

PhD project

Linking forest management and species distribution models: a theoretical approach under climate change

Willian Vieira^{1,*}

¹*Département de Biologie, Université de Sherbrooke, Sherbrooke, Québec, Canada*

^{*}*w.vieiraw@gmail.com*

Abstract

TODO:

- Abiotic and biotic constraints
- Forest management and productivity
- Theoretical approach (SDM, Disturbance, resilience calculus, alternative stable state and early warning signals)
- All study case: Québec Forest ressource
- All methods
- Better description of thesis structure
- Abstract
- Short reference style
- Change L^AT_EXcolor syntax in Atom

Contents

1	What is going on?	3
2	Preliminary objectives	4
3	Mechanisms of delayed biotic response	4
3.1	Biotic Mechanisms	4
3.2	Abiotic Mechanisms	5
4	Forest management	6
4.1	Forest productivity	7
5	Theoretical approach	7
5.1	Range dynamics theory	7
5.2	Disturbance	7
5.3	Resilience	7
5.4	Transition period - Alternative Stable States?	8
5.5	Early warnings?	8
6	Study case: the Quebec forest resource	8
7	Methods	9
7.1	Modeling	9
7.1.1	Species Distribution Models	9
7.1.2	Integral Projection Models	9
7.2	Bayesian approach	9
8	Thesis structure	9

Ecology may provide many of the answers — but only if it is holistic enough to incorporate the human element as part and parcel of the ecosystem.

(Pfister, 1993, p. 231)

1 What is going on?

Climate change is an increasing trending topic both in non-scientific (Capstick et al., 2015) and scientific environment (Figure 1), transforming our world as a metamorphosis of practice and acting (Beck, 2016). According to IPCC (Cubasch et al., 2013), humans activities are contributing to increase the concentration of greenhouse gases, which can lead to increase the mean temperature and the strength of extreme climate events. This global change has an impact in different biological processes, from local species constraints (e.g. low regeneration Treyger and Nowak, 2011), shift in species' range (Boisvert-Marsh et al., 2014; Monleon and Lintz, 2015) and in community composition (Dieleman et al., 2015) to range retractions and extinction (Thomas et al., 2006), impacting biodiversity at different scales (Peñuelas et al., 2013).

Species distribution models (SDM; defined in section 7.1.1) is one of the most popular method to predict species' range shift under climate change, providing a wide range of applications, as in biodiversity conservation and management (Guisan and Thuiller, 2005; Guisan et al., 2013). However, these models are generally phenomenological and distributed at equilibrium with climate (e.g. Pigot and Tobias, 2013), being an issue when species observation does not reflect its niche (Schurr et al., 2012). Furthermore, they do not consider important determinants of range limits as demography (Louthan et al., 2015), ecological constraints (Wisn et al., 2013; Pigot and Tobias, 2013) and species absences data (Koshkina et al., 2017), inducing non-accurately projection of the future spatial distribution of a species (Tavecchia et al., 2016). Considering this determinants, trees' migration rate following climate change will be slower than predicted (Bertrand et al., 2011; Sittaro et al., 2017), increasing the climatic debt (Bertrand et al., 2016).

The climatic debt is a measure of the lag (or disequilibrium) of plant communities with climate change, integrated in an environmental context (Bertrand et al., 2016). Essl et al. (2015) has listed twelve mechanisms that contribute to delayed biodiversity responses, among them, changes appears at ecosystem (loss and degradation), community (secessional, biotic interaction, species removal and invasion) and population (evolutionary and adaptive) levels. Physical changes cause biotic changes that directly and indirectly promotes species' persistence and/or species' migration (Bertrand et al., 2016). This mechanisms of persistence (measured by resistance) and migration (measured by recovery) leads to a climate debt and migration credit, respectively (Bertrand et al., 2016) but also a concept of resilience¹ (Oliver et al., 2015). Therefore, this lag under climate change promotes extinction debt, being a challenging for biodiversity conservation (Kuussaari et al., 2009) and productivity (Lasch et al., 2002). Identify the mechanisms shaping delayed biotic

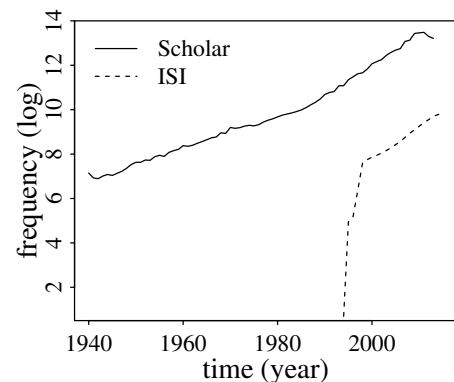


Figure 1: Frequency of the keyword “Climate change” used in publications indexed on Google Scholar (1940 - 2013) and Web of Science (1994 - 2015)

response of systems to environment, its resilience as well as alternatives to mitigate ecological constraints, is crucial to assess the vulnerability of biodiversity to climate change and improve forecasts and biodiversity management (Essi et al., 2015; Oliver et al., 2015; Bertrand et al., 2016).

2 Preliminary objectives

The primary objective of my thesis is to study if forest management can increase the speed of transition (i.e. recovery resilience) from temperate to boreal forests observed in the North Eastern America. To achieve, I will use theoretical models parameterized from a forest inventory database, focusing on tracking uncertainty using Bayesian approach. As an outcome, I will create a decision make tool to improve management strategies that take climate change into account.

My PhD is based in four questions so far:

- (i) Which mechanisms are affecting the delayed biotic response to climate change? What is the origin, direction and intensity of these mechanisms?
- (ii) How can forest management affect these mechanisms to increase resilience and therefore speed up the response?
- (iii) How these mechanisms interact at local and global scale?
- (iv) How can these mechanisms be used to inform applied management to enhance the resilience and productivity?

3 Mechanisms of delayed biotic response

Mechanisms shaping delayed biotic response and ecological resilience act at different scales and usually they interact with each other across scales, which makes the process sometime difficult to track and therefore to mitigate. Furthermore, there is a focus attention in mechanisms at the metapopulation level where local mechanisms are often ignored (Hylander and Ehrlén, 2013); it creates a knowledge gap in understanding all the possible mechanisms as well as its interactions. In this context, I will start my thesis trying to identify how we can increase forest resilience by managing these mechanisms, or more specific, how to decrease the recovery time of a system from a disturbance to a steady state (theories described in section 5). Here, I present some mechanisms that may be affecting the delayed response to climate change, as well as forest resilience, in which may become possible topics I will be testing during my thesis using SDM approach, working both at local and large scale.

3.1 Biotic Mechanisms

Biotic mechanisms affect the delayed response from individual and population species to community level. At the individual scale, the lifecycle elements of a species j , represented by demography patterns, is a mechanism able to alter the time response from environmental perturbations (Bertrand et al., 2016). For example, species with a high growth rate will recover faster (Grman

¹Here I use **recovery resilience** (recovery time to equilibrium) and **resistance** to describe the whole mechanisms of ecological resilience (see why in section 5.3)

et al., 2010), in which we can expect a high recovery resilience; the allee effect can, however, induce the opposite effect by reducing mean vital rates (Dennis and Dennis, 2002). In parallel, the sensitivity of a species also plays an important role in its response to perturbations (Oliver et al., 2015; Bertrand et al., 2016); sensitive species respond faster and also has a high recovery resilience. In other hands, both species (with high growth and sensitivity) have a low resistance to environmental changes; it means that, if they have a low adaptive phenotypic plasticity, they will not be able to survive. Phenotypic plasticity is the (behaviour, morphology or physiology) change of an individual in response to the environmental change (Price et al., 2003); this adaptive process, together with evolutionary adaptation (Bertrand et al., 2016) is a mechanism that increase both species resistance and recovery resilience (Essl et al., 2015; Oliver et al., 2015).

In a metapopulation level, high genetic variability increase both resistance and recovery resilience of species (Hylander and Ehrlén, 2013; Oliver et al., 2015). Dispersal mechanisms can affect genetic variability (the low exchange between individuals, the low variability), in which together with the low dispersal ability of forest species, can lead to an increase in climate debt (Hylander and Ehrlén, 2013; Bertrand et al., 2016). Further than dispersion, the effective population size also affect genetic variability (Oliver et al., 2015), where small populations increase the likelihood for inbreeding and hence the extinction risk (Nieminen et al., 2001). These individual and populational mechanisms are, however, rarely affecting species alone; instated there must be interactions between them (Hylander and Ehrlén, 2013), as well as extra mechanisms acting from different scales and origins.

Because different species are normally distributed together limiting one another (Clark et al., 2014), consider biotic interactions across trophic levels is essential to predict species distribution (Van der Putten et al., 2010), as well as understand its impact on delayed biodiversity response (Essl et al., 2015). For example, trees competition for soil nitrogen has amplified climate debt, but it varies depending on the resource (Bertrand et al., 2016). Species interaction itself is determined by multiple mechanisms (Louthan et al., 2015, for an overview) and a shift from single-species distribution to community distribution is suggested (Cazelles et al., 2016). In a interaction network, the loss of one specie can lead to cascade extinction, reducing network stability (Dunne et al., 2002) and, if the specie is sensitive, the functional resistance. In addition, the recovery resilience and resistance of a system depend if different species perform complementary functions (i.e. functional redundancy) or respond in different ways to perturbation (Winfree and Kremen, 2009); it means resistance increase when the network are dominated by non-specialized interactions (Oliver et al., 2015).

3.2 Abiotic Mechanisms

Abiotic or physical mechanisms can also shape delayed biotic response and ecological resilience, in which a better quality environment will support plant development and therefore its resistance to perturbation. At the soil level, for example, nitrogen availability can limite the growth of trees (Sullivan et al., 2015) and high nitrogen content and low acidity soils impact both species sensitivity and competition, amplifying the climate debt (Bertrand et al., 2016). Likewise, less suitable climates constrained demographic strategies, increasing retrogression and vulberability of plant species (Csergo et al., 2017) and increase in the severity of climate events inflated climate

debt (Bertrand et al., 2016).

Because environmental heterogeneity increases overall species richness (Stein et al., 2014), the resistance of a system is enhanced by functional redundancy (Oliver et al., 2015). Environmental heterogeneity also provides a range of microclimatic refugia, which allow species to persist locally to climate changes (Maclean et al., 2015); however, Bertrand et al. (2016) found that microclimatic refugia plays a minor role comparing with other determinants of climatic debt. Ecosystem loss and degradation are mechanisms that contribute to loss and decrease in species diversity (Essl et al., 2015), as well as decrease landscape connection. Disconnected landscapes have then slow recovery resilience of a system after perturbation, i.e., low functional connectivity (Oliver et al., 2015).

- Disturbance Is important according to Essl but was important according to Bertrand

Human-induced drivers

- Land use by Goring and William 2017

see Cabral 2017

4 Forest management

L'article de Bottero et al. rapporte une augmentation de la résistance à la sécheresse lorsqu'on réduit la densité d'un peuplement forestier. Chase et al. précisent que ce gain en productivité serait attribuable à des conditions d'humidité du sol plus favorables aux printemps. Sohn et al. rajoute que les ÉPC vont, en fait, augmenter la plasticité des réponses physiologiques de l'arbre aux changements environnementaux. Par contre, D'Amato et al. préviennent que ce gain en résistance à la sécheresse disparaît lorsque les peuplements prennent de l'âge.

Lessons from large-scale environmental management successes, for example measures to reduce the causes of 'acid rain' (Fowler et al. 1982), show that action at local and global scales must complement each other if wide-scale environmental management efforts are to be successful. Present some motivations, advantages and disadvantages in considering forest management. (in Rhodes 2015)

It is clear that some factors will be more amenable to management (e.g., population-level genetic variability, landscape structure [18,31]) than others (e.g., environmental sensitivity of individual species, presence of alternative stable states). In Olivier 2015

Four major strategies are available to mitigate carbon emissions through forestry activities: (i) to increase forested land area through reforestation (6), (ii) to increase the carbon density of existing forests at both stand and landscape scales, (iii) to expand the use of forest products that sustainably replace fossil-fuel CO₂ emissions, and (iv) to reduce emissions from deforestation and degradation. in Managing forests for climate change mitigation (Science)

<http://onlinelibrary.wiley.com/doi/10.1111/j.1752-4571.2010.00157.x/full>
<http://www.sciencedirect.com/science/article/pii/S0006320715301762>

Interesting argument about who should peak do winners from Webster et al. (2017). They say that *Predict-and-prescribe management may erode diversity by focusing on 'winners'*.

Forest management in a theoretical view was actually not very much explored and so I consider it a kind of gap we should better explore. Read Becknell et al. (2015) for an overview.

paper: Temporal stability in forest productivity increases with tree diversity due to asynchrony in species dynamics

However, this translation is limited by significant knowledge gaps including the following: (i) difficulties in detecting changes in resilience (Batt et al. 2013), (ii) a lack of evidence and agreement to support successful preventative management actions (Barrett et al. 2014) and (iii) the need to work across multiple geopolitical scales to achieve effective management (Servos et al. 2013). (In Rhodes 2015 at app eco)

An operational model for resilience-based management Step 1: Detecting ecological sensitivity to pressures Step 2: Developing more effective resilience-based management measures Step 3: Achieving adaptive governance

4.1 Forest productivity

Robert m'a envoyé quelques articles qui discutent des facteurs qui contrôlent la dominance des arbustes éricacées en forêt boréale et de leur possible impacte sur la productivité forestière.

Lire toute le mail que je vais arriver avoir une bonne base pour discuter ici.

5 Theoretical approach

Read the section *recent developments in predicting changes in species distribution* from [Ehrlén and Morris \(2015\)](#)

5.1 Range dynamics theory

What theories can help us to describe species range under climate change?

How to integrate forest management in this theory?

-> Metapopulation dynamics theory <-

5.2 Disturbance

Pass through the main disturbance theories basing mainly in [Pulsford et al. \(2016\)](#)

5.3 Resilience

A classical definition of resilience in ecology is the ability of ecosystems to absorb changes and still persist ([Holling, 1973](#)). The concept was further developed in other context (e.g. social-ecological systems), and a more contemporary definition considers resilience as (i) the amount of disturbance the system can absorb, (ii) the degree the system is able to self-organize and (iii) the degree of learning capacity to adapt to disturbance ([Cumming, 2011](#)). We have therefore two concepts, the time to **recovery** to stability and accommodated external changes ([Pimm, 1984](#); [Folke et al., 2002](#)) and the **resistance** of a particular ecological state to change ([Peterson et al., 1998](#)). Although [Oliver et al. \(2015\)](#) treat both resistance and recovery as related aspects of resilience, I prefer to keep these concepts separated in (i) recovery resilience (or engineering resilience) and (ii) resistance where both are englobed in ecological resilience ([Hodgson et al., 2015](#); [Nimmo et al., 2015](#)). Ecological resilience can be affected by different mechanisms from

species to landscape levels, but biodiversity shows to be crucial to maintain long-term resilience of ecosystem services (Oliver et al., 2015).

It is also important to not confuse recovery resilience with stability of a system. Recovery resilience is the rate and extent of “restoration” of a system while stability is when the system maintains stable following small perturbations over time. Before introduce the method to calculate recovery resilience, we must know what is the equilibrium and stability (Box 1) of a system, as well as these measures are relative and careful must be taken when choosing *resilience of what to what* (Carpenter et al., 2001).

Box 1. Equilibrium and Stability

$$E = mc^2 \qquad \text{Formula of the universe} \qquad (1)$$

Box 2. Environmental transition (see Oliver2015)

$$E = mc^2 \qquad \text{Formula of the universe} \qquad (2)$$

(iii) But how to calculate it in a analytical way? To implement the results from these or other studies in management projects, it is necessary to disentangle the many meanings and measures of resilience and related stability concepts (In Mori at TREE). Now introduce the calculus of λ by Jacobian matrix (Box 2). The Jacobian matrix has been used in different applications, from local models [...] to meta-ecosystems models (Gravel et al., 2016)

5.4 Transition period - Alternative Stable States?

The existence of single equilibria is still often assumed in the literature, with critical implications for conservation and restoration. – An important feature of this concept (resilience) is the emphasis on possible alternative system properties that are associated with renewal and reorganization after disturbance (In Mori 2016 at TREE)

Resilience-based management does not typically seek to increase the rate of return to an original state, which often implicitly assumes the existence of a single equilibrium, but instead recognizes that many natural systems could have multiple attractors [2, 3]. (In Mori 2016 at TREE)

5.5 Early warnings?

Resilience indicators: prospects and limitations for early warnings of regime shifts

For precautionary biodiversity management, the identification of robust early-warning signals (e.g., critical slowing down of recovery rates after perturbations) of approaching thresholds (tipping points) of losses of biodiversity or ecosystem services [9] is urgently needed (in Essl2015)

6 Study case: the Quebec forest resource

Explain here where I am going to work and also why I am choosing this area.

7 Methods

Here we see a briefly presentation of possible methods will be used in the thesis.

7.1 Modeling

Why and how modeling?

Morin et thuiller 2009:What then are the best strategies for obtaining accurate predictions for changes in the distributions of deciduous temperate trees? At the scale of the geographic distribution of species, no experiments in situ can be reasonably carried out to predict possible range shifts (Woodward 1987). Modeling therefore appears the most feasible and efficient way to establish useful predictions (Lovejoy and Hannah 2005, Thuiller 2007), and several kinds of models have been developed during the previous decade for this purpose. As reviewed by Midgley et al. (2007), these models fall into two main classes: vegetation-type models (dynamic global vegetation models [DGVMs]) and species-specific models (niche-based and process-based).

L'article de Ashraf et Maclean porte sur un modèle de simulation de croissance d'arbres individuels en fonction des changements climatiques. Leur modèle a été développé avec une technologie d'intelligence artificielle.

7.1.1 Species Distribution Models

Nice resume about SDM in [Morán-Ordóñez et al. \(2016\)](#).

7.1.2 Integral Projection Models

the predictive powers of state and transition models are relatively low and their ability to deal with uncertainty is limited (Bashari, Smith and Bosch, 2008; Phillips, 2011).

7.2 Bayesian approach

I should be writing and not playing with L^AT_EX

8 Thesis structure

The first part of the thesis will be a general introduction where I will probably use a part of this document and present the big picture of my thesis. I believe the introduction part of a thesis is an easy way to welcome the reader through my work, however in the actual context of digital era, no one really reads a whole PhD thesis and an efficient action to welcome and divulge my work is to publish it online. An alternative approach to (sleepers) general introductions that, according to Stephen Heard² no one reads but the author, is to publish it as a general papers in a scientific vulgarization journal. In this way, my work will be easier to understand by both academics and general public, more accessible and the introduction part more useful.

The first chapter will try to answer the question *How can forest management increase forest resilience to climate change?*. The paper will first work with an analytical analysis in a SDM to understand the impact of forest management on increasing forest resilience. Following, as an study case, we will test by sensitivity analysis the effect of forest management

In the second chapter I am going to build a landscape model that will consider both forest management and species interaction.

The third chapter I am going to build another model but in a local scale. *I have to find a good biological reason for that.*

The fourth chapter will then integrate both landscape and local model into one. Here I will also track the uncertainty of the model by bayesian approach.

Finally, I will try to introduce my PhD reflexions into the big picture of ecology, management and ecosystem services. In an integrative and synthetic approach (more appropriate for a *Forum* section), I will discuss my main results, its application and mainly the point of depart for future prosperous work.

²The three functions of a thesis, by Stephen Heard at the [Scientist Sees Squirrel's](#) blog

References

- U. Beck. *The metamorphosis of the world: How climate change is transforming our concept of the world*. Polity Press - John Wiley & Sons, Cambridge, UK, 2016. ISBN 0745690254.
- J. M. Becknell, a. R. Desai, M. C. Dietze, C. a. Schultz, G. Starr, P. a. Duffy, J. F. Franklin, a. Pourmokhtarian, J. Hall, P. C. Stoy, M. W. Binford, L. R. Boring, and C. L. Staudhammer. Assessing Interactions Among Changing Climate, Management, and Disturbance in Forests: A Macrosystems Approach. *BioScience*, 65(3):263–274, 2015. ISSN 0006-3568. doi: 10.1093/biosci/biu234. URL <http://bioscience.oxfordjournals.org/cgi/doi/10.1093/biosci/biu234>.
- R. Bertrand, J. Lenoir, C. Piedallu, G. Riofrío-Dillon, P. de Ruffray, C. Vidal, J.-C. Pierrat, and J.-C. Gégout. Changes in plant community composition lag behind climate warming in lowland forests. *Nature*, 479(7374):517–520, 2011. ISSN 0028-0836. doi: 10.1038/nature10548. URL <http://www.nature.com/doifinder/10.1038/nature10548>.
- R. Bertrand, G. Riofrío-Dillon, J. Lenoir, J. Drapier, P. de Ruffray, J.-C. Gégout, and M. Loreau. Ecological constraints increase the climatic debt in forests. *Nature Communications*, 7(August):12643, 2016. ISSN 2041-1723. doi: 10.1038/ncomms12643. URL <http://www.nature.com/doifinder/10.1038/ncomms12643>.
- L. Boisvert-Marsh, C. Périé, and S. de Blois. Shifting with climate? Evidence for recent changes in tree species distribution at high latitudes. *Ecosphere*, 5(7):art83, 2014. ISSN 2150-8925. doi: 10.1890/ES14-00111.1. URL <http://doi.wiley.com/10.1890/ES14-00111.1>.
- S. Capstick, L. Whitmarsh, W. Poortinga, N. Pidgeon, and P. Upham. International trends in public perceptions of climate change over the past quarter century. *Wiley Interdisciplinary Reviews: Climate Change*, 6(1):35–61, jan 2015. ISSN 17577799. doi: 10.1002/wcc.321. URL <http://doi.wiley.com/10.1002/wcc.321>.
- S. Carpenter, B. Walker, J. M. Anderies, and N. Abel. From Metaphor to Measurement: Resilience of What to What? *Ecosystems*, 4(8):765–781, 2001. ISSN 1435-0629. doi: 10.1007/s10021-001-0045-9. URL <http://dx.doi.org/10.1007/s10021-001-0045-9>.
- K. Cazelles, N. Mouquet, D. Mouillot, and D. Gravel. On the integration of biotic interaction and environmental constraints at the biogeographical scale. *Ecography*, 39(10):921–931, 2016. ISSN 16000587. doi: 10.1111/ecog.01714.
- J. S. Clark, A. E. Gelfand, C. W. Woodall, and K. Zhu. More than the sum of the parts: Forest Climate response from join specise distributions. *Ecological Applications*, 24(5):990–999, 2014. ISSN 10510761. doi: 10.1890/13-1015.1.
- A. M. Csargo, R. Salguero-Gómez, O. Broennimann, S. R. Coutts, A. Guisan, A. L. Angert, E. Welk, I. Stott, B. J. Enquist, B. McGill, J.-C. Svenning, C. Violle, and Y. M. Buckley. Less favourable climates constrain demographic strategies in plants. *Ecology Letters*, 2017. ISSN 1461023X. doi: 10.1111/ele.12794. URL <http://doi.wiley.com/10.1111/ele.12794>.

- U. Cubasch, D. Wuebbles, D. Chen, M. C. Facchini, D. Frame, N. Mahowald, and J. G. Winther. Introduction. In T. F. Stocker, D. Qin, G. K. Plattner, M. Tignor, S. K. Allen, J. Boschung, A. Nauels, Y. Xia, B. V., and P. M. Midgley, editors, *Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*, chapter Introducti, pages 119–158. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA, 2013.
- G. S. Cumming. *Spatial resilience in social-ecological systems*. Springer Science & Business Media, London, 2011. ISBN 9400703074.
- B. Dennis and B. Dennis. Allee effects in stochastic populations. *Oikos*, 96(3):389–401, 2002. ISSN 00301299. doi: 10.1034/j.1600-0706.2002.960301.x.
- C. M. Dieleman, B. A. Branfireun, J. W. Mclaughlin, and Z. Lindo. Climate change drives a shift in peatland ecosystem plant community: Implications for ecosystem function and stability. *Global Change Biology*, 21(1):388–395, 2015. ISSN 13652486. doi: 10.1111/gcb.12643.
- J. A. Dunne, R. J. Williams, and N. D. Martinez. Network structure and biodiversity loss in food webs: robustness increase with connectance. *Ecology Letters*, 5:558–567, 2002. ISSN 1461023X. doi: 10.1046/j.1461-0248.2002.00354.x. URL <http://www.santafe.edu/media/workingpapers/02-03-013.pdf>.
- J. Ehrlén and W. F. Morris. Predicting changes in the distribution and abundance of species under environmental change. *Ecology Letters*, 18(3):303–314, 2015. ISSN 14610248. doi: 10.1111/ele.12410.
- F. Essl, S. Dullinger, W. Rabitsch, P. E. Hulme, P. Pyšek, J. R. U. Wilson, and D. M. Richardson. Delayed biodiversity change: No time to waste. *Trends in Ecology and Evolution*, 30(7):375–378, 2015. ISSN 01695347. doi: 10.1016/j.tree.2015.05.002.
- C. Folke, S. Carpenter, T. Elmqvist, L. Gunderson, C. S. Holling, and B. Walker. Resilience and sustainable development: building adaptive capacity in a world of transformations. *AMBIO: A journal of the human environment*, 31(5):437–440, 2002. ISSN 0044-7447.
- D. Gravel, F. Massol, and M. A. Leibold. Stability and complexity in model meta-ecosystems. *Nature Communications*, 7(10):12457, aug 2016. ISSN 2041-1723. doi: 10.1038/ncomms12457. URL <http://ieeexplore.ieee.org/document/4309856/http://www.nature.com/doifinder/10.1038/ncomms12457>.
- E. Grman, J. A. Lau, D. R. Schoolmaster, and K. L. Gross. Mechanisms contributing to stability in ecosystem function depend on the environmental context. *Ecology Letters*, 13(11):1400–1410, 2010. ISSN 14610248. doi: 10.1111/j.1461-0248.2010.01533.x.
- A. Guisan and W. Thuiller. Predicting species distribution: Offering more than simple habitat models. *Ecology Letters*, 8(9):993–1009, 2005. ISSN 1461023X. doi: 10.1111/j.1461-0248.2005.00792.x.

- A. Guisan, R. Tingley, J. B. Baumgartner, I. Naujokaitis-Lewis, P. R. Sutcliffe, A. I. T. Tulloch, T. J. Regan, L. Brotons, E. McDonald-Madden, C. Mantyka-Pringle, T. G. Martin, J. R. Rhodes, R. Maggini, S. A. Setterfield, J. Elith, M. W. Schwartz, B. A. Wintle, O. Broennimann, M. Austin, S. Ferrier, M. R. Kearney, H. P. Possingham, and Y. M. Buckley. Predicting species distributions for conservation decisions. *Ecology Letters*, 16(12):1424–1435, 2013. ISSN 1461023X. doi: 10.1111/ele.12189.
- D. Hodgson, J. L. McDonald, and D. J. Hosken. What do you mean, ‘resilient’? *Trends in Ecology and Evolution*, 30(9):503–506, 2015. ISSN 01695347. doi: 10.1016/j.tree.2015.06.010. URL <http://dx.doi.org/10.1016/j.tree.2015.06.010>.
- C. S. Holling. Resilience and Stability of Ecological Systems. *Annual Review of Ecology and Systematics*, 4(1):1–23, 1973. ISSN 0066-4162. doi: 10.1146/annurev.es.04.110173.000245. URL <http://www.annualreviews.org/doi/10.1146/annurev.es.04.110173.000245>.
- K. Hylander and J. Ehrlén. The mechanisms causing extinction debts. *Trends in Ecology and Evolution*, 28(6):341–346, 2013. ISSN 01695347. doi: 10.1016/j.tree.2013.01.010.
- V. Koshkina, Y. Wang, A. Gordon, R. M. Dorazio, M. White, and L. Stone. Integrated species distribution models: combining presence-background data and site-occupancy data with imperfect detection. *Methods in Ecology and Evolution*, 8(4):420–430, 2017. ISSN 2041210X. doi: 10.1111/2041-210X.12738.
- M. Kuussaari, R. Bommarco, R. K. Heikkinen, A. Helm, J. Krauss, R. Lindborg, E. Öckinger, M. Pärtel, J. Pino, F. Rodà, C. Stefanescu, T. Teder, M. Zobel, and I. Steffan-Dewenter. Extinction debt: a challenge for biodiversity conservation. *Trends in Ecology and Evolution*, 24(10):564–571, 2009. ISSN 01695347. doi: 10.1016/j.tree.2009.04.011.
- P. Lasch, M. Lindner, M. Erhard, F. Suckow, and a. Wenzel. Regional impact assessment on forest structure and functions under climate change—the Brandenburg case study. *Forest Ecology and Management*, 162(1):73–86, 2002. ISSN 03781127. doi: 10.1016/S0378-1127(02)00051-8.
- A. M. Louthan, D. F. Doak, and A. L. Angert. Where and When do Species Interactions Set Range Limits? *Trends in Ecology and Evolution*, 30(12):780–792, 2015. ISSN 01695347. doi: 10.1016/j.tree.2015.09.011. URL <http://dx.doi.org/10.1016/j.tree.2015.09.011>.
- I. M. D. Maclean, J. J. Hopkins, J. Bennie, C. R. Lawson, and R. J. Wilson. Microclimates buffer the responses of plant communities to climate change. *Global Ecology and Biogeography*, 24(11):1340–1350, 2015. ISSN 14668238. doi: 10.1111/geb.12359.
- V. J. Monleon and H. E. Lintz. Evidence of tree species’ range shifts in a complex landscape. *PLoS ONE*, 10(1):1–17, 2015. ISSN 19326203. doi: 10.1371/journal.pone.0118069.
- A. Morán-Ordóñez, J. J. Lahoz-Monfort, J. Elith, and B. A. Wintle. Evaluating 318 continental-scale species distribution models over a 60-year prediction horizon: what factors influence the reliability of predictions? *Global Ecology and Biogeography*, pages 1–14, 2016. ISSN 1466822X. doi: 10.1111/geb.12545. URL <http://doi.wiley.com/10.1111/geb.12545>.

- M. Nieminen, M. C. Singer, W. Fortelius, K. Schöps, and I. Hanski. Experimental Confirmation That Inbreeding Depression Increases Extinction Risk in Butterfly Populations. *The American Naturalist*, 157(2):237–244, 2001. ISSN 0003-0147. doi: 10.1086/318630. URL <http://www.journals.uchicago.edu/doi/10.1086/318630>.
- D. G. Nimmo, R. Mac Nally, S. C. Cunningham, A. Haslem, and A. F. Bennett. Vive la résistance: Reviving resistance for 21st century conservation. *Trends in Ecology and Evolution*, 30(9):516–523, 2015. ISSN 01695347. doi: 10.1016/j.tree.2015.07.008. URL <http://dx.doi.org/10.1016/j.tree.2015.07.008>.
- T. H. Oliver, M. S. Heard, N. J. B. Isaac, D. B. Roy, D. Procter, F. Eigenbrod, R. Freckleton, A. Hector, C. D. L. Orme, O. L. Petchey, V. Proença, D. Raffaelli, K. B. Suttle, G. M. Mace, B. Martín-López, B. A. Woodcock, and J. M. Bullock. Biodiversity and Resilience of Ecosystem Functions. *Trends in ecology & evolution*, 30(11):673–684, 2015. ISSN 18728383. doi: 10.1016/j.tree.2015.08.009.
- J. Peñuelas, J. Sardans, M. Estiarte, R. Ogaya, J. Carnicer, M. Coll, A. Barbeta, A. Rivas-Ubach, J. Llusà, M. Garbulsky, I. Filella, and A. S. Jump. Evidence of current impact of climate change on life: A walk from genes to the biosphere. *Global Change Biology*, 19(8):2303–2338, 2013. ISSN 13541013. doi: 10.1111/gcb.12143.
- G. Peterson, C. R. Allen, and C. S. Holling. Original Articles: Ecological Resilience, Biodiversity, and Scale. *Ecosystems*, 1(1):6–18, 1998. ISSN 1432-9840. doi: 10.1007/s100219900002. URL <http://link.springer.com/10.1007/s100219900002>.
- R. D. Pfister. The need and potential for ecosystem management in forests of the inland west. In G. N. Aplet, N. Johnson, J. T. Olson, and V. A. Sample, editors, *Defining sustainable forestry*, chapter The need a, pages 217–239. Island Press, The Wilderness Society, Washington, DC, 1993.
- A. L. Pigot and J. A. Tobias. Species interactions constrain geographic range expansion over evolutionary time. *Ecology Letters*, 16(3):330–338, 2013. ISSN 1461023X. doi: 10.1111/ele.12043. URL <http://doi.wiley.com/10.1111/ele.12043>.
- S. L. Pimm. The complexity and stability of ecosystems. *Nature*, 307(26):321–326, 1984. ISSN 0028-0836. doi: 10.1038/315635c0. URL <http://www.nature.com/doifinder/10.1038/315635c0>.
- T. D. Price, A. Qvarnstrom, and D. E. Irwin. The role of phenotypic plasticity in driving genetic evolution. *Proceedings of the Royal Society B: Biological Sciences*, 270(1523):1433–1440, 2003. ISSN 0962-8452. doi: 10.1098/rspb.2003.2372. URL <http://rspb.royalsocietypublishing.org/cgi/doi/10.1098/rspb.2003.2372>.
- S. A. Pulsford, D. B. Lindenmayer, and D. A. Driscoll. A succession of theories: Purging redundancy from disturbance theory. *Biological Reviews*, 91(1):148–167, 2016. ISSN 1469185X. doi: 10.1111/brv.12163.

- F. M. Schurr, J. Pagel, J. S. Cabral, J. Groeneveld, O. Bykova, R. B. O'Hara, F. Hartig, W. D. Kissling, H. P. Linder, G. F. Midgley, B. Schröder, A. Singer, and N. E. Zimmermann. How to understand species' niches and range dynamics: A demographic research agenda for biogeography. *Journal of Biogeography*, 39(12):2146–2162, 2012. ISSN 03050270. doi: 10.1111/j.1365-2699.2012.02737.x.
- F. Sittaro, A. Paquette, C. Messier, and C. A. Nock. Tree range expansion in eastern North America fails to keep pace with climate warming at northern range limits. *Global Change Biology*, pages 1–10, 2017. ISSN 13652486. doi: 10.1111/gcb.13622.
- A. Stein, K. Gerstner, and H. Kreft. Environmental heterogeneity as a universal driver of species richness across taxa, biomes and spatial scales. *Ecology Letters*, 17(7):866–880, 2014. ISSN 14610248. doi: 10.1111/ele.12277.
- P. F. Sullivan, S. B. Z. Ellison, R. W. McNown, A. H. Brownlee, and B. Sveinbjörnsson. Evidence of soil nutrient availability as the proximate constraint on growth of treeline trees in northwest Alaska. *Ecology*, 96(3):716–727, 2015. ISSN 00129658. doi: 10.1890/14-0626.1. URL <http://scholar.google.com/scholar?hl=en&btnG=Search&q=intitle:No+Title{#}0>.
- G. Tavecchia, S. Tenan, R. Pradel, J. M. Igual, M. Genovart, and D. Oro. Climate-driven vital rates do not always mean climate-driven population. *Global Change Biology*, 22(12):3960–3966, 2016. ISSN 13652486. doi: 10.1111/gcb.13330.
- C. D. Thomas, A. M. A. Franco, and J. K. Hill. Range retractions and extinction in the face of climate warming. *Trends in Ecology and Evolution*, 21(8):415–416, 2006. ISSN 01695347. doi: 10.1016/j.tree.2006.05.012.
- A. L. Treyger and C. A. Nowak. Changes in tree sapling composition within powerline corridors appear to be consistent with climatic changes in New York State. *Global Change Biology*, 17(11):3439–3452, 2011. ISSN 13541013. doi: 10.1111/j.1365-2486.2011.02455.x.
- W. H. Van der Putten, M. Macel, and M. E. Visser. Predicting species distribution and abundance responses to climate change: why it is essential to include biotic interactions across trophic levels. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 365(1549):2025–2034, 2010. ISSN 0962-8436. doi: 10.1098/rstb.2010.0037. URL <http://rstb.royalsocietypublishing.org/cgi/doi/10.1098/rstb.2010.0037>.
- M. S. Webster, M. A. Colton, E. S. Darling, J. Armstrong, M. L. Pinsky, N. Knowlton, and D. E. Schindler. Who Should Pick the Winners of Climate Change? *Trends in Ecology & Evolution*, 32(3):167–173, 2017. ISSN 01695347. doi: 10.1016/j.tree.2016.12.007. URL <http://linkinghub.elsevier.com/retrieve/pii/S0169534716302415>.
- R. Winfree and C. Kremen. Are ecosystem services stabilized by differences among species? A test using crop pollination. *Proceedings of the Royal Society B: Biological Sciences*, 276(1655):229–237, 2009. ISSN 0962-8452. doi: 10.1098/rspb.2008.0709. URL <http://rspb.royalsocietypublishing.org/cgi/doi/10.1098/rspb.2008.0709>.

M. S. Wisz, J. Pottier, W. D. Kissling, L. Pellissier, J. Lenoir, C. F. Damgaard, C. F. Dormann, M. C. Forchhammer, J. A. Grytnes, A. Guisan, R. K. Heikkinen, T. T. Høye, I. Kühn, M. Luoto, L. Maiorano, M. C. Nilsson, S. Normand, E. Öckinger, N. M. Schmidt, M. Termansen, A. Timmermann, D. A. Wardle, P. Aastrup, and J. C. Svenning. The role of biotic interactions in shaping distributions and realised assemblages of species: Implications for species distribution modelling. *Biological Reviews*, 88(1):15–30, 2013. ISSN 14647931. doi: 10.1111/j.1469-185X.2012.00235.x.