \right\}, \quad (\text{A3})$$

where  $z$  is a time span measured in real time.

Equation (A3) yields a sufficient condition to consider that species  $i$  relative abundance is constant over time span  $z$

$$\begin{aligned}
 1 - \left[ 1 - 2 \left( \frac{K_{\text{reg}}}{K_{\text{reg}} - 1} \right) df^2 \right]^{K_{\text{reg}}(z/\Lambda)} &\ll 1 \Rightarrow \\
 \left[ 1 - 2 \left( \frac{K_{\text{reg}}}{K_{\text{reg}} - 1} \right) df^2 \right]^{K_{\text{reg}}(z/\Lambda)} &\approx 1 \Rightarrow \\
 e^{-2z/\Lambda(K_{\text{reg}}-1)} \approx 1 &\Rightarrow \frac{2z}{\Lambda K_{\text{reg}}} \ll 1.
 \end{aligned} \tag{A4}$$

Coming back to the model and combining equation (A1) and condition (A4), one obtains a sufficient condition on local immigration rate to consider the structure of the regional species pool as a constant at the local timescale

$$1 \ll K_{\text{reg}} m. \tag{A5}$$

A sufficient condition justifying that the impact of speciation on regional relative abundances can be neglected at the local timescale is

$$\frac{S}{m} \Lambda K_{\text{reg}} \nu \ll K_{\text{reg}} \Rightarrow \nu \ll m, \tag{A6}$$

where  $\nu$  would be a punctual “per cycle” speciation rate. We assume that both conditions are verified in this work.

#### Condition to Neglect Mutation at Local Timescale

We consider an infinite-alleles model with mutation rate  $\mu$ . The probability of observing no mutation at the local scale during coalescence is less than  $(1 - \mu)^{S/m} \approx e^{-\mu S/m}$ . The condition  $m \gg \mu$  ensures that mutation can be locally neglected. We refer to this situation as the “weak mutation regime.” By analogy with condition (A6) above, this condition also ensures that the allelic frequencies in the regional population of the focal species can be considered constant at the local timescale.

We also consider the “strong mutation” situation, in which  $m \approx \mu$ . Assuming that the focal species is not rare (a necessary assumption to perform sampling, as shown in app. A), inequality (A1) implies  $\theta = K_{\text{reg}} f_e \mu \gg 1$ . The regional population of the focal species shows enough genetic variability to ensure that any new immigrant in local sites harbors an allele that never occurred locally before.

### Complete Analysis of the Neutral Model of the SGDC under the Weak Mutation Regime

We consider local sites with parameters  $(K, m)$ , and we define  $I = (K - 1)m/(1 - m)$ . We assume that condition (A6) is verified. First, we establish the joint sampling formula for species and genetic samples and show that both sample composition are probabilistically independent given  $s_e$ . Then, we develop the case of species richness and genetic richness. We finally discuss how these theoretical results may be biased when neglecting the assumption that  $s_e \geq k$  in the site.

#### Joint Sampling Formula and Independence of $\mathbf{s}$ and $\mathbf{u}$

When the condition  $s_e \geq k$  is neglected, species sample structure follows the distribution described in Etienne and Alonso (2005),

$$\mathbb{P}(\mathbf{s}) = \frac{S!}{\prod_{i=1}^B s_i!} \times \frac{\prod_{i=1}^B (If_i)_{(s_i)}}{(I)_{(S)}}, \tag{A7}$$

where  $x_{(n)} = \prod_{i=0}^{n-1} (x + i)$ . In the following, we note  $\mathbb{P}_{s_e}$  probabilities conditionally on  $s_e$ . Using the sampling formula of Etienne and Alonso (2005), we derive the probability of  $\mathbf{t}$  composition conditionally on  $s_e$ ,

$$\begin{aligned} \mathbb{P}_{(s_e)}(\mathbf{t}) &= \frac{\mathbb{P}(s_e \cap \mathbf{t})}{\mathbb{P}(s_e)} \\ &= \frac{s![I(1-f_e)]_{(s-s_e)} \prod_{j=1}^A (If_e g_j)/(s-s_e)! \prod_{j=1}^A t_j!(I)_{(S)}}{s!(If_e)_{(s_e)} [I(1-f_e)]_{(s-s_e)} / s_e!(s-s_e)!(I)_{(S)}} \\ &= \frac{s_e!}{\prod_{j=1}^A t_j!} \times \frac{\prod_{j=1}^A (If_e g_j)_{(t_j)}}{(If_e)_{(s_e)}}, \end{aligned} \quad (\text{A8})$$

where  $\mathbf{g} = (g_1, g_2, \dots)$  is the allelic frequencies distribution for the genetic marker of the focal species (and  $g_1 > g_2 > \dots$   $\mathbf{g}$ ). It follows a Ewens distribution as described in Ewens and Tavaré (2006). This distribution is, in principle, infinite, but we truncated here at rank  $A$  (very large), leading to a renormalized frequency distribution  $\mathbf{g} = (g_1, g_2, \dots, g_A)$ . This allows us to use the sampling formulae of Etienne and Alonso (2005). Equation (A8) shows that, when  $s_e$  is known, the composition of  $\mathbf{t}$  follows a sampling formula that is similar to the one described in Etienne and Alonso (2005). This implies that  $\mathbf{t}$  structure verifies the “subsampling property” so that  $\mathbf{u}$  composition can be inferred as follows:

$$\mathbb{P}_{s_e}(\mathbf{u}) = \frac{k!}{\prod_{j=1}^A u_j!} \times \frac{\prod_{j=1}^A (If_e g_j)_{(u_j)}}{(If_e)_{(k)}}. \quad (\text{A9})$$

Equation (A9) does not depend on  $s_e$ , so the unconditional distribution of  $\mathbf{u}$  is given by

$$\mathbb{P}(\mathbf{u}) = \frac{k!}{\prod_{j=1}^A u_j!} \times \frac{\prod_{j=1}^A (If_e g_j)_{(u_j)}}{(If_e)_{(k)}}. \quad (\text{A10})$$

In particular, equation (A10) shows that the relative strength of migration compared with drift in the local populations of the focal species is  $If_e$ , instead of  $I$  for the whole community.

Using the sampling formula from Etienne and Alonso (2005), one can verify that

$$\begin{aligned} \mathbb{P}_{s_e}(\mathbf{s} \cap \mathbf{t}) &= \frac{S! / \prod_{i \neq e}^B s_i! \prod_{j=1}^A t_j! \times \prod_{i \neq e}^B (If_i)_{(s_i)} \prod_{j=1}^A (If_e g_j)_{(t_j)} / (I)_{(S)}}{S! / s_e!(S-s_e)! \times (If_e)_{(s_e)} (I(1-f_e))_{(S-s_e)} / (I)_{(S)}} \\ &= \frac{(S-s_e)!}{\prod_{i \neq e}^B s_i!} \times \frac{\prod_{i \neq e}^B (If_i)_{(s_i)}}{(I(1-f_e))_{(S-s_e)}} \times \frac{s_e!}{\prod_{j=1}^A t_j!} \times \frac{\prod_{j=1}^A (If_e g_j)_{(t_j)}}{(If_e)_{(s_e)}} \\ &= \mathbb{P}_{s_e}(\mathbf{s}) \mathbb{P}_{s_e}(\mathbf{t}). \end{aligned} \quad (\text{A11})$$

Equation (A11) shows that the composition of the remaining part of the species sample  $\mathbf{s}$  is independent from  $\mathbf{t}$  composition given  $s_e$ . With  $\mathbf{u}$  being a subsample of  $\mathbf{t}$ , this result also applies to  $\mathbf{u}$

$$\mathbb{P}_{s_e}(\mathbf{s} \cap \mathbf{u}) = \mathbb{P}_{s_e}(\mathbf{s}) \mathbb{P}_{s_e}(\mathbf{u}). \quad (\text{A12})$$

As shown in equation (A9),  $\mathbb{P}_{s_e}(\mathbf{u})$  does not depend on  $s_e$ . Thus, taking the expectation of equation (A12), we obtain the independence of  $\mathbf{s}$  and  $\mathbf{u}$  compositions

$$\mathbb{P}(\mathbf{s} \cap \mathbf{u}) = \mathbb{P}(\mathbf{s}) \mathbb{P}(\mathbf{u}). \quad (\text{A13})$$

### Species Richness and Allelic Richness

Using the sampling formula of Etienne and Alonso (2005), the probability  $\mathbb{P}_{s_e}(\mathbf{s})$  of observing a composition of the species sample given the number of individuals belonging to species  $e$  can be written as

$$\mathbb{P}_{s_e}(\mathbf{s}) = \frac{(S-s_e)!}{\prod_{i \neq e}^B s_i!} \times \frac{\prod_{i \neq e}^B (If_i)_{(s_i)}}{(I(1-f_e))_{(S-s_e)}}. \quad (\text{A14})$$



From equation (A14), we derive the probability  $p_i$  of species  $i$  occurring in the sample, given the number of individuals belonging to species  $e$

$$p_i = 1 - \frac{[I(1 - f_e - f_i)]_{(S-s_e)}}{[I(1 - f_e)]_{(S-s_e)}}. \quad (\text{A15})$$

Equation (A15) implies that the expectation for species richness in the species sample  $s$ , given the number of individuals belonging to species  $e$ , is equal to

$$\overline{R}_{\text{spe}}(s_e, I) = 1 + \sum_{i=1, i \neq e}^B p_i = B - \sum_{i=1, i \neq e}^B \frac{[I(1 - f_e - f_i)]_{(S-s_e)}}{[I(1 - f_e)]_{(S-s_e)}}. \quad (\text{A16})$$

It can be shown on the basis of a simple development of equation (A16) that  $\overline{R}_{\text{spe}}(s_e, I)$  is a decreasing function of  $s_e$ .

When not specifying the value of  $s_e$ , and neglecting the assumption that  $s_e \geq k$ , the species sample structure follows the distribution described in equation (A7). Therefore, the probability of species  $i$  occurring in the sample  $q_i$  is equal to

$$q_i = 1 - \frac{[I(1 - f_i)]_{(S)}}{(I)_{(S)}}. \quad (\text{A17})$$

Equation (A17) implies that the expectation for species richness in the species sample  $s$  is equal to

$$\overline{R}_{\text{spe}}(I) = \sum_{i=1}^B q_i = B - \sum_{i=1}^B \frac{[I(1 - f_i)]_{(S)}}{(I)_{(S)}}. \quad (\text{A18})$$

Equation (A18) is the expectation on species richness when no condition is put on the number of individuals belonging to species  $e$ . Little calculation from equation (A18) shows that  $\overline{R}_{\text{spe}}(I)$  is an increasing function of  $I$ .

Equation (A10) shows that  $\mathbf{u}$  sampling formula can be obtained from  $\mathbf{s}$  sampling formula by replacing  $I$  by  $If_e$ ,  $S$  by  $k$ , and  $f$  by  $g$ . Therefore, expected allelic richness in a site can be directly deduced from expected species richness in a site given by equation (A18),

$$\overline{R}_{\text{all}}(I) = A - \sum_{i=1}^A \frac{[If_e(1 - g_i)]_{(k)}}{(If_e)_{(k)}}, \quad (\text{A19})$$

and  $\overline{R}_{\text{all}}(I)$  is an increasing function of  $I$ .

#### Effects of Neglecting the Assumption That $s_e \geq k$

Neglecting the assumption that  $s_e \geq k$  leads to use equation (A7) instead of the true sampling formula that writes

$$\mathbb{P}(\mathbf{s}) = \begin{cases} 0 & \text{if } s_e < k \\ \frac{1}{1-P} \times \frac{S!}{\prod_{i=1}^B s_i!} \times \frac{\prod_{i=1}^B (If_i)_{(s_i)}}{(I)_{(S)}} & \text{if } s_e \geq k \end{cases}, \quad (\text{A20})$$

where  $P = \sum_{j=0}^{k-1} P_j$  is the probability of observing fewer than  $k$  individuals in the species sample, and  $P_j$  is the probability of observing exactly  $j$  individuals of species  $e$  in the sample.

We chose to work with equation (A7), because it leads to a more tractable derivation, but one needs to quantify the potential bias of such an approximation. The condition  $s_e \geq k$  has little effect on species sample when  $P \ll 1$ . To assess when this occurs, we place ourselves under the diffusion limit, where  $K \rightarrow +\infty$ ;  $m \rightarrow 0$ ;  $Km \rightarrow I$  finite.

Assuming that  $S \gg 1$  and defining  $\chi$  as the proportion of the species sample occupied by species  $e$  (i.e.,  $s_e/S$ ) density  $\phi$  of  $\chi$  writes (Wright 1931)

$$\phi(\chi; I, f_e) = \begin{cases} \frac{\Gamma(I)}{\Gamma(If_e)\Gamma[I(1-f_e)]} \chi^{If_e-1} (1-\chi)^{I(1-f_e)-1} & \text{if } \chi \in [0, 1] \\ 0 & \text{else} \end{cases}, \quad (\text{A21})$$

and probability  $P$  defined above asymptotically verifies

$$P = \int_0^{(k/S)} \phi(\chi; I, f_e) d\chi. \quad (\text{A22})$$

$P$  increases with  $k$ . According to the properties of the  $\beta$  distribution, one can predict that  $P$  decreases with  $f_e$ .

For given values of  $k/S$  and  $f_e$ , figure A1 shows that there exists a threshold of  $I$  above which  $P$  is negligible (i.e., below .05). It also shows that, for a given value of  $k/S$ , this threshold is a decreasing function of  $f_e$ . In the whole study, we consider situations in which  $P$  is negligible. To perform fast simulations, we focus on the case where  $k = 5$  and  $S = 50$  (i.e., a  $k/S$  ratio of 0.1; fig. A1A). We consider a focal species with regional relative abundance of 0.8 so that we have a threshold for  $I$  of 1. With those parameters,  $s$  composition could be considered to follow the distribution described in equation (A7).

## Analysis of the Variation in $\overline{R}_{\text{all}}(I, m)$ under the Strong Mutation Regime

Within local sites,  $R_{\text{all}}$  depends on two features: the number of migrants that funded the genetic sample  $\mathbf{u}$ , called  $N_A$  (for number of ancestors), and the number of mutation events that occur in the coalescence tree associated to  $\mathbf{u}$  (that we call the  $\mathbf{u}$  tree), called  $M$ .  $R_{\text{all}}$  is an increasing function of  $N_A$  ( $M$  being kept constant) and an increasing function of  $M$  ( $N_A$  being kept constant).

$N_A$  only depends on the topology of the  $\mathbf{u}$  tree (i.e., which lineages coalesce and which ones emigrate), which is exclusively driven by parameter  $I$ . Expectation of  $N_A$  is given by

$$\overline{N_A} = \sum_{n=1}^k \frac{If_e}{If_e + n - 1}. \quad (\text{A23})$$

The expected number of birth-death events in a lineage of the  $\mathbf{s}$  tree during the phase where the  $\mathbf{s}$  tree has exactly  $n$  local lineages  $\overline{B_n}$  is  $\overline{B_n} = [1/(nm)][I/(I + n - 1)]$ . Thus, the overall expected number of mutation events in the lineage during the same phase is given as  $\overline{F_n} = [\mu/(nm)][I/(I + n - 1)]$ . The  $\mathbf{u}$  tree is a subset of the branches of the  $\mathbf{s}$  tree. We define the set of random variables  $\mathcal{D} = \{D_1, \dots, D_S\}$ , where  $D_i$  is the number of branches of the  $\mathbf{u}$  tree during the phase where the  $\mathbf{s}$  tree has  $i$  lineages. The expectation of  $M$  writes

$$\overline{M} = \sum_{n=1}^S \overline{D_n} \overline{F_n} = \frac{\mu}{m} \sum_{n=1}^S \frac{\overline{D_n}}{n} \left( \frac{I}{I + n - 1} \right), \quad (\text{A24})$$

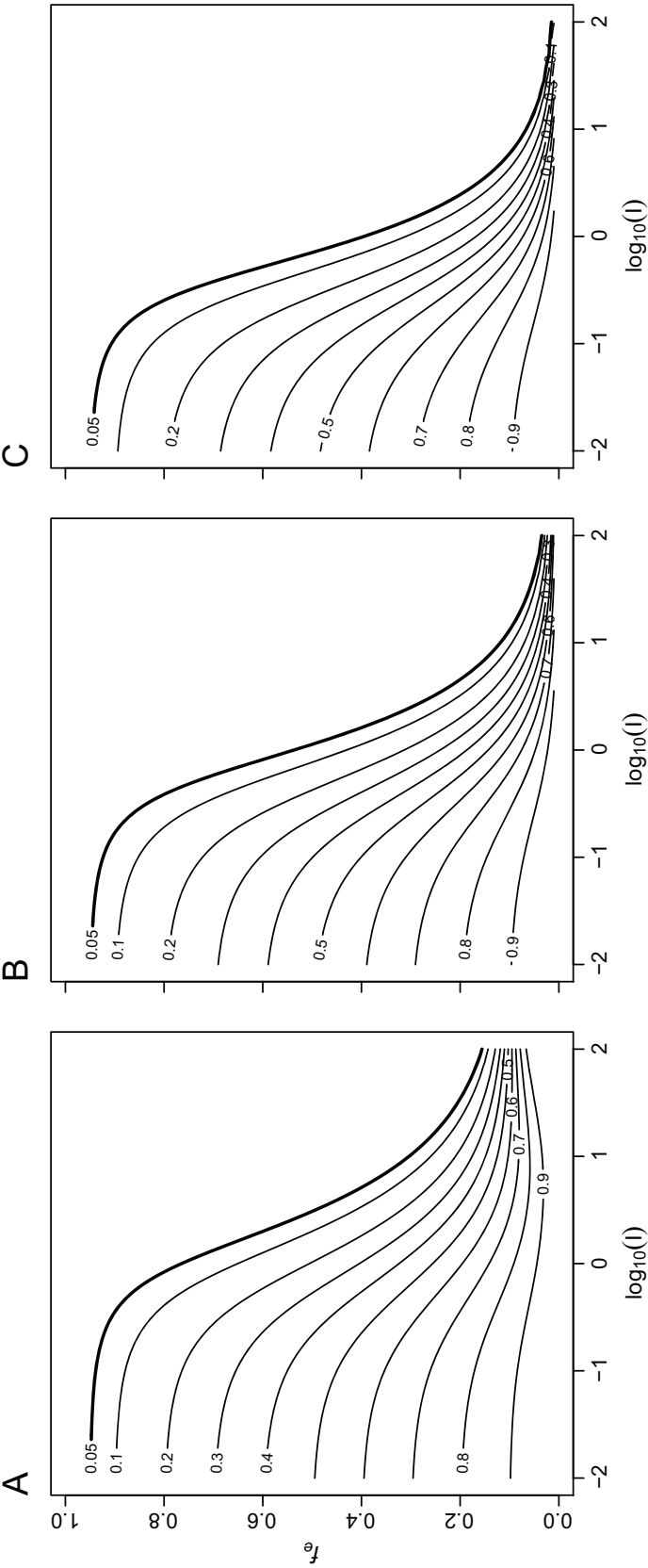
where  $\overline{D_n}$  is the expectation of  $D_n$  and depends on  $\mathbf{s}$  tree topology (i.e., on  $I$  parameter) and  $f_e$ .

We assume that  $R_{\text{all}}$  is an increasing function of  $\overline{N_A}$  and  $\overline{M}$ . Then, equations (A23) and (A24) imply that,  $I$  being kept constant,  $R_{\text{all}}$  is a decreasing function of  $m$  because  $\overline{M}$ , the mean number of mutation events in the  $\mathbf{u}$  tree, is proportional to the mutation to migration ratio  $\mu/m$ , whereas the number of ancestors  $N_A$  is unaffected by the value of  $m$ . Formally, we obtain

$$\frac{\partial \overline{R}_{\text{all}}(I, m)}{\partial m} > 0. \quad (\text{A25})$$

Under the weak mutation regime, similarly to species level, we have  $\partial \overline{R}_{\text{all}}(I)/\partial I > 0$ . This pattern may change when mutation is strong because of the impact of  $I$  on  $\overline{D_n}$  values. However, on the basis of a continuity argument, we expect this property to be maintained until a certain level of mutation rate, so that  $\partial \overline{R}_{\text{gen}}(I, m)/\partial I > 0$ . Unfortunately, we could not establish the generality of this result.





**Figure A1:** Value of  $P$  as a function of  $I$  and  $f_e$  for various values of  $k/S$ : (A)  $k/S = 0.1$ , (B)  $k/S = 0.01$ , and (C)  $k/S = 0.001$ . Bold line materializes the threshold of  $I$  above which  $P < .05$  as a function of  $f_e$ .

## Appendix B from F. Laroche et al., “A Neutral Theory for Interpreting Correlations between Species and Genetic Diversity in Communities” (Am. Nat., vol. 185, no. 1, p. 000)

### Modeling the Landscape through a “Discretized” Bivariate Gaussian Distribution of $K$ and $m$

#### Building $(K, m)$ Distribution

We model  $(K, m)$  distribution across sites as follows:

$$\left[ \log(K-1), \log\left(\frac{m}{1-m}\right) \right] = [f(\mathbf{X}), \mathbf{Y}], \quad (\text{B1})$$

where  $(\mathbf{X}, \mathbf{Y})$  is a Gaussian vector with mean  $(\alpha_K, \alpha_m)$  and variance/covariance matrix

$$\Sigma = \begin{pmatrix} \sigma_K^2 & \rho\sigma_K\sigma_m \\ \rho\sigma_K\sigma_m & \sigma_m^2 \end{pmatrix},$$

$\rho \in [-1, 1]$ , and  $f(x) = \log(\lfloor 10^x \rfloor + 1)$ , where  $\lfloor \cdot \rfloor$  is the integer part operator. Here we worked with given  $\sigma_K^2$  and explored variation in  $\sigma_m^2$  and  $\rho_{Km}$ .

#### Linking $(K, m)$ and $(I, m)$ Distribution

$\sigma_I^2 = \text{Var}[\log(I)]$  and  $C_{Im} = \text{Cov}\{\log(I), \log[m/(1-m)]\}$  can be linked to  $(K, m)$  distribution. Considering that

$$\log(I) = \log(K-1) + \log\left(\frac{m}{1-m}\right), \quad (\text{B2})$$

and assuming that discretization through  $f$  has no important effect, which is likely to be true when  $K$  is high enough (e.g., when  $\mu_K$  is higher than 2 and  $\sigma_K < \mu_K/2$ ),  $\sigma_I^2$  and  $C_{Im}$  write

$$\sigma_I^2 = \sigma_K^2 + \sigma_m^2 + 2\rho_{Km}\sigma_K\sigma_m, \quad (\text{B3})$$

$$C_{Im} = \rho_{Km}\sigma_K\sigma_m + \sigma_m^2. \quad (\text{B4})$$

Equation (B3) shows that a high variance in  $K$  and  $m$  does not necessarily lead to a high variance in  $I$  if  $\rho_{Km}$  is strongly negative. For a given value of  $\sigma_I^2$ , equations (B3) and (B4) yield

$$C_{Im} = \frac{\sigma_I^2 + \sigma_m^2 - \sigma_K^2}{2}. \quad (\text{B5})$$

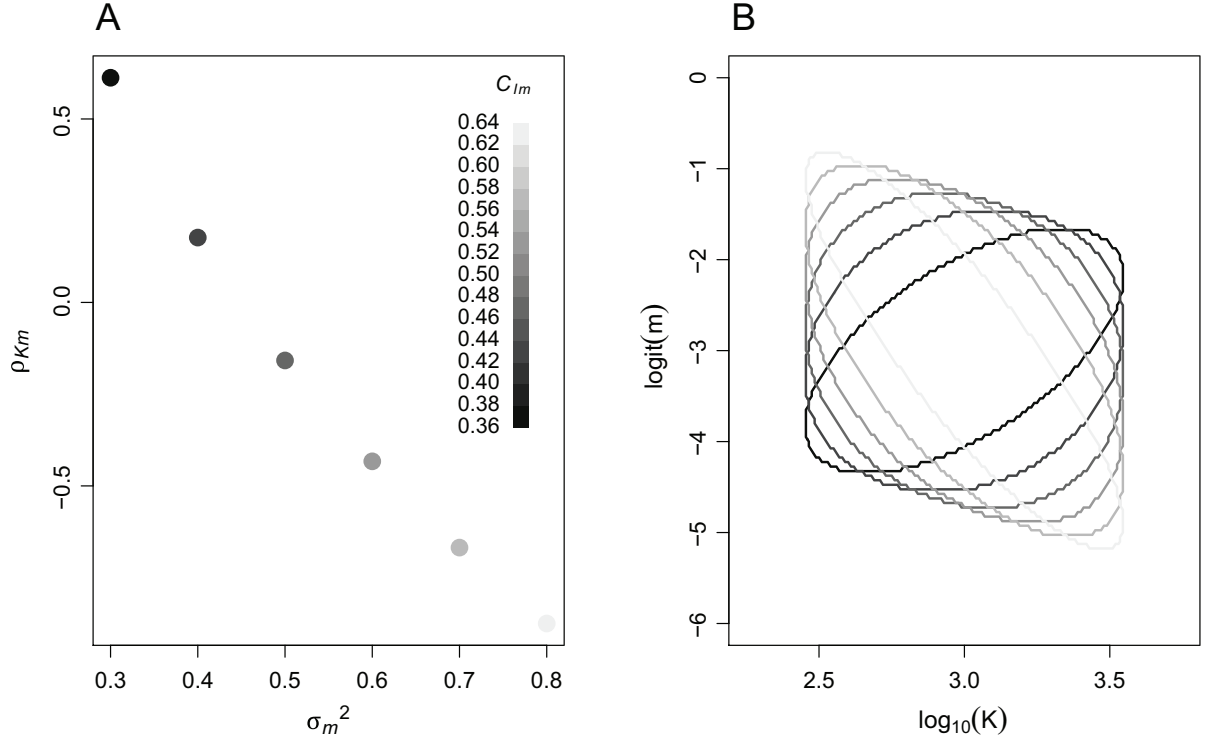
Equation (B5) implies that, for a given value of  $\sigma_I^2$  and  $\sigma_K^2$ , landscapes with higher variance in  $m$  harbor stronger  $C_{Im}$ , as illustrated in figure B1, whereas for a given value of  $\sigma_I^2$  and  $\sigma_m^2$ , landscapes with lower variance in  $K$  harbor stronger  $C_{Im}$ .

For a given value of  $\sigma_K^2$ , increasing  $\sigma_m^2$  keeping  $\sigma_I^2$  constant can be obtained by compensatory variation of  $\rho_{Km}$  verifying

$$\begin{aligned} \frac{\partial \sigma_I^2}{\partial \sigma_m} &= 2\sigma_m + 2\rho_{Km}\sigma_K + 2\frac{\partial \rho_{Km}}{\partial \sigma_m}\sigma_K\sigma_m \\ &= 0 \Leftrightarrow \frac{\partial \rho_{Km}}{\partial \sigma_m} \\ &= -\frac{\sigma_m + \rho_{Km}\sigma_K}{\sigma_K\sigma_m} = -\frac{C_{Im}}{\sigma_K\sigma_m^2}. \end{aligned} \quad (\text{B6})$$

Equation (B6) implies that, among landscapes sharing the same values of  $\sigma_I^2$  and  $\sigma_K^2$  and harboring positive  $C_{Im}$  values,  $\sigma_m^2$

and  $\rho_{Km}$  are negatively related, and a higher value of  $\sigma_m^2$  along with a lower value of  $\rho_{Km}$  leads to a higher  $C_{Im}$  value (fig. B1). By contrast, among landscapes sharing the same values of  $\sigma_I^2$  and  $\sigma_K^2$  and harboring negative  $C_{Im}$  value,  $\sigma_m^2$  and  $\rho_{Km}$  are positively related, and higher values of  $\sigma_m^2$  and  $\rho_{Km}$  lead to higher  $C_{Im}$  value.



**Figure B1:** Features of various distributions of  $\{\log(K-1), \log[m/(1-m)]\}$  with the same value of  $\sigma_I^2$ . Distributions were generated by exploring values of  $\sigma_m^2$  while keeping  $\alpha_K$ ,  $\alpha_m$ , and  $\sigma_K^2$  constant.  $\rho_{Km}$  was adjusted so as to keep  $\sigma_I^2$  constant in every distribution, using equation (B3). In A, distributions are represented as dots in the  $(\sigma_m^2, \rho_{Km})$  plan. The levels of gray indicate the corresponding value of  $C_{Im}$ . In B, the same distributions were represented using ellipsoids encompassing a 0.95 probability zone around the distribution mode. The levels of gray indicate the corresponding value of  $C_{Im}$  according to the color key described in A. Constant parameters were set to  $\alpha_K = 3$ ,  $\alpha_m = -3$ ,  $\sigma_K^2 = 3$ , and  $\sigma_I^2 = 0.5$ .

## Appendix C from F. Laroche et al., “A Neutral Theory for Interpreting Correlations between Species and Genetic Diversity in Communities” (Am. Nat., vol. 185, no. 1, p. 000)

### Decomposition of Covariance

Let  $X, Y, \mathbf{Z} = (Z_1, Z_2, \dots, Z_k)$  be random variables. We use the following lemma:

$$\text{Cov}(X, Y) = \text{Cov}(\bar{X}(\mathbf{Z}), \bar{Y}(\mathbf{Z})) + \mathbb{E}[\text{Cov}_{\mathbf{Z}}(X, Y)], \quad (\text{C1})$$

where  $\bar{X}(\mathbf{Z})$  is the conditional expectation of  $X$  knowing  $\mathbf{Z}$  values,  $\bar{Y}(\mathbf{Z})$  is the conditional expectation of  $Y$  knowing  $\mathbf{Z}$  values, and  $\text{Cov}_{\mathbf{Z}}(X, Y)$  is the conditional covariance between  $X$  and  $Y$  knowing  $\mathbf{Z}$  values.  $\bar{X}(\mathbf{Z})$ ,  $\bar{Y}(\mathbf{Z})$ , and  $\text{Cov}_{\mathbf{Z}}(X, Y)$  are then three deterministic functions of  $\mathbf{Z}$  values.

Applying equation (C1) with  $X = R_{\text{spe}}$ ,  $Y = R_{\text{all}}$ ,  $\mathbf{Z} = (K, m)$  yields equation (1) of the main text,

$$\begin{aligned} \text{Cov}(R_{\text{spe}}, R_{\text{all}}) &= \text{Cov}[\bar{R}_{\text{spe}}(K, m), \bar{R}_{\text{all}}(K, m)] \\ &\quad + \mathbb{E}[\text{Cov}_{K, m}(R_{\text{spe}}, R_{\text{all}})]. \end{aligned}$$

Equation (C1) can be applied conditionally to the fact that some other variables  $\mathbf{U} = (U_1, \dots, U_l)$  are known, such that

$$\text{Cov}_{\mathbf{U}}(X, Y) = \text{Cov}_{\mathbf{U}}[\bar{X}(\mathbf{Z}, \mathbf{U}), \bar{Y}(\mathbf{Z}, \mathbf{U})] + \overline{\text{Cov}_{\mathbf{U}, \mathbf{Z}}(X, Y)}(\mathbf{U}). \quad (\text{C2})$$

In equation (C2),  $\text{Cov}_{\mathbf{U}}$  means conditional covariance knowing  $\mathbf{U}$  values and  $\bar{X}(\mathbf{Z}, \mathbf{U})$  and  $\bar{Y}(\mathbf{Z}, \mathbf{U})$  are the conditional expectation of  $X$  and  $Y$  knowing both  $\mathbf{Z}$  values and  $\mathbf{U}$  values. As  $\mathbf{U}$  is supposed to be known, we consider  $\bar{X}(\mathbf{Z}, \mathbf{U})$  and  $\bar{Y}(\mathbf{Z}, \mathbf{U})$  as deterministic functions of random variables contained in  $\mathbf{Z}$ .  $\text{Cov}_{\mathbf{U}}(\bar{X}(\mathbf{Z}, \mathbf{U}), \bar{Y}(\mathbf{Z}, \mathbf{U}))$  is then the covariance between these functions for a given  $\mathbf{U}$  when  $\mathbf{Z}$  varies.

$\text{Cov}_{\mathbf{U}, \mathbf{Z}}(X, Y)$  is the covariance of  $X$  and  $Y$  knowing  $\mathbf{U}$  and  $\mathbf{Z}$  values. As  $\mathbf{U}$  is known, we consider  $\text{Cov}_{\mathbf{U}, \mathbf{Z}}(X, Y)$  as a deterministic function of random variables contained in  $\mathbf{Z}$ .  $\overline{\text{Cov}_{\mathbf{U}, \mathbf{Z}}(X, Y)}(\mathbf{U})$  is then the expectation for a given  $\mathbf{U}$  of this function, taken over all possible values of  $\mathbf{Z}$ .

Applying equation (C2) with  $X = R_{\text{spe}}$ ,  $Y = R_{\text{all}}$ ,  $\mathbf{Z} = s_e$ , and  $\mathbf{U} = (K, m)$  yields

$$\begin{aligned} \text{Cov}_{K, m}(R_{\text{spe}}, R_{\text{all}}) &= \text{Cov}_{K, m}[\bar{R}_{\text{spe}}(s_e, K, m), \bar{R}_{\text{all}}(s_e, K, m)] \\ &\quad + \overline{\text{Cov}_{K, m, s_e}(R_{\text{spe}}, R_{\text{all}})}(K, m). \end{aligned} \quad (\text{C3})$$

We show in appendix A that  $R_{\text{spe}}$  and  $R_{\text{all}}$  are probabilistically independent when  $K$ ,  $m$ , and  $s_e$  are known, which implies for any value of  $K$ ,  $m$ , and  $s_e$ ,

$$\text{Cov}_{K, m, s_e}(R_{\text{spe}}, R_{\text{all}}) = 0. \quad (\text{C4})$$

Applying equation (C3), equation (C4) simplifies to

$$\text{Cov}_{K, m}(R_{\text{spe}}, R_{\text{all}}) = \text{Cov}_{K, m}[\bar{R}_{\text{spe}}(s_e, K, m), \bar{R}_{\text{all}}(s_e, K, m)]. \quad (\text{C5})$$

Under the weak mutation regime,  $\bar{R}_{\text{all}}$  does not depend on  $s_e$  (app. A). Then equation (C5) yields

$$\text{Cov}_{K, m}(R_{\text{spe}}, R_{\text{all}}) = 0. \quad (\text{C6})$$

Under the strong mutation regime,  $\bar{R}_{\text{spe}}(s_e, K, m)$  decreases with  $s_e$ , whereas  $\bar{R}_{\text{all}}(s_e, K, m)$  increases with  $s_e$ . Thus equation (C5) yields

$$\text{Cov}_{K, m}(R_{\text{spe}}, R_{\text{all}}) < 0. \quad (\text{C7})$$

RESEARCH ARTICLE

# The Robustness of Plant-Pollinator Assemblages: Linking Plant Interaction Patterns and Sensitivity to Pollinator Loss

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## Abstract

Most flowering plants depend on pollinators to reproduce. Thus, evaluating the robustness of plant-pollinator assemblages to species loss is a major concern. How species interaction patterns are related to species sensitivity to partner loss may influence the robustness of plant-pollinator assemblages. In plants, both reproductive dependence on pollinators (breeding system) and dispersal ability may modulate plant sensitivity to pollinator loss. For instance, species with strong dependence (e.g. dioecious species) and low dispersal (e.g. seeds dispersed by gravity) may be the most sensitive to pollinator loss. We compared the interaction patterns of plants differing in dependence on pollinators and dispersal ability in a meta-dataset comprising 192 plant species from 13 plant-pollinator networks. In addition, network robustness was compared under different scenarios representing sequences of plant extinctions associated with plant sensitivity to pollinator loss. Species with different dependence on pollinators and dispersal ability showed similar levels of generalization. Although plants with low dispersal ability interacted with more generalized pollinators, low-dispersal plants with strong dependence on pollinators (i.e. the most sensitive to pollinator loss) interacted with more particular sets of pollinators (i.e. shared a low proportion of pollinators with other plants). Only two assemblages showed lower robustness under the scenario considering plant generalization, dependence on pollinators and dispersal ability than under the scenario where extinction sequences only depended on plant generalization (i.e. where higher generalization level was associated with lower probability of extinction). Overall, our results support the idea that species generalization and network topology may be good predictors of assemblage robustness to species loss, independently of plant dispersal ability and breeding system. In contrast, since ecological specialization among partners may increase the probability of disruption of interactions, the fact that the plants most sensitive to pollinator loss interacted with more particular pollinator assemblages suggest that the persistence of these plants and their pollinators might be highly compromised.

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## Introduction

The robustness of plant-pollinator assemblages to species loss is a main concern of basic and applied Ecology since 87.5% of flowering plants and most crops directly consumed by humans depend in some degree on pollinators to reproduce [1, 2, 3]. Understanding how the organization of plant-pollinator interactions may influence species persistence is central to predict the consequences of species loss [4]. Ultimately, ecological interactions are shaped by traits and therefore trait-based descriptions of species interactions may provide insights into the organization of interacting assemblages [5]. In this context, a main challenge is to understand how traits shaping species interaction patterns also influence the sensitivity of species to the loss of interaction partners [6, 7].

Plant-pollinator assemblages show consistent patterns in the organization of interactions among species [8]. In these assemblages, only a few species of plants and pollinators are extremely generalized i.e. interact with a high number of species [8]. Generalists are central to the nested structure of plant-pollinator assemblages, in which ecologically specialized species interact with subsets of species interacting with more generalized species [9, 10]. As a consequence, the loss of generalized species decreases the robustness of plant-pollinator assemblages to subsequent species loss [11–13]. Thus, the persistence of generalists may increase the persistence of the whole assemblage [11–13].

In plants, pollination of generalists should be less affected by pollinator loss due to pollinator redundancy [14–18, 19]. Indeed, generalized plants tend to interact both with generalized and specialized pollinators [20], which may lead to lower fluctuation of pollinator service [15] and to lower risk of reproductive failure when specialized pollinators go extinct [21]. However, plant sensitivity to pollinator loss is not only affected by interaction patterns among plants and pollinators but also by plant breeding system [22–24].

Plant breeding systems modulate the dependence of plants on pollinators to produce seeds [22, 24]. Among biotically pollinated plants, self-incompatible and dioecious species are strongly dependent on pollinator services, since pollination will only occur when pollinators have previously visited flowers of compatible and male conspecific plants, respectively. In contrast, self-compatible species may be less dependent on pollinators because a single visit of pollinators to each individual flower may allow reproduction. Plants having mechanisms to produce seeds without pollinator visits may be even less dependent. As generalization on pollinators may evolve if it decreases the risk of reproductive failure when pollinators fluctuate in abundance [15], plants with different breeding systems may show different levels of generalization [25]. Species depending more on pollinators may interact with multiple pollinator species [26] whereas plants interacting with fewer pollinator species may be less dependent on pollinators [27–29]. Moreover, pollinator-dependent plants would be expected to interact with more generalized pollinators, minimizing temporal fluctuation in pollination services [15, 29].

Plant dispersal ability may also modulate plant sensitivity to pollinator loss. Higher dispersal ability has been associated with lower dependence on pollinators (i.e. self-compatibility or autonomous self-pollination) because only plants with the ability to produce seeds without pollinators should reproduce in sites where pollinators are absent (Baker's law) [30, 31]. In contrast, it has recently been shown in theoretical studies that fluctuations in pollination levels may lead to the evolution of two alternative syndromes: outcrossers with high dispersal ability or selfers with low dispersal [32, 33]. Indeed, high dispersal ability may increase the persistence of dioecious species [34]. In this sense, if strongly dependent species can locally persist by dispersing seeds from sites where pollinators are present, then their persistence may be less dependent on local pollinator services. Thus, the patterns of interaction of plants may also be modulated by dispersal ability, with highly dispersing plants interacting with fewer and/or more specialized

pollinator species and low-dispersal plants being more generalists and/or interacting with generalized pollinators.

In this study, we investigated how plant interaction patterns varied with plant sensitivity to pollinator loss. We also explored how this variation might influence the robustness of plant-pollinator assemblages. We compiled information on plant breeding system and dispersal mode for 192 species from 13 published plant-pollinator networks. We described the patterns of interaction for each plant species, i.e. its contribution to network nestedness, its degree of ecological generalization on pollinators [35], and the mean level of generalization of its pollinators. Specifically, we asked how these patterns were associated with the dependence of plants on pollinators and their dispersal ability. We predicted that plants with strong dependence on pollinators or low dispersal ability may show higher degree of generalization on pollinators, higher contribution to nestedness and interact with more generalized pollinators. In addition, we investigated how the association of plant generalization, dependence on pollinators and dispersal ability may affect the robustness of plant-pollinator assemblages by simulating sequences of species extinctions. We expected that scenarios where plant generalization level and biological traits affected the probability of extinction of plants would lead to less robust networks than scenarios only considering plant generalization and as robust as the random scenario—i.e. where no plant trait affected plant sensitivity.

## Methods

### Plant interaction patterns and sensitivity to pollinator loss

We characterized the interaction pattern of 339 plant species belonging to 13 qualitative plant-pollinator networks available at the interaction web database (<http://www.nceas.ucsb.edu/interactionweb/>; S1 Table). We used three network metrics to characterize the patterns of interaction of each species: plant contribution to nestedness, plant ecological generalization on pollinators (hereafter plant generalization) and mean ecological generalization of plant interaction partners (hereafter mean pollinator generalization). Plant contribution to nestedness measured how much the interactions of a given plant species overlapped, on average, with those of other plant species in the network, following [36] (see “Plant contribution to nestedness” in the [supporting information](#)). We first calculated the proportion of pollinator species shared between a given plant and each plant species of the network. Then, for each plant, the average proportion of pollinators shared with the other plant species represented its contribution to nestedness. To calculate plant contribution to nestedness we used the ANINHADO software [37]. The generalization of a given plant species was characterized by the proportion of pollinator species that interacted with it [38],  $k_p/S_A$ , where  $k_p$  was the number of pollinator species interacting with the focal plant species and  $S_A$  was the number of pollinator species of the network. The generalization level of each pollinator interacting with a given plant species was calculated as  $k_a/S_p$ , where  $k_a$  was the number of plant species that interacted with a given pollinator and  $S_p$  was the plant richness species of the network. The mean pollinator generalization for a given plant species was obtained as the mean of the generalization level of all pollinators interacting with the focal plant species.

We used information on breeding system and dispersal mode to estimate, respectively, plant dependence on pollinators and dispersal ability. Data on breeding system and dispersal mode was obtained for 192 of the initial 339 species (58%; S2 Table). For most of the plant species, data on these traits was extracted from published articles (S2 Table). When different studies were available for the same species, we prioritized information obtained in the same study region where networks were characterized. Data on the two traits for 6% of species was obtained from researchers working with those plants. Dispersal mode was also obtained from



seed-trait databases (7.5% of species; [S2 Table](#)). In 7% of plants, dispersal mode was assigned by the analysis of images of the dispersal units and according to [\[39\]](#).

We grouped the large diversity of plant breeding systems in three categories depicting the degree of dependence of plants on pollinators to produce seeds. Species were classified as: (i) strongly dependent plants, including self-incompatible and dioecious species, and obligate outcrossers; (ii) intermediately dependent plants, including self-compatible species and facultative outcrossers; and (iii) slightly dependent plants, including autonomous self-pollinating, agamospermous, cleistogamous, and facultative autogamous species. Dispersal mode was coded in two classes depicting dispersal ability: (i) low-dispersal plants, including species dispersed by gravity (with or without diaspore explosion), and ants; (ii) high-dispersal plants, including species dispersed by vertebrates, wind and water.

## Statistical analyses

We evaluated how plant interaction patterns varied among plants differing in their dependence on pollinators and dispersal ability. In our analysis, plant generalization, contribution to nestedness and mean generalization of pollinators were the response variables, and dependence on pollinators and dispersal ability the explanatory factors. Since residuals of linear models were not normally distributed but variances among groups were homogeneous, we chose to use the distance-based non-parametric analysis of variance introduced by Anderson [\[40, 41\]](#). Thus, we computed p-values using permutation tests ( $n = 9999$  permutations). We performed these permutation analyses using the Adonis function included in the Vegan package on R [\[42\]](#). Particularities of each assemblage such as species richness and connectance (i.e. the proportion of possible interactions actually recorded) could influence the value of the response variables. Thus, permutations were performed among species within networks. To determine *a posteriori* pair-wise differences between levels of factors that influenced the response variables, we performed separated permutation tests following [\[40\]](#). Data on plants occurring in more than one network (6 species) were included only once in the analyses by randomly choosing one of these networks. Including or not these 6 species in the analyses did not change the results.

## Plant sensitivity to pollinator loss and network robustness

We evaluated how plant sensitivity to pollinator loss might influence network robustness by simulating plant extinctions. We used 10 networks, excluding three networks from this analysis due to limited information on both the dependence of plants on pollinators and plant dispersal abilities ( $< 60\%$  of the species) ([S1 Table](#)). Among these 10 networks, species without information on a given trait were randomly assigned with equal probability to one category of the trait at the beginning of each simulation of extinction events.

We evaluated network robustness under different simulated scenarios of plant extinctions. We used a fully factorial design leading to eight simulated scenarios in which each plant trait (i.e. plant generalization, dependence on pollinators or dispersal ability) or the combination of these traits determined plant sensitivity to pollinator extinction (see [S3 Table](#) for a full description of the scenarios). Plant sensitivity depending on species generalization represented the ability of plants to cope with fluctuations on the abundances of pollinators or even pollinator loss, associated with pollinator redundancy (e.g. the reproduction of plants interacting with few pollinators is more likely to be pollen limited [\[43\]](#)). Thus, plants interacting with multiple pollinators were considered to be less sensitive to pollinator loss than those interacting with a few species. In the case of plant dependence on pollinators and dispersal ability, plant sensitivity represented the ability of plants to cope with pollinator decline with alternative strategies, e.g. autonomous self-pollination or seeds arriving from other sites. Then, species with slight



dependence on pollinators and/or high dispersal ability (e.g. wind or animal dispersed) were less sensitive to pollinator loss. Simulated scenarios also included a random scenario under which no plant trait affected plant sensitivity. This random scenario represented a null model to compare the effects of the other scenarios on assemblage robustness [11, 13, 44].

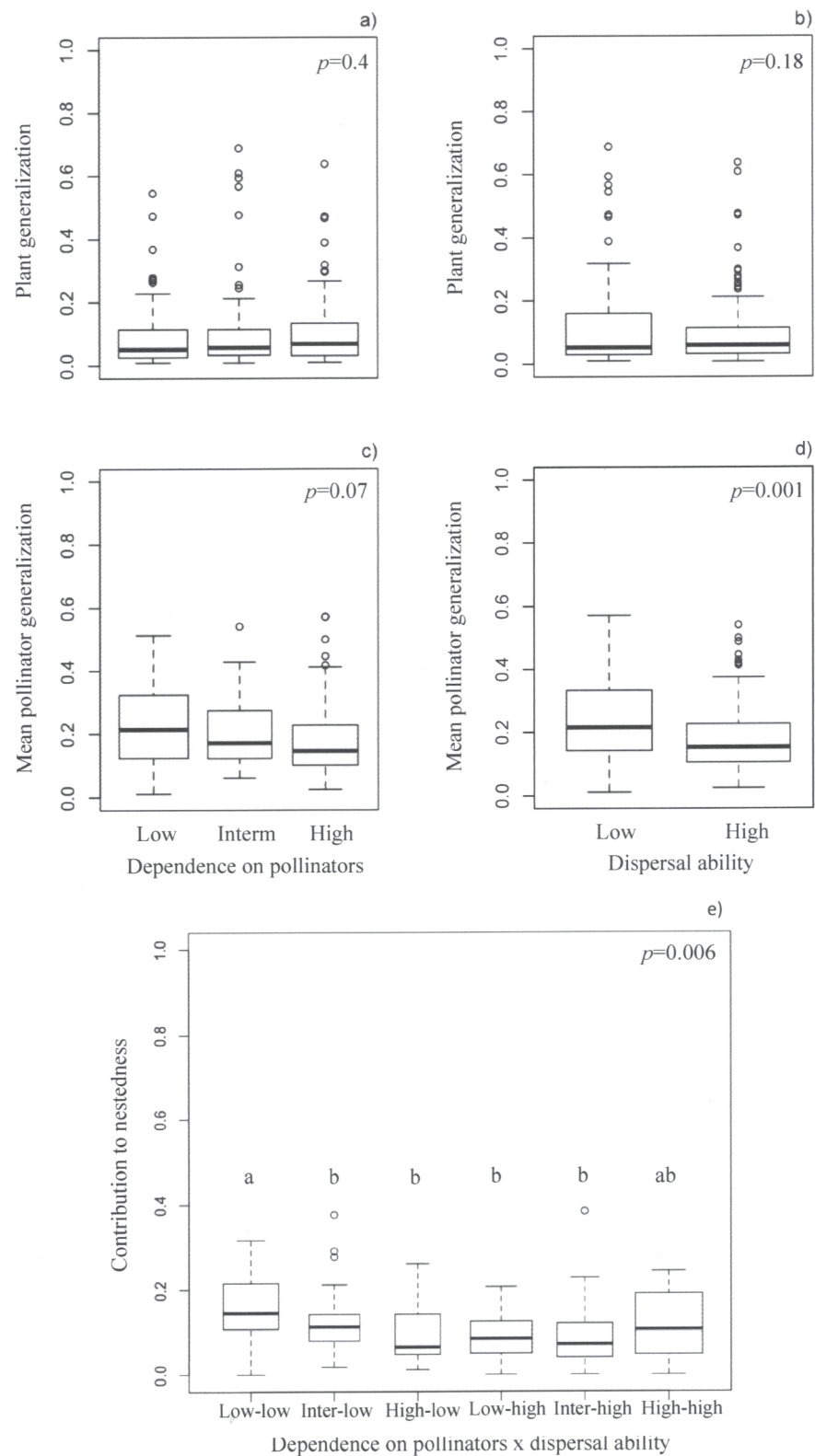
To perform extinction sequences, we assigned probabilities of extinction to each plant species according to plant generalization, dependence on pollinators and dispersal ability as follows. For scenarios only considering one of these traits, we first ranked all the species according to a decreasing order of sensitivity to pollinator loss, as explained above. Thus, in the case of plant dependence on pollinators, strongly dependent species were considered the most sensitive whereas slightly dependent species were the least sensitive. In relation to dispersal ability, low-dispersal plants were considered the most sensitive whereas high-dispersal species were the least sensitive. In the case of plant generalization on pollinators, higher generalization was associated with lower sensitivity to pollinator loss. Secondly, for the  $N$  species within each category of each trait we sampled  $N$  extinction probabilities from a truncated exponential distribution, where the lambda parameter was randomly chosen among values ranging from 10 to 25. Thus, species belonging to more sensitive categories were first ranked and received higher extinction probabilities. Then, we computed the mean extinction probability of the sampled values for each trait category and assigned this mean value to all plants within the category. Finally, we normalized the probability values across all species (i.e. we made the sum of all probabilities equal to 1) to obtain the final probability of extinction for each species. In scenarios taking into account any combination of traits, we assigned extinction probabilities according to each trait as explained above, and we multiplied the set of probabilities for each species. Then, we normalized these probability values across species in order to obtain the final probability of extinction for each species. In the random scenario, all species received the same probability of extinction calculated as  $1/S_p$ .

We performed 1000 sequences of plant extinction for each scenario. Each sequence included the sequential removal of all plant species. A pollinator species died out if all their interacting plants were extinct. After the removal of each plant species, we computed the percentage of surviving pollinator species. Then, we assessed the robustness of the networks following each sequence of extinction by computing the area under the curve describing the proportion of remaining pollinator species against the proportion of plants that went extinct [45, 46]. Areas that are close to one represent networks that are robust to plant extinction, since large percentages of extinctions are needed until significant secondary extinctions of pollinators are observed. On the other hand, areas that are close to zero correspond to very fragile networks, in which extinction of a small proportion of plant species leads to the extinction of a high proportion of pollinator species [45]. Simulations were performed in MATLAB [47]. We obtained mean values of robustness for each scenario and then we compared the differences between means of a-priori planned pair-wise comparisons (see S5–S12 Tables). We calculated the 95% confidence intervals for differences between means and we considered that the difference between scenarios was significant when the confidence interval did not include the zero value [48].

## Results

### Plant interaction patterns and sensitivity to pollinator loss

Plant generalization did not differ among species with different dependence on pollinators ( $F_{1, 192} = 0.68$ ,  $P = 0.4$ ; Fig. 1A and B; S4 Table) or dispersal ability ( $F_{1, 192} = 1.85$ ,  $P = 0.18$ ; Fig. 1A and B; S4 Table). However, low-dispersal plants interacted, on average, with more generalized pollinators ( $F_{1, 192} = 11.26$ ,  $P = 0.0013$ ; Fig. 1D; S4 Table). Low-dispersal plants showed



**Figure 1. Plant interaction patterns and sensitivity to pollinator loss.** Box-plots of plant generalization (“a” and “b”), mean pollinator generalization (“c” and “d”) and plant contribution to nestedness (“e”) of species differing in dependence on pollinators and dispersal ability. Black lines within boxes represent median values.

Upper and lower limits of boxes represent 1<sup>st</sup> and 3<sup>rd</sup> quartiles, respectively. Boxes were drawn with widths proportional to the number of observations in each group. In (a) and (c), “Strong”, “Inter” and “Slight” refer to strongly, intermediately and slightly dependent plants, respectively. In (b) and (d), “Low” and “High” refer to high and low-dispersal plants, respectively. In (e) “Strong-Low”, “Inter-Low” and “Slight-Low” refer to plants with strong, intermediate and low dependence on pollinators and slight dispersal ability, whereas “Strong-high”, “Inter-high” and “Slight-high” refer to plants with high, intermediate and low dependence on pollinators and high dispersal ability. The probability of obtaining a difference higher than that observed among groups is also shown. Abbreviations: Inter = intermediate.

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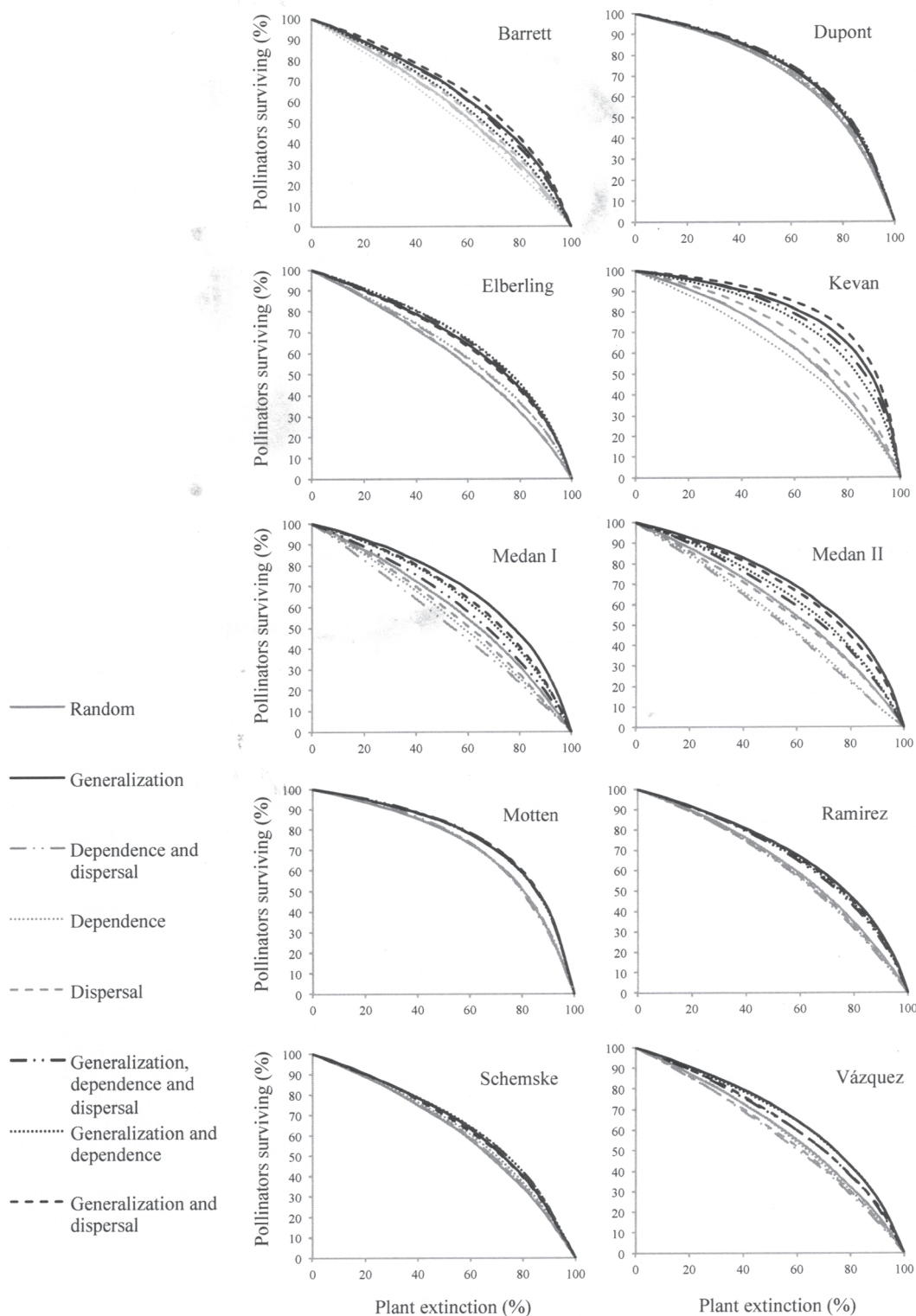
higher contribution to nestedness than high-dispersal plants ( $F_{1, 192} = 7.62$ ,  $P = 0.006$ ; [Fig. 1E](#); [S4 Table](#) and [S1 Fig.](#)). However, the relationship between dispersal ability and nestedness was modulated by plant dependence on pollinators ( $F_{1, 192} = 7.19$ ,  $P = 0.006$ ; [Fig. 1E](#) and [S4 Table](#)). Thus, species with low dispersal ability and slight dependence on pollinators showed the highest contribution to nestedness ([Fig. 1E](#)). Species with strong dependence on pollinators and high dispersal ability showed intermediate mean values of contribution to nestedness ([Fig. 1E](#)) that did not differ significantly from the other groups. By contrast, low-dispersal plants with strong dependence on pollinators were among those that showed the lowest contributions to nestedness ([Fig. 1E](#)).

## Plant sensitivity to pollinator loss and network robustness

The proportion of pollinator species surviving after plant extinction followed a slow-decaying curve under most of the scenarios ([Fig. 2](#)). The robustness of plant-pollinator networks varied depending on which plant trait or combination of traits influenced plant probability of extinction ([Fig. 2](#); [S5–S12 Tables](#)). In most assemblages (80%), networks were more robust when the sequence of extinctions depended on differences in generalization among plant species whether or not the other biological traits affected extinction probabilities ([Fig. 2](#); [S5–S12 Tables](#)). Seven networks (70%) showed lower robustness when all species had the same probability of extinction (random scenario) and under scenarios where plant loss was influenced only by plant dependence on pollinators, dispersal ability or these two traits (80%; [Fig. 2](#)). In two networks (Schemske and Dupont) robustness was similar among all scenarios and in two networks (Ramirez and Vázquez) robustness under the random scenario was similar to robustness observed under the scenario considering plant generalization and the two biological traits ([Fig. 2](#); [S6](#) and [S12–S14 Tables](#)).

Differences in the robustness of networks among the set of scenarios where plant generalization influenced the sequence of extinctions varied across assemblages. Most networks (80%) showed similar robustness to extinction sequences determined by the combination of the three traits and to extinctions only based on plant generalization ([Fig. 2](#); [S5–S8](#), [S11–S14 Tables](#)). Only two networks were less robust when the three traits were considered (Medan I and Medan II; [Fig. 2](#); [S9](#) and [S10 Tables](#)).

Differences in the robustness of networks between the random scenario and the set of scenarios where extinction sequences were determined by plant dependence and/or dispersal also varied across assemblages. Half of assemblages showed similar robustness between scenarios where extinction probabilities were associated to either one or both biological traits and random scenarios (Barrett, Dupont, Elberling, Motten and Vázquez; [Fig. 2](#); [S5–S7](#), [S11](#) and [S14 Tables](#)). The scenario considering plant dispersal and dependence on pollinators led to less robust networks than the random scenario in three assemblages (Medán I, Medán II and Ramirez; [Fig. 2](#); [S9](#), [S10](#) and [S12 Tables](#)).



**Figure 2. Plant sensitivity to pollinator loss and network robustness.** Proportion of pollinator species surviving under different scenarios of plant extinction representing plant sensitivity to pollinator loss in 10 plant-pollinator networks. Scenarios where plant extinction probability was linked to plant generalization (with or without taking into account other traits) were drawn in black. Scenarios that did not consider plant generalization into plant extinction probability were drawn in grey.

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## Discussion

Focusing on how traits determining species sensitivity to partner loss may influence species patterns of interaction may improve our understanding of the impacts of species loss on assemblage maintenance [6, 7]. Contrary to what we hypothesized, generalist plants were not more sensitive to pollinator loss. We showed that low dispersal plants interacted with more generalized pollinators and that the contribution of plants to nestedness was associated with the interaction among biological traits. Slightly dependent low dispersal plants were those contributing more to nestedness whereas species showing the highest sensitivity to pollinator loss were among those species showing the lowest contribution. Finally, in most assemblages (80%) considering plant generalization and biological traits as determinants of species probability of extinction led to networks of similar robustness to scenarios only including plant generalization. Below, we discuss the implications of our results in light of how plant species may persist locally and how this persistence will maintain plant-pollinator assemblages.

### Plant interaction patterns and sensitivity to pollinator loss

Since functional redundancy among pollinators may lead to less fluctuating pollination service in generalist plants [15–17, 49], species depending more on pollinators to produce seeds (e.g. dioecious or self-incompatible species) are expected to be more generalists. Alternatively, to cope with fluctuations in pollinator service species depending more on pollinators may be expected to be better dispersers [32], as a way to buffer local pollination limitation. Although a good ability to colonize has traditionally been associated with low dependence on pollinators—i.e., self-compatibility or autonomous self-pollination [30, 31]—, the association between strong dependence on pollinators and high dispersal has been predicted by theoretical studies and both trends have been observed in empirical studies [32, 34, 50]. Our results showed that plants more sensitive to pollinator loss did not show higher ecological generalization on pollinators. Species with strong dependence on pollinators and high dispersal ability might persist under unfavorable pollination environments by receiving seeds from other sites whereas low-dispersal plants with autonomous self-pollination mechanisms might assure their reproduction by performing self-pollination.

Moreover, low-dispersal plants interacted with more generalized pollinators which might fluctuate less in abundance and thus may provide a more reliable pollination service [15, 26, 51]. Thus, the interaction with pollinators that visit multiple plant species—a pervasive pattern in pollination networks [20]—might also be an alternative pathway for the persistence of low-dispersal plants. However, the interaction with more generalized pollinators might also increase the arrival of heterospecific pollen to stigmas, negatively affecting the reproduction of plants [52, 53]. The quantity of heterospecific pollen delivered by generalist pollinators might depend on how pollinator foraging behavior can be affected by the more likely patchy distribution of low dispersal plants [54].

Higher overlap of interactions with other species may also increase species persistence [55]. An indirect positive effect may exist among plants interacting with the same pollinators since the persistence of any of the plant species may allow the persistence of pollinators and thus maintain the pollination service of other plants [56]. The highest contribution to nestedness was observed in plants with slight dependence on pollinators, i.e. plants that can reproduce even when pollinators are scarce. Therefore, the persistence of slightly dependent plants despite temporal fluctuations of pollinator abundance might facilitate the persistence of more sensitive plants. However, we also found that plants having the highest sensitivity to pollinator loss—i.e., strongly dependent, low-dispersal species—where among the groups of plants showing the lowest contribution to nestedness. Ecological specialization between interacting partners may

contribute to increase the vulnerability of interactions to disruption [57], which might compromise the persistence of these highly sensitive plants and their pollinators.

## Plant sensitivity to pollinator loss and network robustness

Plant-pollinator assemblages may show high robustness on average to the random extinction of species, but face higher fragility when generalists are lost earlier in the sequence of extinctions [11, 13]. We assessed network robustness under scenarios of plant extinction representing plant sensitivity to pollinator loss associated with two key biological traits: plant dependence on pollinators and dispersal ability. In accordance with previous studies [11, 13], the early collapse of networks was not observed under the different scenarios of species extinction. Thus, plant-pollinator networks may be tolerant to the loss of more sensitive plants. However, this tolerance relies on the assumption that pollinators are functionally redundant which is still unknown for most of plant-pollinator networks [13].

Since generalization implies redundancy of interaction partners, more robust assemblages can be expected when extreme generalists are the least likely to be lost [11, 13]. The higher robustness of scenarios where extinction sequences depended on plant generalization compared to scenarios where generalization was not considered is in agreement with that expectation. Moreover, the lower robustness of networks under scenarios where extinction order depended only on either plant dependence on pollinators or dispersal ability may be explained by the earlier removal of generalized plants. The early extinction of generalists lies with the similar generalization levels we found among plants with different dependence on pollinators and dispersal ability, i.e. generalist plants may show both high and low sensitivity to pollinator loss. However, as the nested structure of interactions may explain the robustness of plant-pollinator assemblages [11, 13, 56, 58, 59], differences in network robustness among scenarios might be associated, indeed, to differences in contribution to nestedness among species. When extinction sequences depended on dispersal, plants being removed earlier may decrease network nestedness, as low-dispersal (more sensitive) plants were those contributing more to the nested structure. The interaction of strongly dependent, low-dispersal plants with more particular sets of pollinators may explain why scenarios considering dependence on pollinators with or without dispersal ability led to less robust networks than scenarios including plant generalization. Contribution to nestedness may partially increase with species ecological generalization [9], which may explain why scenarios where generalists were less likely to be lost were more robust.

Plant sensitivity to pollinator loss has been included into simulated scenarios of plant extinction in two previous studies, by using plant-pollinator frequency of interactions as a surrogate of species dependence on interaction partners [13, 60]. By removing either pollinators or plants, Kaiser-Bunbury et al. [13] showed that the early removal of most important interaction partners (i.e. with the strongest interaction frequencies) led to less robust networks than scenarios assuming the early removal of generalists. Vieira & Almeida-Neto [60] included plant dependence on pollinators into extinction scenarios by considering interaction frequency among plants and pollinators, and by assigning different levels of dependence on pollinators to whole plant communities of real networks (i.e. plants of the same community had the same ability to self-pollinate). They showed that lower mean plant ability to self-pollinate increased the number of co-extinctions per extinction event, decreasing network robustness to the loss of generalists [60]. In contrast, we found that when breeding system, dispersal ability and plant generalization influenced the sequences of plant extinction only two networks showed lower robustness than under the generalization scenario. Thus, one of the next questions to be addressed is to what extent adding pollinator effectiveness may evidence the influence of biological traits on network robustness. Asymmetric dependencies seem to be the rule in mutualistic



networks [61, 62] and species importance for interaction partners (i.e. species strength) has been reported to be positively associated with species generalization [61]. Thus, we hypothesize that the extinction of more sensitive plants does not cause the co-extinction of shared pollinators and other plants, because highly sensitive plants interacted with more particular sets of pollinators. However, we recognize that the influence of pollinator effectiveness on plant persistence and thus on community robustness remains to be empirically tested.

## Conclusions and Future Directions

Our results suggest that networks might be tolerant to pollinator loss because plants that are central to network organization may have alternative strategies to cope with pollen limitation, which may allow their persistence under unfavorable pollinator environments. Thus, focusing on network organization as a determinant of assemblage robustness might be a good approximation to estimate the fragility of plant-pollinator networks to species loss. However, more complete understanding of the importance of plant sensitivity to pollinator loss should be achieved by studying the effects of functional redundancy within pollinators of more generalist species, including how per-visit effectiveness and species local abundance relate to each other and with temporal fluctuation in pollinator abundance, three important features that may influence species generalization level [15]. Moreover, although the nested structure of plant-pollinator assemblages may provide higher metacommunity robustness to habitat loss [63], more sensitive plants interacting with more particular pollinator assemblages may be more prone to be lost. Since plant breeding system and dispersal ability may modulate plant response to habitat fragmentation [24, 64], future studies assessing how changes in landscape configuration affect the relationships between plant interaction patterns and plant sensitivity to pollinator loss may improve our understanding of the effects of one of the major threats to biodiversity.

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## Supporting Information

**S1 Table. General information of the plant-pollinator networks from the Interaction Web Database used in this study.** Network, Habitat type, localization, total number of plant and pollinator species (Sp), connectance (c), degree of nestedness (NODF), and percentage of plant species with information on dependence on pollinators and dispersal ability (% Plants DP & DA) are shown for each network. References as stated at the IWDB are also shown. Networks with their original name in *italic* are those that were used in simulations of plant extinction. For abbreviation purposes we used the surname of the first author to refer to each network. (PDF)

**S2 Table. Plant interaction patterns and sensitivity to pollinator loss.** Network, species, family, dependence on pollinators (DP), dispersal ability (DA), plant generalization, contribution to nestedness (nestedness) and mean generalization of pollinators of the plant species used in this study. Data on plant generalization, nestedness and mean generalization of pollinators were obtained as described in the M&M section. The first citation appearing in the column “Reference” refers to the bibliographic source from which data on dependence on pollinators was extracted and the second one refers to data on dispersal ability. Only one reference is presented when information on both traits was extracted from the same source. Three references

are shown when more than one reference was available for one of the traits. “Strong”, “Inter” and “Slight” refer to strongly, intermediately and slightly dependent plants, respectively, in the column referring to dependence on pollinators (DP). “Low” and “High” refer to high and low-dispersal plants, respectively, in the column referring to dispersal ability (DA).  
(PDF)

**S3 Table. Plant sensitivity to pollinator loss and network robustness.** Scenarios linking plant probability of extinction to different plant traits associated with plant sensitivity to pollinator loss (i.e. plant generalization, dependence on pollinators, dispersal ability) or combinations of these traits. The random scenario (no trait is considered) was also explored.  
(PDF)

**S4 Table. Plant interaction patterns and sensitivity to pollinator loss: partition of variation and permutation analyses results.** Sum of squares (SS), degrees of freedom (df), mean squares (MS), and F-ratio are shown for plant generalization on pollinators, contribution to nestedness and mean pollinator generalization. Probability values (p) obtained from permutation analyses are also shown.  
(PDF)

**S5 Table. Plant sensitivity to pollinator loss and network robustness.** Mean differences of robustness (Mean) between pairs of scenarios, and minimum (CI min) and maximum (CI max) limits of the 95% confidence interval of each difference are shown for the Barrett network. Pairwise comparisons were planned a-priori. Scenarios: dependence on pollinators (DP), dispersal ability (DA), dependence on pollinators and dispersal ability (DPDA), random (R), dependence on pollinators and generalization (DPG), dispersal ability and generalization (DAG), dependence on pollinators, dispersal ability and generalization (DPDAG) and generalization (G).  
(PDF)

**S6 Table. Plant sensitivity to pollinator loss and network robustness.** Mean differences of robustness (Mean) between pairs of scenarios, and minimum (CI min) and maximum (CI max) limits of the 95% confidence interval of each difference are shown for the Dupont network. Pairwise comparisons were planned a-priori. Scenarios: dependence on pollinators (DP), dispersal ability (DA), dependence on pollinators and dispersal ability (DPDA), random (R), dependence on pollinators and generalization (DPG), dispersal ability and generalization (DAG), dependence on pollinators, dispersal ability and generalization (DPDAG) and generalization (G).  
(PDF)

**S7 Table. Plant sensitivity to pollinator loss and network robustness.** Mean differences of robustness (Mean) between pairs of scenarios, and minimum (CI min) and maximum (CI max) limits of the 95% confidence interval of each difference are shown for the Elberling network. Pairwise comparisons were planned a-priori. Scenarios: dependence on pollinators (DP), dispersal ability (DA), dependence on pollinators and dispersal ability (DPDA), random (R), dependence on pollinators and generalization (DPG), dispersal ability and generalization (DAG), dependence on pollinators, dispersal ability and generalization (DPDAG) and generalization (G).  
(PDF)

**S8 Table. Plant sensitivity to pollinator loss and network robustness.** Mean differences of robustness (Mean) between pairs of scenarios, and minimum (CI min) and maximum (CI max) limits of the 95% confidence interval of each difference are shown for the Kevan network.



Pairwise comparisons were planned a-priori. Scenarios: dependence on pollinators (DP), dispersal ability (DA), dependence on pollinators and dispersal ability (DPDA), random (R), dependence on pollinators and generalization (DPG), dispersal ability and generalization (DAG), dependence on pollinators, dispersal ability and generalization (DPDAG) and generalization (G).

(PDF)

**S9 Table. Plant sensitivity to pollinator loss and network robustness.** Mean differences of robustness (Mean) between pairs of scenarios, and minimum (CI min) and maximum (CI max) limits of the 95% confidence interval of each difference are shown for the Medán II network. Pairwise comparisons were planned a-priori. Scenarios: dependence on pollinators (DP), dispersal ability (DA), dependence on pollinators and dispersal ability (DPDA), random (R), dependence on pollinators and generalization (DPG), dispersal ability and generalization (DAG), dependence on pollinators, dispersal ability and generalization (DPDAG) and generalization (G).

(PDF)

**S10 Table. Plant sensitivity to pollinator loss and network robustness.** Mean differences of robustness (Mean) between pairs of scenarios, and minimum (CI min) and maximum (CI max) limits of the 95% confidence interval of each difference are shown for the Medán I network. Pairwise comparisons were planned a-priori. Scenarios: dependence on pollinators (DP), dispersal ability (DA), dependence on pollinators and dispersal ability (DPDA), random (R), dependence on pollinators and generalization (DPG), dispersal ability and generalization (DAG), dependence on pollinators, dispersal ability and generalization (DPDAG) and generalization (G).

(PDF)

**S11 Table. Plant sensitivity to pollinator loss and network robustness.** Mean differences of robustness (Mean) between pairs of scenarios, and minimum (CI min) and maximum (CI max) limits of the 95% confidence interval of each difference are shown for the Motten network. Pairwise comparisons were planned a-priori. Scenarios: dependence on pollinators (DP), dispersal ability (DA), dependence on pollinators and dispersal ability (DPDA), random (R), dependence on pollinators and generalization (DPG), dispersal ability and generalization (DAG), dependence on pollinators, dispersal ability and generalization (DPDAG) and generalization (G).

(PDF)

**S12 Table. Plant sensitivity to pollinator loss and network robustness.** Mean differences of robustness (Mean) between pairs of scenarios, and minimum (CI min) and maximum (CI max) limits of the 95% confidence interval of each difference are shown for the Ramirez network. Pairwise comparisons were planned a-priori. Scenarios: dependence on pollinators (DP), dispersal ability (DA), dependence on pollinators and dispersal ability (DPDA), random (R), dependence on pollinators and generalization (DPG), dispersal ability and generalization (DAG), dependence on pollinators, dispersal ability and generalization (DPDAG) and generalization (G).

(PDF)

**S13 Table. Plant sensitivity to pollinator loss and network robustness.** Mean differences of robustness (Mean) between pairs of scenarios, and minimum (CI min) and maximum (CI max) limits of the 95% confidence interval of each difference are shown for the Schemske network. Pairwise comparisons were planned a-priori. Scenarios: dependence on pollinators (DP),

dispersal ability (DA), dependence on pollinators and dispersal ability (DPDA), random (R), dependence on pollinators and generalization (DPG), dispersal ability and generalization (DAG), dependence on pollinators, dispersal ability and generalization (DPDAG) and generalization (G).  
(PDF)

**S14 Table. Plant sensitivity to pollinator loss and network robustness.** Mean differences of robustness (Mean) between pairs of scenarios, and minimum (CI min) and maximum (CI max) limits of the 95% confidence interval of each difference are shown for the Vazquez network. Pairwise comparisons were planned a-priori. Scenarios: dependence on pollinators (DP), dispersal ability (DA), dependence on pollinators and dispersal ability (DPDA), random (R), dependence on pollinators and generalization (DPG), dispersal ability and generalization (DAG), dependence on pollinators, dispersal ability and generalization (DPDAG) and generalization (G).  
(PDF)

**S1 Fig. Plant contribution to nestedness and dispersal ability.** Box-plots of plant contribution to nestedness of species with different dispersal ability. Black lines within boxes represent median values. Upper and lower limits of boxes represent 1<sup>st</sup> and 3<sup>rd</sup> quartiles, respectively. Boxes were drawn with widths proportional to the number of observations in each group. “Low” and “High” refer to low and high-dispersal plants, respectively.  
(TIFF)

## Author Contributions

Conceived and designed the experiments: JA FM POC PRG. Performed the experiments: JA MMV. Analyzed the data: JA MMV. Contributed reagents/materials/analysis tools: JA FM MMV POC PRG. Wrote the paper: JA FM MMV POC PRG.

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## ABSTRACT / RÉSUMÉ

Ecological systems are all spatially structured to some extent, with fluxes of individuals, matter and energy linking habitat patches and, thus, connecting local and regional dynamics. This synthesis is an attempt at summarising work I have performed since 2008 on the following topics:

- (i) The emergence and coexistence of phenotypically distinct types, be they genotypes within a species or species within a community, in particular in models explaining the evolution of dispersal polymorphisms and their consequences for communities;
- (ii) The complexity and functioning of ecological networks. This more recent part of my work has led me to consider models of interaction networks and models of spatially structured ecological systems on directed networks;
- (iii) The dynamics of spatially structured ecological systems, in particular the consequences of perturbation dynamics in metacommunities and a re-examination of the stability-complexity issue in metaecosystems;
- (iv) The geographic distributions of species, notably through the improvement of current methods to estimate consensus and uncertainty among different species distribution models and through theoretical models linking maladaptation and gene flow to species range limits.

Current perspectives on these topics include developing spatial evolutionary models interaction network, applying network approaches to the prediction of ecosystem services, and improving the general framework of spatially structured ecological systems, *e.g.* by taking into account symbiotic interactions and their evolution in spatially heterogeneous settings.

**Keywords:** adaptive dynamics; complexity; dispersal; metacommunity; metaecosystem; metapopulation; network; species distribution; stability.

Dans une certaine mesure, les systèmes écologiques sont tous structurés spatialement, les flux d'individus, de matière et d'énergie connectant les taches d'habitat et, ainsi, liant les dynamiques locales et régionales. Cette synthèse tente de résumer mon travail depuis 2008 sur les thèmes suivants :

- (i) L'émergence et la coexistence de types phénotypiquement distincts, que ce soient des génotypes au sein d'une espèce ou des espèces au sein d'une communauté, en particulier via des modèles expliquant l'évolution de polymorphismes de traits de dispersion et leurs conséquences pour les communautés écologiques ;
- (ii) La complexité et le fonctionnement des réseaux écologiques. Cette partie plus récente de mon travail m'a amené à considérer des modèles de réseaux d'interaction et des modèles de systèmes écologiques spatialisés évoluant sur un réseau dirigé ;
- (iii) La dynamique de systèmes écologiques spatialement structurés, en particulier les conséquences de la dynamique des perturbations dans les métacommunautés et un réexamen du problème complexité-stabilité sous l'angle des métaécosystèmes ;
- (iv) La distribution géographique des espèces, notamment via l'amélioration des méthodes d'estimation de consensus et d'incertitude entre modèles de distribution différents et à travers des modèles théoriques liant maladaptation et flux de gènes aux limites des aires de distribution.

Mes perspectives actuelles sur ces thèmes incluent le développement de modèles spatiaux et évolutifs de réseaux d'interaction, l'application des approches « réseau » à la prédiction des services écosystémiques et une amélioration du cadre général des systèmes écologiques spatialement structurés, notamment en prenant en compte les interactions symbiotiques et leur évolution dans un environnement hétérogène.

**Mots-clés :** complexité ; dispersion ; distribution des espèces ; dynamique adaptative ; métacommunauté ; métaécosystème ; métapopulation ; réseau ; stabilité.