

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

Shift in species distribution under climate change has been largely predicted by species distribution models, where biotic and physics mechanisms at fine- and landscape scale leads to an improvement in forecast. However, the potential of forest management to mitigate climate change impacts on forest dynamics remains poorly understood. My primary objective is to test if forest management can increase the speed of transition from temperate to boreal forests observed in the North Eastern America. By using theoretical models parameterized from a forest inventory database, I expect to find a positive effect of forest management on accelerating forest migration towards the north. As an outcome, I will create a decision make tool to improve management strategies that take climate change into account.

Contents

1	Context	2
2	Preliminary objectives	3
3	Mechanisms of delayed biotic response	3
4	Forest management	6
5	Theoretical approach	7
6	Study case: the Quebec forest resource	8
7	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 Context

Climate change is an increasing trending topic in both non-scientific (Capstick *et al.* 2015) and scientific environment (Figure 1), transforming our world as a metamorphosis of practice and acting (Beck 2016). In the holocene epoch, the world’s climate has never been completely stable, mainly impacted by different forces as, e.g., orbital, solar and volcanic (Wanner *et al.* 2008). However, in the last 200 years humans activities are contributing to increase the concentration of greenhouse gases, which can lead to increase the mean temperature, changes in precipitation patters and the strength of extreme climate events (Cubasch *et al.* 2013). These changes on climate are not only impacting the functionality of ecosystems and their capacity to provide essential ecological services for human well-being (Cardinale *et al.* 2012), but also (surprisingly) the risk of human’s death (Mora *et al.* 2017).

Recent global changes have an impact on different biological mechanisms, then an immediate key question is to understand the patters of this process. Impacts of climate change go from local species constraints (e.g. low regeneration; Treyger & Nowak 2011), shift in species’ range (Boisvert-Marsh *et al.* 2014; Monleon & Lintz 2015) and in community composition (Dieleman *et al.* 2015), to range retractions and extinction (Thomas *et al.* 2006), modifying biodiversity in all scales (Peñuelas *et al.* 2013). To understand this link, climate variables are often used as predictors of trees site occupancy (Canham *et al.* 2010) and range limits (Morin *et al.* 2007), in which, modeling approach projects a range shift to both higher elevations and higher latitudes under climate change (Chen *et al.* 2011).

Species distribution models (SDM) 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 & Thuiller 2005; Guisan *et al.* 2013). However, these models are generally phenomenological and distributed at equilibrium with climate (e.g. Pigot & 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 (Pigot & Tobias 2013; Wisz *et al.* 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 cli-

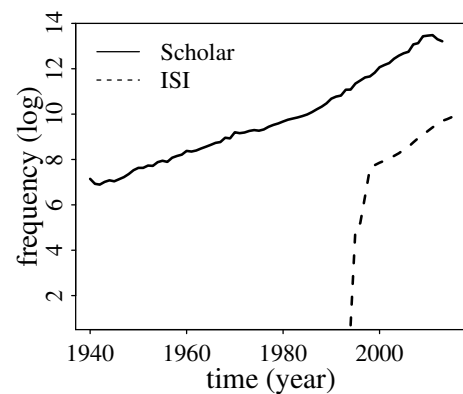


Figure 1: Frequency of the keyword “Climate change” used in publications indexed on Google Scholar (1940 - 2013) and Web of Science (1994 - 2015)

mate 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, climate lag promotes extinction debt (temporarily persistence of population under unsuitable conditions) and colonization credit (suitable locations are not occupied due species constraints; Talluto *et al.* 2017), being a challenging for biodiversity conservation (Kuussaari *et al.* 2009) and productivity (Lasch *et al.* 2002). Identify the mechanisms shaping delayed biotic response of systems to environment, its resilience as well as alternatives to mitigate ecological constraints, is crucial to access the vulnerability of biodiversity to climate change and improve forecasts and biodiversity management (Bertrand *et al.* 2016; Essl *et al.* 2015; Oliver *et al.* 2015).

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.

During these first few months of reading, I asked myself the following questions that may direct my PhD:

- (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 interact with these mechanisms to increase resilience to climate change and therefore speed up the response?
- (iii) What if we consider demography patterns, species interaction and natural disturbance in both local and global scale models?
- (iv) Which role plays the interaction of forest management, climate change and disturbance on provision of ecosystem services? Which scale is the most important?
- (v) How can the mechanisms we will find 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

¹Here I use **recovery resilience** (recovery time to equilibrium) and **resistance** to describe the whole mechanisms of ecological resilience (see why in section 5)

the metapopulation level where local mechanisms are often ignored (Hylander & 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 specifically, 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.

Biotic Mechanisms

Biotic mechanisms change the response from individual and population species to community level. At the individual scale, the lifecycle elements of any species, 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 *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 & Dennis 2002). In parallel, the sensitivity of a species also plays an important role in its response to perturbations (Bertrand *et al.* 2016; Oliver *et al.* 2015); sensitive species respond faster and also has a high recovery resilience. Alternatively, 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 behavior, morphology or physiology change of an individual in response to the environmental change (T. D. Price *et al.* 2003); this adaptive process, together with evolutionary adaptation (Bertrand *et al.* 2016) are mechanisms 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 & 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 (Bertrand *et al.* 2016; Hylander & Ehrlén 2013). Dispersion itself is a key mechanisms that can increase range shift under climate change (González-Varo *et al.* 2017). Yet, this mechanism is poorly supported by data; alternatively, species' demographic rates are sufficient to predict population spread when dispersal data is absent (Hemrová *et al.* 2017). In addition to 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; instead there must be interactions between them (Hylander & 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 instance, trees competition for soil nitrogen has amplified climate debt, but it varies depending on the resource (Bertrand *et al.* 2016). Generally, 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 interaction networks, the loss of one specie can lead to cascade extinction, reducing the 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 & Kremen 2009); it means resistance increase when the network are dominated by non-specialized interactions (Oliver *et al.* 2015).

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 limit 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 vulnerability of plant species (Csergo *et al.* 2017) and increase the severity of climate events, inflating climate debt (Bertrand *et al.* 2016). In contrast, warming temperatures and higher CO₂ concentration did not amplify ring growth (Girardin *et al.* 2017).

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. Species in disconnected landscapes have then slow recovery resilience after perturbation, that is, low functional connectivity (Oliver *et al.* 2015).

Disturbance can have different sources (natural or anthropic) and the response of forest to disturbance can be positive, negative or even neutral depending on the intensity of disturbance. Natural disturbance are diverse and normally act quickly with high effect as, e.g., fire, flooding, pest outbreaks. These disturbances are often negative as generate decline in species density, community richnesses and connectivity, in other words, reduce forest resilience (Buma & Wessman 2011; Essl *et al.* 2015) but see Bertrand *et al.* (2016). However, according to the famous intermediate disturbance hypothesis, too little disturbance induces competitive exclusion and and too much disturbance long-lived species elimination (Connell 1978; Grime 1973; Horn 1975); between extremes, higher species richness is expected and hence higher forest resilience. Human-induced disturbances is becoming increasingly frequent and, not surprisingly, climate change is one of the most important (Bellard *et al.* 2012). But beyond that, human's disturbance is present almost everywhere, from local impacts, as soil degradations, to global ones, as mining disaster (Garcia *et al.* 2017); it implies that all mechanisms of disturbance, as well as its interaction (Goring & Williams 2017), has to be considered to a better understand of forest resilience and, hence,

biodiversity management.

4 Forest management

Forest managers have an important (and challenging) mission to create strategies that will both adapt and mitigate forest under climate change (Millar *et al.* 2007). Mitigative practices are often addressed, forest management can affect carbon cycle and retention, hydrology dynamics and the maintenance of rich suitable habitats (Becknell *et al.* 2015); however, adaptive ones are not that evident. Currently, management practices are usually based in mechanisms of immediate action-effects and not in theoretical concepts. Also, some factors are more amenable to manage (as e.g. genetic variability) than others (e.g. individual sensitivity, presence of alternative stable states; Oliver *et al.* 2015). Therefore, a theoretical approach can improve our understand of forest management and help we move towards a more sustainable intervention.

Looking analytically, practices as plantation, cutting and pre-commercial thinning can be used to change the mechanisms of colonization, perturbation and succession, respectively (Figure 2). For example, plantation cannot just enhance colonization but also determine future forest structure by choosing what species to plant. Similarly, reduce forest density by silvicultural thinning can enhance diameter growth (Rytter & Stener 2014) [but depend on thinning intensity (Fuller 2013; Olivar *et al.* 2014)], forest productivity (Chase *et al.* 2016), drought resilience (Bottero *et al.* 2017; Sohn *et al.* 2013) and accelerate succession; however, birds respond different to thinning and decrease in some species were observed (Hayes *et al.* 2003). Forest harvest can equally enhance disturbance and, by the fact that intermediate disturbance can enhance biodiversity (Connell 1978; Grime 1973; Horn 1975), the intensity and frequency of harvest can be important to decide whereas productivity will increase or not.

In contrast, we cannot consider management as a single solution by the fact that managing practices can have different action depending on the context (Millar *et al.* 2007), also external factors and interaction between practices can lead forest management to be complex (Becknell *et al.* 2015). For instance, theoretical methods, based in a macrosystem ecology approach, can access the interaction between forest management, climate change and disturbances to better provide

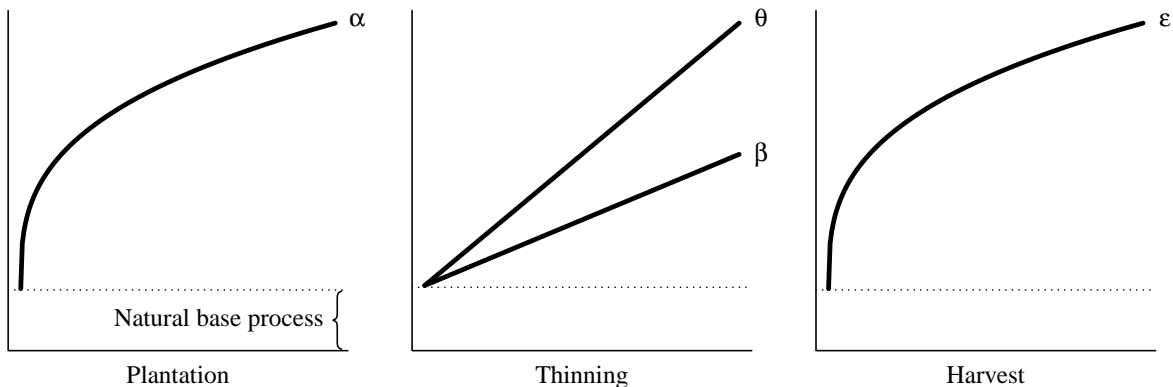


Figure 2: Hypothesized interaction between forest management and state transition processes. Plantation can enhance colonization (α), pre-commercial thinning can enhance both competitive exclusion (θ) and succession (β) and cutting can enhance disturbance (ϵ). Dotted line is the base natural process that occur without intervention.

ecosystems services (Becknell *et al.* 2015; Heffernan *et al.* 2014). Briefly, data synthesis can combine different methods as monitoring networks, remote-sensing, field studies and modeling to create an integrative approach able to evaluate forest change under different contexts (Becknell *et al.* 2015). Furthermore, ecological conditions, economic trends, policy and social priorities can influence forest management, where these practices vary in intensity, spatial extent and in frequency (Becknell *et al.* 2015).

The adaptation process described above has two interpretations, the first one is a directed management to whereas the manager wants to go, mainly based in productivity of target species. instead, the second one is a natural adaptation, which includes acclimatization, ecological reorganization and evolution through natural selection (Webster *et al.* 2017). The Predict-and-prescribe approach aims to protect target species based in predicting future environmental conditions, however, the uncertainty of predictions still high, hence the effectiveness of this approach is limited (Schindler & Hilborn 2015). Based on the portfolio theory, a successful approach happens when a diversity of portfolios environments, species, and communities promote a wide diversity of options, where in the end, nature is the one that peaks the “winners” (Webster *et al.* 2017).

5 Theoretical approach

Metapopulation dynamics theory

Metapopulation theory, or a population of populations (Levins 1968), is simply represented by patches that are either occupied or not. Further extended by Holt & Keitt (2000), the follow metapopulation dynamic equation has its parameters as a function of landscape position along the gradient (E):

$$\frac{dp(E)}{dt} = \underbrace{c(E)p(E)[1 - p(E)]}_{\text{colonization}} - \underbrace{e(E)p(E)}_{\text{extinction}} \quad (1)$$

Let p be the fraction of patches occupied at a given time, each unoccupied patch $[1 - p(E)]$ can become occupied with a defined colonization rate $c(E)$, in function of already occupied patches $p(E)$. In the other way, each occupied patch can become unoccupied with a defined extinction rate $e(E)$, in function of already occupied patches.

Solving equation (1) to equilibrium, we obtain the follow equation, which is pretty straightforward in the interaction between colonization and extinction:

$$\hat{p}(E) = 1 - \frac{e(E)}{c(E)} \quad (2)$$

In the context of forest management, we can analytically joint some practices into the metapopulation theory, and that is why I will do in the first chapter. For example the colonization rate $c(E)$ can be decomposed in the sum of natural colonization by migration $I(E)$ with human colonization by plantation $P(E)$: $c(E) = I(E) + P(E)$. The same can be done for all transition processes, as represented in Figure 2.

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 (Folke *et al.* 2002; Pimm 1984) 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.

Measure resilience can be sometimes mathematically difficult, however, with help from computational ecology, this calculus is becoming more accessible. To summarize, after a tiny perturbation to equilibrium, the linearization of the dynamic of this perturbation, given by the eigenvalue, is the recovery resilience rate. The eigenvalue, obtained by the Jacobian matrix, has been used in different applications, from local models to meta-ecosystems models (Gravel *et al.* 2016)

Alternative Stable States

In contrast of what is often assumed in the literature, systems can have multiple equilibria and alternative states can be reached after a perturbation. This implies that recovery resilience does not need to return to equilibrium but can go to an alternative one based in the renewal and reorganization after disturbance (Mori 2016). In the forest management context, resilience-based management will not just seek the old equilibrium but the most sustainable one after a disturbance (Chapin *et al.* 2009).

6 Study case: the Quebec forest resource

The present forest in the Québec province is mainly occupied by temperate species, with a land cover over 200 000 km² (Boulay 2015). Further than climate impacts on temperate forests (McKenney *et al.* 2011), clear-cutting and colonization after fire disturbances are changing forest composition (Dupuis *et al.* 2011). It happens because temperate forests are distributed in the region with more human demography concentration, instead, boreal forests distribution is farther north, where climate changes has a stronger affect. According to D. T. Price *et al.* (2013), models and observations has indicated that boreal forests will continue to be exposed to warmer temperatures compared with other biomes.

Both temperate, boreal and mixed forests are culturally, ecologically and economically important for the province. For example, white pine is a cultural species for the Kitcisakik Algonquin

community in Québec (Upreti *et al.* 2013), but clearly, economic pressures plays a more important role. The Canadian forest sector is dominated by the industrial forestry model, where the economical value is emphasized over cultural and ecological ones (Howlett & Rayner 2001), even though, sometimes, ecosystems services' value can be higher (Costanza *et al.* 1997). In this context where both global change and forest management are a strong influence to the Québec forest resource, this area will be an important study case to answer my questions.

7 Thesis structure

The first part of the thesis will be a general introduction where I will 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. 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 work with a four states transition model and, by analytical analysis, we will try (i) to identify the most important mechanisms shaping transition processes, (ii) measure how can forest management change these mechanisms, and (iii) understand the impact of these changes on forest resilience. In this part, resilience will be measured by the dominant eigenvalue (section 5) and forest management by increasing the model parameters (Figure 2). Furthermore, as a study case in the North Eastern America forest, we will run simulations with the most effective management practices, found from the analytical analysis, under different scenarios of climate change. Based in the real historical climate data from North Eastern America forest, the model will be run from the actual climate scenario to an increasing growth in temperature; and the probability of transition between temperate, boreal or mixed state will be extracted from the transition matrix. We expect forest management to enhance recovery resilience by the hypothesis that plantation and thinning will increase colonization and succession (This chapter answers questions I and II from section 2).

In the second chapter I will build a landscape Integral Projection Model (IPM) that will take forest management, species interaction and natural and human disturbance into account. State and transition models has a low predictive power and limited ability to track uncertainty (Bashari *et al.* 2008; Phillips 2011), IPMs are then an interesting alternative that can increase both of these weakness (Elderl & Miller 2016). The IPM will consider the mechanisms of management, species interaction and disturbance to reduce uncertainly of the transition matrix. Based in the correlation between these mechanisms and climate change, we expect to have a higher prediction power of the impact of each mechanism in the probability of transition (This chapter answers questions III and IV from section 2).

The third chapter is dedicated to another IPM but at fine-scale. As discussed earlier, fine-scale mechanisms are often ignored (Hylander & Ehrlén 2013); at this time, we will consider,

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

beyond forest management, species interaction and disturbance, the demography patterns of trees species. The objective of this chapter is similar to the previous one, but focusing in a different level of details. By calculating the capacity of prediction for each mechanism, we will have a more consistent argument about what mechanisms to use or not, increasing both prediction and efficiency in simulation time. As local demography patterns can influence the metapopulation, we expect a shift in the interaction between forest management, climate change and disturbance; these new mechanisms can improve the prediction of range distribution.

However, consider fine-scale patterns alone will not be the solution, alternatively, integrate models at multiple levels can be very powerful. The fourth chapter will, based in a metapopulation framework (Talluto *et al.* 2016), integrate both landscape model (from chapter 2) and local model (from chapter 3) into one. With the integration, correlative analysis between mechanisms and scale will give the relative importance of each process at each level, which is important to future researchers seeking to predict range distribution but also managers to effectively understand their impact on forest dynamics. Also, this approach allows a translucent track of uncertainty using Bayesian approach, where new methodology may be presented (This chapter answers question IV from section 2).

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. In parallel, I will create a decision make tool to improve management strategies that take the main outcomes of my thesis into account (This chapter answers question V from section 2).

References

- Bashari, H., Smith, C. & Bosch, O. (2008). Developing decision support tools for rangeland management by combining state and transition models and Bayesian belief networks. *Agricultural Systems*, 99, 23–34.
- Beck, U. (2016). *The metamorphosis of the world: How climate change is transforming our concept of the world*. Ed. by Beck, U. Polity Press - John Wiley & Sons. Cambridge, UK.
- Becknell, J. M., Desai, a. R., Dietze, M. C., Schultz, C. a., Starr, G., Duffy, P. a., *et al.* (2015). Assessing Interactions Among Changing Climate, Management, and Disturbance in Forests: A Macrosystems Approach. *BioScience*, 65, 263–274.
- Bellard, C., Bertelsmeier, C., Leadley, P., Thuiller, W. & Courchamp, F. (2012). Impacts of climate change on the future of biodiversity. *Ecology Letters*, 15, 365–377.
- Bertrand, R., Lenoir, J., Piedallu, C., Riofrío-Dillon, G., Ruffray, P. de, Vidal, C., *et al.* (2011). Changes in plant community composition lag behind climate warming in lowland forests. *Nature*, 479, 517–520.
- Bertrand, R., Riofrío-Dillon, G., Lenoir, J., Drapier, J., Ruffray, P. de, Gégout, J.-C. & Loreau, M. (2016). Ecological constraints increase the climatic debt in forests. *Nature Communications*, 7, 12643.
- Boisvert-Marsh, L., Périé, C. & Blois, S. de (2014). Shifting with climate? Evidence for recent changes in tree species distribution at high latitudes. *Ecosphere*, 5, 1–33.

- Bottero, A., D'Amato, A. W., Palik, B. J., Bradford, J. B., Fraver, S., Battaglia, M. A. & Asherin, L. A. (2017). Density-dependent vulnerability of forest ecosystems to drought. *Journal of Applied Ecology*, ed. by Bugmann, H.
- Boulay, É. (2015). *Ressources et industries forestières - portrait statistique*, p. 106.
- Buma, B. & Wessman, C. A. (2011). Disturbance interactions can impact resilience mechanisms of forests. *Ecosphere*, 2, 1–13.
- Canham, C. D., Thomas, R. Q. & Quinn, R. (2010). Frequency, not relative abundance, of temperate tree species varies along climate gradients in eastern North America. *Ecology*, 91, 3433–3440.
- Capstick, S., Whitmarsh, L., Poortinga, W., Pidgeon, N. & Upham, P. (2015). International trends in public perceptions of climate change over the past quarter century. *Wiley Interdisciplinary Reviews: Climate Change*, 6, 35–61.
- Cardinale, B. J., Duffy, J. E., Gonzalez, A., Hooper, D. U., Perrings, C., Venail, P., *et al.* (2012). Corrigendum: Biodiversity loss and its impact on humanity. *Nature*, 489, 326–326.
- Cazelles, K., Mouquet, N., Mouillot, D. & Gravel, D. (2016). On the integration of biotic interaction and environmental constraints at the biogeographical scale. *Ecography*, 39, 921–931.
- Chapin, F. S., Kofinas, G. P., Folke, C. & Chapin, M. C. (2009). *Principles of ecosystem stewardship: resilience-based natural resource management in a changing world*. Springer Science & Business Media.
- Chase, C. W., Kimsey, M. J., Shaw, T. M. & Coleman, M. D. (2016). The response of light, water, and nutrient availability to pre-commercial thinning in dry inland Douglas-fir forests. *Forest Ecology and Management*, 363, 98–109.
- Chen, I.-C., Hill, J. K., Ohlemüller, R., Roy, D. B. & Thomas, C. D. (2011). Rapid range shifts of species associated with high levels of climate warming. *Science*, 333, 1024–1026.
- Clark, J. S., Gelfand, A. E., Woodall, C. W. & Zhu, K. (2014). More than the sum of the parts: Forest Climate response from joint species distributions. *Ecological Applications*, 24, 990–999.
- Connell, J. H. (1978). Diversity in tropical rain forests and coral reefs. *Science*, 199, 1302–1310.
- Costanza, R., D'Arge, R., De Groot, R., Farber, S., Grasso, M., Hannon, B., *et al.* (1997). The value of the world's ecosystem services and natural capital. *nature*, 387, 253–260.
- Csergo, A. M., Salguero-Gómez, R., Broennimann, O., Coutts, S. R., Guisan, A., Angert, A. L., *et al.* (2017). Less favourable climates constrain demographic strategies in plants. *Ecology Letters*,
- Cubasch, U., Wuebbles, D., Chen, D., Facchini, M. C., Frame, D., Mahowald, N. & Winther, J. G. (2013). Introduction. In: *Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change* (eds. Stocker, T. F.; Qin, D.; Plattner, G. K.; Tignor, M.; Allen, S. K.; Boschung, J., *et al.*). Cambridge University Press. Cambridge, United Kingdom and New York, NY, USA. Chap. Introducti, pp. 119–158.
- Cumming, G. S. (2011). *Spatial resilience in social-ecological systems*. Springer Science & Business Media. London, pp. 1–254.
- Dennis, B. & Dennis, B. (2002). Allee effects in stochastic populations. *Oikos*, 96, 389–401.

- Dieleman, C. M., Branfireun, B. A., Mclaughlin, J. W. & Lindo, Z. (2015). Climate change drives a shift in peatland ecosystem plant community: Implications for ecosystem function and stability. *Global Change Biology*, 21, 388–395.
- Dunne, J. A., Williams, R. J. & Martinez, N. D. (2002). Network structure and biodiversity loss in food webs: robustness increase with connectance. *Ecology Letters*, 5, 558–567.
- Dupuis, S., Arseneault, D. & Sirois, L. (2011). Change from pre-settlement to present-day forest composition reconstructed from early land survey records in eastern Québec, Canada. *Journal of Vegetation Science*, 22, 564–575.
- Elder, B. D. & Miller, T. E. X. (2016). Quantifying demographic uncertainty: Bayesian methods for integral projection models. *Ecological Monographs*, 86, 125–144.
- Essl, F., Dullinger, S., Rabitsch, W., Hulme, P. E., Pyšek, P., Wilson, J. R. U. & Richardson, D. M. (2015). Delayed biodiversity change: No time to waste. *Trends in Ecology and Evolution*, 30, 375–378.
- Folke, C., Carpenter, S., Elmqvist, T., Gunderson, L., Holling, C. S. & Walker, B. (2002). Resilience and sustainable development: building adaptive capacity in a world of transformations. *AMBIO: A journal of the human environment*, 31, 437–440.
- Fuller, R. J. (2013). FORUM: Searching for biodiversity gains through woodfuel and forest management. *Journal of Applied Ecology*, 50. Ed. by McKenzie, A., 1295–1300.
- Garcia, L. C., Ribeiro, D. B., Oliveira Roque, F., Ochoa-Quintero, J. M. & Laurance, W. F. (2017). Brazil’s worst mining disaster: corporations must be compelled to pay the actual environmental costs. *Ecological applications*, 27, 5–9.
- Girardin, M. P., Bouriaud, O., Hogg, E. H., Kurz, W., Zimmermann, N. E., Metsaranta, J. M., *et al.* (2017). No growth stimulation of Canada’s boreal forest under half-century of combined warming and CO₂ fertilization. *Proceedings of the National Academy of Sciences*, 201610156.
- González-Varo, J. P., López-Bao, J. V. & Guitián, J. (2017). Seed dispersers help plants to escape global warming. *Oikos*, 1–7.
- Goring, S. J. & Williams, J. W. (2017). Effect of historical land-use and climate change on tree-climate relationships in the upper Midwestern United States. *Ecology Letters*, 20, 461–470.
- Gravel, D., Massol, F. & Leibold, M. A. (2016). Stability and complexity in model meta-ecosystems. *Nature Communications*, 7, 12457.
- Grime, J. P. (1973). Competitive exclusion in herbaceous vegetation. *Nature*, 242, 344–347.
- Grman, E., Lau, J. A., Schoolmaster, D. R. & Gross, K. L. (2010). Mechanisms contributing to stability in ecosystem function depend on the environmental context. *Ecology Letters*, 13, 1400–1410.
- Guisan, A. & Thuiller, W. (2005). Predicting species distribution: Offering more than simple habitat models. *Ecology Letters*, 8, 993–1009.
- Guisan, A., Tingley, R., Baumgartner, J. B., Naujokaitis-Lewis, I., Sutcliffe, P. R., Tulloch, A. I. T., *et al.* (2013). Predicting species distributions for conservation decisions. *Ecology Letters*, 16, 1424–1435.
- Hayes, J. P., Weikel, J. M. & Huso, M. M. P. (2003). Response of birds to thinning Young Douglas-Fir forests. *Ecological Applications*, 13, 1222–1232.

- Heffernan, J. B., Soranno, P. A., Angilletta, M. J., Buckley, L. B., Gruner, D. S., Keitt, T. H., *et al.* (2014). Macrosystems ecology: understanding ecological patterns and processes at continental scales. *Frontiers in Ecology and the Environment*, 12, 5–14.
- Hemrová, L., Bullock, J. M., Hooftman, D. A. P., White, S. M. & Münzbergová, Z. (2017). Drivers of plant species' potential to spread: the importance of demography versus seed dispersal. *Oikos*, 125, 336–342.
- Hodgson, D., McDonald, J. L. & Hosken, D. J. (2015). What do you mean, 'resilient'? *Trends in Ecology and Evolution*, 30, 503–506.
- Holling, C. S. (1973). Resilience and Stability of Ecological Systems. *Annual Review of Ecology and Systematics*, 4, 1–23.
- Holt, R. D. & Keitt, T. H. (2000). Alternative causes for range limits: a metapopulation perspective. *Ecology Letters*, 3, 41–47.
- Horn, H. S. (1975). Markovian Properties of Forest Succession. In: *The ecology and evolution of communities* (ed.). Harvard University Press, pp. 196–211.
- Howlett, M. & Rayner, J. (2001). The business and government nexus: principal elements and dynamics of the Canadian forest policy regime. *Canadian forest policy: Adapting to change*, 23–64.
- Hylander, K. & Ehrlén, J. (2013). The mechanisms causing extinction debts. *Trends in Ecology and Evolution*, 28, 341–346.
- Koshkina, V., Wang, Y., Gordon, A., Dorazio, R. M., White, M. & Stone, L. (2017). Integrated species distribution models: combining presence-background data and site-occupancy data with imperfect detection. *Methods in Ecology and Evolution*, 8, 420–430.
- Kuussaari, M., Bommarco, R., Heikkinen, R. K., Helm, A., Krauss, J., Lindborg, R., *et al.* (2009). Extinction debt: a challenge for biodiversity conservation. *Trends in Ecology and Evolution*, 24, 564–571.
- Lasch, P., Lindner, M., Erhard, M., Suckow, F. & Wenzel, a. (2002). Regional impact assessment on forest structure and functions under climate change—the Brandenburg case study. *Forest Ecology and Management*, 162, 73–86.
- Levins, R. (1968). Some Demographic and Genetic Consequences of Environmental Heterogeneity for Biological Control. *Bulletin of the Entomological Society of America*, 15, 237–240.
- Louthan, A. M., Doak, D. F. & Angert, A. L. (2015). Where and When do Species Interactions Set Range Limits? *Trends in Ecology and Evolution*, 30, 780–792.
- Macleán, I. M. D., Hopkins, J. J., Bennie, J., Lawson, C. R. & Wilson, R. J. (2015). Microclimates buffer the responses of plant communities to climate change. *Global Ecology and Biogeography*, 24, 1340–1350.
- McKenney, D. W., Hutchinson, M. F., Papadopol, P., Lawrence, K., Pedlar, J., Campbell, K., *et al.* (2011). Customized Spatial Climate Models for North America. *Bulletin of the American Meteorological Society*, 92, 1611–1622.
- Millar, C. I., Stephenson, N. L. & Stephens, S. L. (2007). Climate change and forest of the future: Managing in the face of uncertainty. *Ecological Applications*, 17, 2145–2151.
- Monleon, V. J. & Lintz, H. E. (2015). Evidence of tree species' range shifts in a complex landscape. *PLoS ONE*, 10, 1–17.

- Mora, C., Dousset, B., Caldwell, I. R., Powell, F. E., Geronimo, R. C., Bielecki, C., *et al.* (2017). Global risk of deadly heat. *Nature Climate Change*,
- Mori, A. S. (2016). Resilience in the Studies of Biodiversity-Ecosystem Functioning. *Trends in Ecology and Evolution*, 31, 87–89.
- Morin, X., Augspurger, C. & Chuine, I. (2007). Process-based modeling of species' distributions: what limits temperate tree species' range boundaries? *Ecology*, 88, 2280–2291.
- Nieminen, M., Singer, M. C., Fortelius, W., Schöps, K. & Hanski, I. (2001). Experimental Confirmation That Inbreeding Depression Increases Extinction Risk in Butterfly Populations. *The American Naturalist*, 157, 237–244.
- Nimmo, D. G., Mac Nally, R., Cunningham, S. C., Haslem, A. & Bennett, A. F. (2015). Vive la résistance: Reviving resistance for 21st century conservation. *Trends in Ecology and Evolution*, 30, 516–523.
- Olivar, J., Bogino, S., Rathgeber, C., Bonnesoeur, V. & Bravo, F. (2014). Thinning has a positive effect on growth dynamics and growth?climate relationships in Aleppo pine (*Pinus halepensis*) trees of different crown classes. *Annals of Forest Science*, 71, 395–404.
- Oliver, T. H., Heard, M. S., Isaac, N. J. B., Roy, D. B., Procter, D., Eigenbrod, F., *et al.* (2015). Biodiversity and Resilience of Ecosystem Functions. *Trends in ecology and evolution*, 30, 673–684.
- Peñuelas, J., Sardans, J., Estiarte, M., Ogaya, R., Carnicer, J., Coll, M., *et al.* (2013). Evidence of current impact of climate change on life: A walk from genes to the biosphere. *Global Change Biology*, 19, 2303–2338.
- Peterson, G., Allen, C. R. & Holling, C. S. (1998). Original Articles: Ecological Resilience, Biodiversity, and Scale. *Ecosystems*, 1, 6–18.
- Pfister, R. D. (1993). The need and potential for ecosystem management in forests of the inland west. In: *Defining sustainable forestry* (eds. Aplet, G. N.; Johnson, N.; Olson, J. T. & Sample, V. A.). Island Press, The Wilderness Society. Washington, DC. Chap. The need a, pp. 217–239.
- Phillips, J. D. (2011). Predicting modes of spatial change from state-and-transition models. *Ecological Modelling*, 222, 475–484.
- Pigot, A. L. & Tobias, J. A. (2013). Species interactions constrain geographic range expansion over evolutionary time. *Ecology Letters*, 16, 330–338.
- Pimm, S. L. (1984). The complexity and stability of ecosystems. *Nature*, 307, 321–326.
- Price, D. T., Alfaro, R. I., Brown, K. J., Flannigan, M. D., Fleming, R. A., Hogg, E. H., *et al.* (2013). Anticipating the consequences of climate change for Canada ' s boreal forest ecosystems. *Environmental Reviews*, 365, 322–365.
- Price, T. D., Qvarnstrom, A. & Irwin, D. E. (2003). The role of phenotypic plasticity in driving genetic evolution. *Proceedings of the Royal Society B: Biological Sciences*, 270, 1433–1440.
- Rytter, L. & Stener, L.-G. (2014). Growth and thinning effects during a rotation period of hybrid aspen in southern Sweden. *Scandinavian Journal of Forest Research*, 29, 747–756.
- Schindler, D. E. & Hilborn, R. (2015). Prediction, precaution, and policy under global change. *Science*, 347, 953–954.

- Schurr, F. M., Pagel, J., Cabral, J. S., Groeneveld, J., Bykova, O., O'Hara, R. B., *et al.* (2012). How to understand species' niches and range dynamics: A demographic research agenda for biogeography. *Journal of Biogeography*, 39, 2146–2162.
- Sittaro, F., Paquette, A., Messier, C. & Nock, C. A. (2017). Tree range expansion in eastern North America fails to keep pace with climate warming at northern range limits. *Global Change Biology*, 1–10.
- Sohn, J. A., Gebhardt, T., Ammer, C., Bauhus, J., H?berle, K.-H., Matyssek, R. & Grams, T. E. (2013). Mitigation of drought by thinning: Short-term and long-term effects on growth and physiological performance of Norway spruce (*Picea abies*). *Forest Ecology and Management*, 308, 188–197.
- Stein, A., Gerstner, K. & Kreft, H. (2014). Environmental heterogeneity as a universal driver of species richness across taxa, biomes and spatial scales. *Ecology Letters*, 17, 866–880.
- Sullivan, P. F., Ellison, S. B. Z., McNown, R. W., Brownlee, A. H. & Sveinbjörnsson, B. (2015). Evidence of soil nutrient availability as the proximate constraint on growth of treeline trees in northwest Alaska. *Ecology*, 96, 716–727.
- Talluto, M. V., Boulangeat, I., Ameztegui, A., Aubin, I., Berteaux, D., Butler, A., *et al.* (2016). Cross-scale integration of knowledge for predicting species ranges: a metamodeling framework. *Global Ecology and Biogeography*, 25, 238–249.
- Talluto, M. V., Boulangeat, I., Vissault, S., Thuiller, W. & Gravel, D. (2017). Extinction debt and colonization credit delay range shifts of eastern North American trees. *Nature Ecology & Evolution*, 1, 0182.
- Tavecchia, G., Tenan, S., Pradel, R., Igual, J. M., Genovart, M. & Oro, D. (2016). Climate-driven vital rates do not always mean climate-driven population. *Global Change Biology*, 22, 3960–3966.
- Thomas, C. D., Franco, A. M. A. & Hill, J. K. (2006). Range retractions and extinction in the face of climate warming. *Trends in Ecology and Evolution*, 21, 415–416.
- Treyger, A. L. & Nowak, C. A. (2011). Changes in tree sapling composition within powerline corridors appear to be consistent with climatic changes in New York State. *Global Change Biology*, 17, 3439–3452.
- Upreti, Y., Asselin, H. & Bergeron, Y. (2013). Cultural importance of white pine (*Pinus strobus* L.) to the Kitcisakik Algonquin community of western Quebec, Canada. *Canadian Journal of Forest Research*, 43, 544–551.
- Van der Putten, W. H., Macel, M. & Visser, M. E. (2010). 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, 2025–2034.
- Wanner, H., Beer, J., Bütikofer, J., Crowley, T. J., Cubasch, U., Flückiger, J., *et al.* (2008). Mid-to Late Holocene climate change: an overview. *Quaternary Science Reviews*, 27, 1791–1828.
- Webster, M. S., Colton, M. A., Darling, E. S., Armstrong, J., Pinsky, M. L., Knowlton, N. & Schindler, D. E. (2017). Who Should Pick the Winners of Climate Change? *Trends in Ecology and Evolution*, 32, 167–173.

- Winfree, R. & Kremen, C. (2009). Are ecosystem services stabilized by differences among species? A test using crop pollination. *Proceedings of the Royal Society B: Biological Sciences*, 276, 229–237.
- Wisz, M. S., Pottier, J., Kissling, W. D., Pellissier, L., Lenoir, J., Damgaard, C. F., *et al.* (2013). The role of biotic interactions in shaping distributions and realised assemblages of species: Implications for species distribution modelling. *Biological Reviews*, 88, 15–30.