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Regeneration of spruce - fir - beech mixed forests under climate and ungulate pressure

Mithila Unkule

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THÈSE

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préparée au sein du **Laboratoire INRAE - LESSEM Laboratoire
EcoSystèmes et Sociétés En Montagne**
dans l'**École Doctorale Chimie et Sciences du Vivant**

Régénération des forêts mixtes épicéa - sapin - hêtre sous la pression du climat et des ongulés

Regeneration of spruce - fir - beech mixed forests under climate and ungulate pressure

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“Those who contemplate the beauty of the earth find reserves of strength that will endure as long as life lasts. There is something infinitely healing in the repeated refrains of nature—the assurance that dawn comes after night, and spring after winter.”

— **Rachel Carson, catalyst for the modern environmental movement and author of *Silent Spring***

*I dedicate this thesis to my mother,
who has been my rock in life;
and to all the other women out there,
who's courage and struggle we stand upon..*

—

Thank you.

Baba, I hope you are smiling down at me..

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Abstract

Global environmental changes are affecting tree population demography with potentially significant impacts on forest biodiversity and wood industry. Forest regeneration processes include seed production and dispersal, seedling establishment, growth and survival of saplings till they reach adulthood, at which point, they become part of the adult tree stand. Changes in regeneration dynamics, thus, directly affect forest composition and structure and can jeopardize the sustainability of forest management. This is especially the case in mountain forests where environmental gradients are strong and where forests are often uneven-aged, i.e. combining trees of all ages in a single stand. Regeneration processes are difficult to monitor at large spatial or temporal scales. There is also often, absence of large scale historical datasets that can help recognize patterns of regeneration processes in different environmental conditions. In this thesis, I quantified the effects of different biotic and abiotic factors on regeneration dynamics of Norway spruce (*Picea abies*), silver fir (*Abies alba*) and European beech (*Fagus sylvatica*) in the French Alps and Jura mountains. I also predicted changes in tree recruitment fluxes in these forests for different climate change situations projected by the IPCC, and different ungulate browsing pressures.

I carried out field sampling in which I recorded sapling densities and height increments of spruce, fir and beech, along with potential environmental drivers of regeneration, such as altitude, slope, aspect, light availability, soil characteristics, ungulate browsing pressure, temperature, precipitation evapotranspiration and many more climatic variables, in 152 plots across the French Alps and Jura mountains. I then established patterns of the effects of these biotic and abiotic factors on sapling density and growth using non-linear mixed models. I showed that temperature and water demand, in the form of potential evapotranspiration has a negative effect on sapling density and height increments, and height increments are also affected positively by canopy openness, in addition to climate variables. Browsing of the terminal shoot by ungulates, which prevents sapling height growth and reduces survival, is especially frequently observed on fir.

Using these established patterns, I calibrated a more comprehensive model of regeneration dynamics, representing the processes of new seedling production, sapling growth, browsing and survival of saplings, and finally their recruitment into adult trees.

I estimated parameters for these processes in combination, using Approximate Bayesian Computation (ABC), based on the field data collected earlier. The results imply that with frequent and intense heat and drought events, by the year 2100, sapling growth and survival of the three species will be highly impaired, with a substantial reduction of forest renewal fluxes, with species specific differences. An increase of ungulate populations leading to increased browsing could be especially damaging for fir saplings, and beech saplings to a lesser extent. Within the range of climate sampled by me, the cumulative effect of rising temperatures and browsing intensities is most detrimental for fir, followed by spruce, whereas beech fares comparatively better in future climate conditions, indicating the possibility of a shift in forest species compositions in these stands in the absence of forest management strategies adapted to mitigate the effects of these disturbances.

In addition to establishing the susceptibility of regeneration to climate and browsing pressure, this study confirms the potential of Approximate Bayesian Computation (ABC) to estimate dynamic regeneration and tree recruitment processes based on a screenshot of field conditions. It also highlights the importance of regeneration processes in determining forest dynamics and tree species compositions. I conclude that future forest regeneration is vulnerable to temperature, water demand and ungulate presence, urging researchers and forest managers alike to take management measures that align with anticipated future conditions in the mountain forests.

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CHAPTER 1

Introduction

Anthropogenic activities in the past couple of centuries have been recognized as the main cause of major environmental changes (Lewis and Maslin (2015)). Climate change (Parmesan and Yohe (2003)), along with increasing disturbances (storms, fires) (Seidl et al. (2017)), global land use changes (deforestation, fragmentation) (Song et al. (2018)) contribute to current threats to many ecological systems around the world. Extreme climatic events lead to unfavorable conditions for plants and animals to thrive, by reducing productivity in current species niches, along with slow but steady species range shifts towards more favorable climates (Wason and Dovciak (2017); Renwick and Rocca (2015); Sekercioglu et al. (2008)) and species interactions. For example, consistent changes induced by human footprint impact animal movements, their expansion and food webs globally (Tucker et al. (2018)). However, more locally, an absence of a significant number of natural predators has resulted in a continuously increasing wild ungulate population in many European forests (Valente et al. (2020)), as well as in North America (Clark et al. (2021)), New Zealand (Caughley (1970)), Zimbabwe (Valeix et al. (2007)). This has led to disproportionate browsing of the vegetation among which tree saplings are often most highly favored (Valente et al. (2020)). The objective of this thesis is to understand the role of climate change and wild ungulate browsing in forest renewal, in mixed and uneven aged stands of Norway spruce (*Picea abies* H.), Silver fir (*Abies alba* Mill. L) and European beech (*Fagus sylvatica*) in the French Alps and Jura mountains, and to estimate present and future tree recruitment rates using a regeneration dynamics model.

1.1 Spruce-fir-beech forests and their management

Spruce, fir and beech mixed forests make up an important ecosystem in the European mountains, and are of considerable ecological and commercial importance (Orman et al. (2021); Vencurik et al. (2020); Vitasse et al. (2019); Hasenauer and Kindermann (2002)). They occupy a large area in mountain forests in France, as represented in 1.1 (Toïgo et al. (2015)). Spruce and fir are of high economic importance and commonly used as a source of wood for construction (e.g. carpentry, boats), as well as for firewood and pulp wood (Caudullo et al. (2016); Tinner et al. (2013)). Beech growing in mountainous regions, however, is not as popular as the prior two, due to its lower wood quality, mainly used as firewood and pulp (Brunet et al. (2010)). They are present between altitudes of 400 to 2000 m, depending on latitudes, with beech being more prevalent in lower altitudes and spruce in higher altitudes. Spruce goes higher than fir and is the major species at the sub-alpine level in the Alps, usually in almost pure stands (Vallet and Pérot (2011)). Recent studies have shown that forests globally are under threat from global changes such as

changes in land use (Pettersson et al. (2019)), climate (Canham and Murphy (2016)), herbivory (Nagel et al. (2014)) and other disturbances such as storms (Csilléry et al. (2017)), fires (Boucher et al. (2020)), droughts (Martínez-Vilalta and Lloret (2016)), frost and insect parasitism (Vitasse et al. (2019)). Most of the spruce-fir-beech forests in Europe are under active management regimes of different intensities (Hilmers et al. (2020); Klopčič et al. (2017)). These management interventions are focused on maintaining productivity of the stand by preserving its biodiversity (Heller and Zavaleta (2009); Mielikäinen and Hynynen (2003)), at the same time also trying to meet the economic demands (Sousa-Silva et al. (2018)). The concept of "continuous cover forestry" (Ficko et al. (2016)) management practices and programs have grown popular in the last few decades in order to practice sustainable management (O'Hara (2016); Brang et al. (2014)). These include silvicultural practices such as uneven-aged silviculture (O'Hara and Gersonde (2004)) and natural disturbance based management (Kuuluvainen et al. (2021)). Numerous studies have also shown the importance of maintaining mixtures of spruce-fir and beech rather than monocultures, as mixtures are more productive and stable (Pretzsch et al. (2021)), and more resistant to pests, pathogens, and other disturbances (Jactel et al. (2017); Pretzsch et al. (2017)).

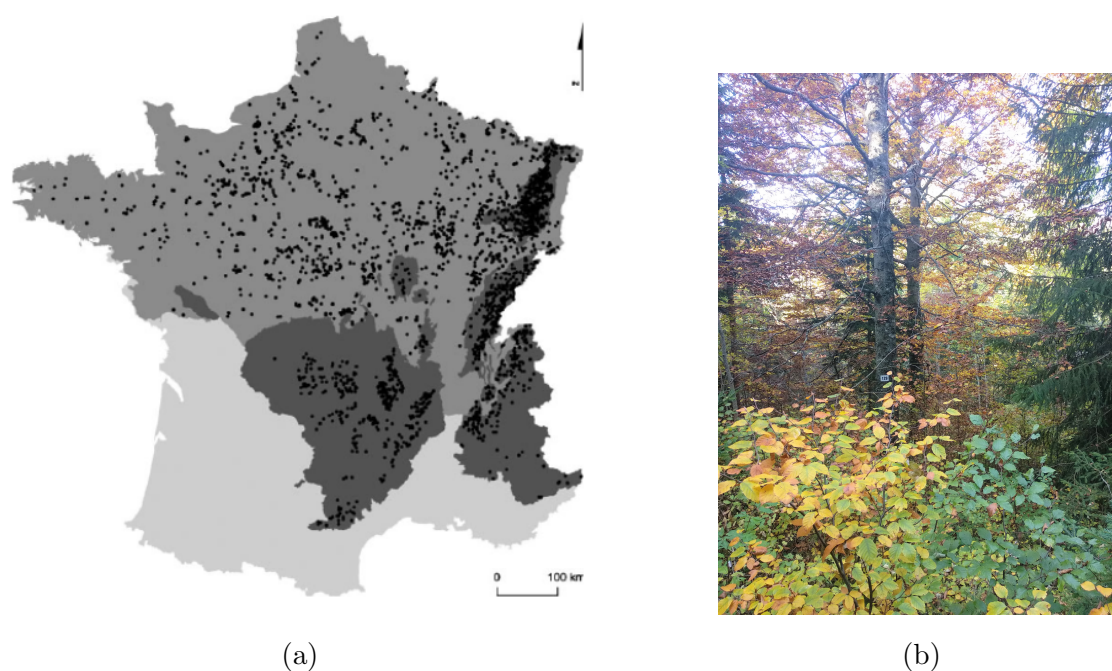


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1.2 Drivers of regeneration dynamics and tree recruitment

Global changes have led to difficulties in regeneration and renewal of forests around the world ([Tucker et al. \(2018\)](#)). In this thesis, the focus will be on understanding regeneration of spruce, fir and beech and recognize where they differ in their vulnerability. For example, fir is known to be most susceptible to browsing by ungulates, and in regions with high ungulate populations, spruce and beech are at an advantage ([Bernard et al. \(2017\)](#)). Reduced regeneration, and as a result, reduced tree recruitment in forests has led to not only ecological, but also economic difficulties ([Wagner et al. \(2010\)](#)). This makes it even more important to ensure a flux of newly recruited trees in the forests. There are many studies trying to understand the different environmental drivers and limiters of regeneration processes. However, the results are likely to be specific to the

field site, conditions, species composition, and other environmental factors and may be difficult to generalize. Additionally, studying the dynamic process from regeneration to tree recruitment is a difficult task, and most of the studies are focused on either regeneration, or adult trees, but not the transition between the two. For instance, [Käber et al. \(2021\)](#) explored the relation between tree recruitment rates and environmental factors surrounding it, but it is difficult to estimate the number of tree recruits without any information on regenerated sapling numbers, as shown by [Lines et al. \(2020\)](#).

Regeneration dynamics consists of many processes. Each process in the forest succession cycle plays a role in determining the future forest structures, and it is crucial to understand the factors driving each process ([Clark et al. \(1999\)](#)). The processes include: 1. Seed formation, viability and dispersal, 2. seed germination and establishment of seedling, 3. growth of sapling, 4. Survival/mortality of sapling, 5. tree recruitment and maturity (figure 1.3). Each process depends on one or more biotic or abiotic factors in the surrounding environment, as described in figure 1.3, and this effect is often dependent on the species and age class of the sapling. The most popular known drivers of forest regeneration are light ([Helluy et al. \(2021\)](#)), temperature ([Tingstad et al. \(2015\)](#)), precipitation ([Gwitira et al. \(2014\)](#)), soil conditions and water availability ([Moser et al. \(2017\)](#); [Piedallu and claude Gégout \(2008\)](#)), inter and intra-specific competition ([Pretzsch \(2013\)](#)), disturbances such as fires ([Sáenz-Ceja and Pérez-Salicrup \(2019\)](#)), droughts ([Vitasse et al. \(2019\)](#)), storms ([Csilléry et al. \(2017\)](#)) or frost, or damage due to biotic interactions such as herbivores, insect infestations, fungi or other diseases, etc. Recent studies have attempted to understand the role of these different factors in determining tree regeneration dynamics ([Axer et al. \(2021\)](#); [Kremer and Bauhus \(2020\)](#); [Tinya et al. \(2019\)](#); [Vacek et al. \(2019a\)](#)). However, in order to better quantify specific mechanisms through which variables affect each other, it is more practical to study only the effects of few variables at a time. For instance, ([Lombaerde et al. \(2020\)](#)) described the effects of light and climate on tree seedlings, whereas ([Barrere et al. \(2021\)](#)) documented the combined effect of canopy openness and ungulate browsing on oak regeneration.

This thesis identified different environmental drivers of different demographic processes of spruce, fir and beech, before understanding the regeneration dynamics and suggesting management measures in these forests.

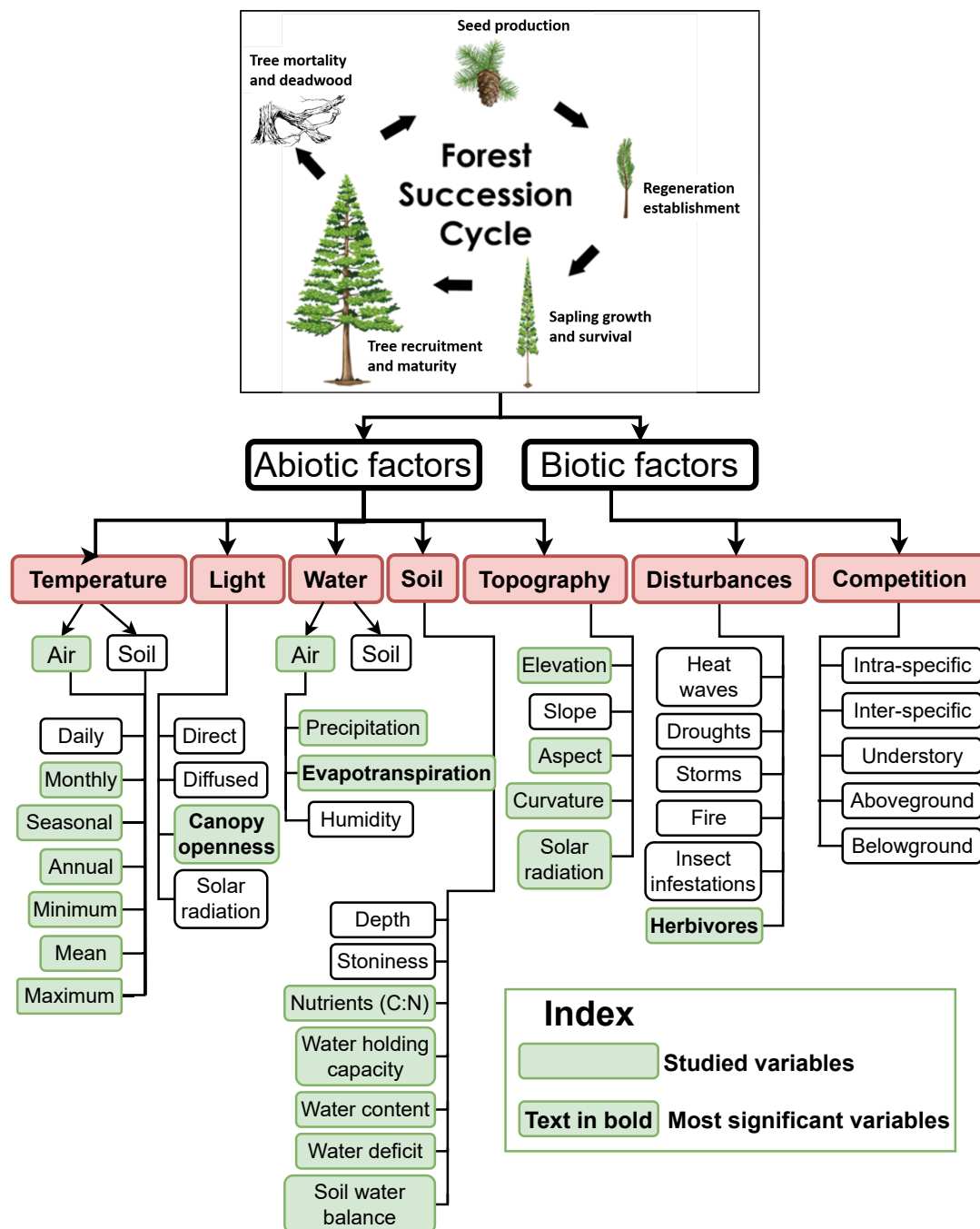


Figure 1.3: Schematic representing the main processes of the forest succession cycle, followed by the different biotic and abiotic environmental factors known to be responsible for driving regeneration dynamics. The variables tested in models during the thesis are labelled in green boxes, and the ones that had the most significant effect on spruce, fir and beech are marked in bold lettering.

1.3 Global changes disrupt ecosystem dynamics

Climate is getting warmer with more frequent extreme events, which increase in their intensity and frequency, for example, with drought events, forest fires, storms, late frost etc. By the year 2100, average earth temperatures are expected to rise anywhere between 1 to 4 °C, as illustrated in figure 1.4 (IPCC (2014)). Natural ecosystems are under great threat with this increasing temperature, as growth and survival of organism is highly compromised in sub-optimal environmental conditions. Due to global warming, there could be an expected extinction of 27-63 % of the current species diversity (in different climate scenarios, averaged over Europe) (Thuiller et al. (2005)). In Europe, drought is a major cause of tree mortality at the continental scale, impacting almost 500,000 hectares of forests (Senf et al. (2020)). Tree species in mountain ranges of the Alps and Carpathians are already shifting towards higher altitudes and latitudes in search of more optimal climate, and this rate is higher for lower altitude forests (Aitken et al. (2008)). This would mean a significant loss of species, and changes in forest structures, affecting the biodiversity, as well as ecosystem functioning and productivity. In warm and dry climates, there is also an increase in biotic disturbances such as spread of invasive species, pathogens and insect infestations (McDowell et al. (2020)). Invasive species often outgrow native species, change the soil composition and nutrient cycling, reducing ecosystems to single species dominated ecosystems (Crespo et al. (2018); Ramaswami and Sukumar (2013)). In addition to mass mortality of all vulnerable tree species, infestations of insects such as bark beetles also alter soil sequestration properties and change stand compositions and complexity (Fernandez-Carrillo et al. (2020); Orman and Dobrowolska (2017)). In addition to disturbances, changing land use patterns due to increasing human activities has also proved to detrimental to forests and other ecosystems alike. Activities such as deforestation, habitat fragmentation, conversion of natural ecosystems to fields for agriculture or as pastures, are grounds for habitat reduction (Thomas et al. (2004)), local species extinctions (Ruosch et al. (2016)), species range shifts (Pettersson et al. (2019)), changes in soil properties (Baeten et al. (2010)).

Another increasing disturbance, which is the result of many accumulating global changes, is the increase in ungulate browsing pressure in different forests in Europe and North America (Côté et al. (2004); Gill et al. (1992)). Ungulates such as roe deer, red deer, chamois rely on tree species (eg. fir, oak, maple) for their dietary requirements, and are known to disrupt growth patterns of saplings and damage barks of trees (Vacek et al. (2017); Heuze et al. (2005); Jorritsma et al. (1999); Amrner (1996)).

Thus, we can confirm with conviction that the occurrence of multiple global changes and disturbances simultaneously, or through interactions, are making natural ecosystems, and especially forests, even more vulnerable to these changes.

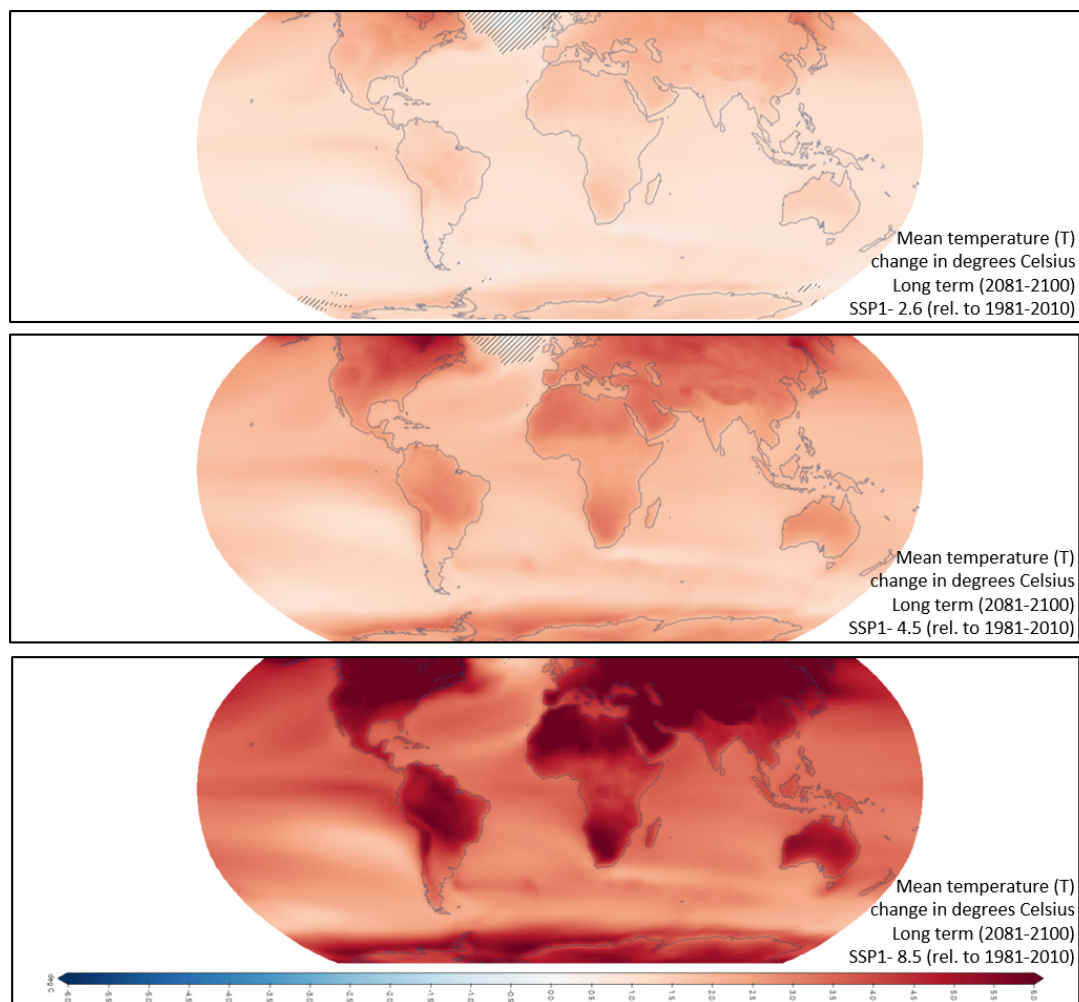


Figure 1.4: IPCC projections for mean annual temperatures around the globe for the year 2100, in three distinct climate change scenarios (optimistic (SSP2.6), intermediate (SSP4.5), pessimistic (SSP8.5))

1.4 Potential for adapting forest management strategies to changing environmental conditions

There are currently different types of forest management strategies adopted by foresters in France. Depending on the strategies used, and the conditions of the forest, the motives of these practices vary, from maintaining biodiversity and specific forest cover (Santopuoli et al. (2021); Brunet et al. (2010)), to harvesting a target amount of wood for economic gains (Pretzsch et al. (2021); Li and Lo (2014)), with varying focus on different intentions (Lafond et al. (2015)). In the Alps, some forests are also managed for purposes other than wood production, such as protection against rocks and avalanches, landscape, recreation, and maintaining biodiversity (Hilmers et al. (2020); Leuschner and Ellenberg (2017); Boncina (2011)). In these situations, managers could accept lower wood productivity if the other functions are secured. This can also be termed as "sustainable silviculture" (Santopuoli et al. (2021)).

Maintaining forests sustainably is one of the main goals of continuous cover forestry (Tudoran et al. (2021)). This type of silviculture is also motivated by "natural consideration", miming in a sense the natural dynamic of forest stands as periodically affected by disturbances and tree mortality creating some small gaps in the forest cover. Continuous cover requires uneven-aged stands (young trees ready to replace harvested trees), and maintaining a balanced uneven-aged stand requires that the production between two harvest is equal to the harvested volume, and the recruitment of new trees between two harvests is the sum of the number of harvested trees and unharvested tree mortality. Production of more forest cover, i.e. recruitment of trees depends in turn on the regeneration flux. Hence, decent management practices carried out to ensure enough renewal at the regeneration stage are essential to guarantee a continuous cover forest. This involves strategies such as maintaining a threshold of adult tree cover in a stand to ensure enough seed production, harvesting only after maintaining a particular number of individuals of each species, creating gaps by way of cluster thinning to ensure light availability to growing saplings. However, many new questions are arising with increasing amount of changes and disturbances in these forests. What are the predicted future species compositions in forests? If economically important species are not able to persist, should they be replaced with species more adapted to various global changes? How will plasticity and genetic adaptation of species work in warming scenarios? How can management practices adapt to future climate conditions? Can we predict future regeneration of forests? Can

forests renew naturally if harvesting continues at current rates? Foresters and researchers alike are asking such questions more often.

1.5 Methodological difficulties of studying regeneration dynamics

Classical forest dynamics studies usually depend on large historical datasets to establish temporal patterns between different demographic processes, and use them to predict future dynamics. For example, [Borderieux et al. \(2021\)](#) used the French National Forest Inventory (NFI) dataset to understand drivers of *Quercus Petrea* regeneration. However, there is often a lack of large historical data to implement into various methods, which rely on small specific areas, or limited number of years, or they address a specific process in the regeneration dynamics. To quote the above example again, [Borderieux et al. \(2021\)](#) could not study all regeneration processes, but only the factors driving oak cover. Sometimes, smaller datasets are combined together to form a larger one. But there is often absence of homogeneity, as different datasets have different protocols of data collection, different variables measured, making it difficult to build a good dataset ([Sirén et al. \(2018\)](#)). Additionally, it is practically very difficult to monitor and observe the evolution of individual saplings over time, especially in field conditions. Small, recently established seedlings are very sensitive to any disturbance and many of them disappear without any visible remaining, or even if present, are difficult to find in places with thick litter ([Collet and Le Moguedec \(2007\)](#)).

Alternatively, it is possible to study these processes using experimental approaches in controlled setups ([Chang-Yang et al. \(2021\)](#); [Zang et al. \(2021\)](#); [Lombaerde et al. \(2020\)](#); [Lendzion and Leuschner \(2008\)](#)). [Zang et al. \(2021\)](#) created a soil drought gradient in an experimental setup to test the responses of European beech (*Fagus sylvatica L.*) saplings. [Lombaerde et al. \(2020\)](#) planted saplings of different species in different forest conditions in order to study their growth. However, it is time consuming to setup and monitor experimental plots at large scales. They often cannot replicate field conditions, as at least some variables are fixed. They cannot be carried out over large gradients of environmental conditions. Moreover, it is not practical to follow the life cycle of saplings as they grow into adults. The strongest difficulty is to estimate each process composing the whole regeneration cycle, so generally you only have a truncated view of one or few of the processes.

In the context of these difficulties, using computational methods to build a model mimicking these processes of interest, and testing the influence of different environmental factors on demographic processes is a more robust methodology. However, it can also come with its limitations as discussed in section 1.6.

1.6 Regeneration dynamics modelling

The last few decades have seen a massive increase in computational capacities and power, and well as development of many new computational methodologies in almost every field of research, from drug discovery (Leelananda and Lindert (2016)) to cognition (Xirogiannis et al. (2010)) and material sciences (Kshirsagar et al. (2021)). It is especially valuable when research questions are too complex to address experimentally, or the data is too noisy, or worse, inaccessible, which is often the case in ecology (Green et al. (2005)). It is also becoming an increasingly popular and emerging tool in the field of ecology, and is known as "computational ecology" (Petrovskii and Petrovskaya (2012)).

In forest ecology, tree species regeneration, and the transition from seed germination to an adult is a complex process, involving many sub-processes and environmental variables, and is often overlooked in forest dynamics research (Larson and Funk (2016)). In section 1.5, I described the methodological challenges involved in studying these processes in the field. The most promising alternative to this approach, which is also practically feasible, is to build and use computational models to understand the different processes and also make predictions into the future (Petrovskii and Petrovskaya (2012)).

Modelling forest tree dynamics is a fast emerging approach, with a large number of studies investigating different aspects of tree growth, mortality, stand structures (Ligot et al. (2020a); Manso et al. (2020); Gratzer and Waagepetersen (2018); Lagarrigues et al. (2015); Parveaud et al. (2008); Wallentin et al. (2008); Seagle and Liang (2001)). Modelling forest regeneration, however, is not as common, possibly due to difficulties mentioned in section 1.5 (Eerikäinen et al. (2007); Zumrawi et al. (2005)), with not many models studying the transition from saplings to recruited trees (Hackett-Pain and Bogdziewicz (2021); Lines et al. (2020); Klopčič et al. (2012b)). There are only very few studies trying to simultaneously model the effects of changing climate and increasing ungulate browsing, both important threats to regeneration (Cailleret et al. (2014)). In this thesis, I attempt to build a model that can integrate the impacts of these two threats on regeneration, and

quantify their effects on tree recruitment rates in the present and future.

1.7 Objectives of the thesis

This introductory chapter highlighted some knowledge gaps in the estimation of regeneration dynamics and future forest compositions of mixed uneven-aged forests of Norway Spruce (*Picea abies* L.), Silver fir (*Abies alba* Mill.) and European beech (*Fagus sylvatica*) in the French Alps and Jura mountains, in the context of changing climate and increasing ungulate herbivory. Based on these gaps, I attempt to answer the following questions in the thesis:

- What are the magnitudes of sapling growths and densities of spruce, fir, and beech in the French Alps and Jura mountains?
- What are the key environmental factors affecting regeneration?
- In the absence of any temporal data, or data on regeneration survival, can we predict tree recruitment rates?
- What will be the fate of tree recruitment rates in different projected climate and browsing conditions?

To that end, I conducted two main studies: one empirical study in which I gathered information about regeneration and related environmental factors and identified its key drivers, and the other one is a predictive model that estimated different demographic processes involved in regeneration dynamics, leading to tree recruitment predictions in the future. These studies are divided into 2 articles, that are included as chapter 3 and 4 of the thesis:

Chapter 3: Climate and ungulate browsing impair regeneration dynamics in spruce-fir-beech forests in the French Alps

Chapter 4: Spruce and fir tree recruitment at risk: estimating regeneration processes under climate change and ungulate browsing in forests of the Alps

The methods used for each study, and the justification of their use are presented in the dedicated chapters, there is thus no need to repeat these elements in the present chapter. They are preceded by an analysis of the literature leading to the main hypothesis of the thesis (chapter 2). In this chapter, I summarize the different vegetation dynamics and community assembly theories that help in understanding mechanisms behind progression

of regeneration in stands, both spatially and temporally. I also describe how species and individuals interact with each other, and which theories could govern their establishment and evolution. I try to put this in the context of global changes, especially climate and ungulate browsing, which are the focus topics of this thesis. Global warming may play a big role in modifying these interactions and changing the course of advancement of forests, and having a fundamental knowledge of these theories aides the understanding of adaptations of forests to such novel situations. As climate change mitigation of forests involves human interventions in the form of forest management, I also touch upon the various forms of forest management practices and emphasize the use of sustainable management strategies. After a description of the study species and field sites, I move on to a short description of the computational methods that I used during the thesis. I end chapter 2 with the hypotheses of my thesis and explain the scientific approach used in the thesis.

In chapter 5, I summarize results of both my studies and discuss perspectives, including knowledge gaps, scientific challenges and forest management implications, opened up by this study.

Lastly, I end with chapter 6, in which I state the general conclusions of my thesis.

CHAPTER 2

Theoretical framework

2.1 Regeneration processes and vegetation dynamics theories

2.1.1 Vegetation dynamics

Vegetation dynamics, as a concept, is based on the fundamental idea that different capacities of plants to match the existing environment, determine the nature of plant assemblage that will exist in the place. The environment includes both biotic and abiotic factors (Clark and McLachlan (2003)). Thus, vegetation in a site may not remain constant unless the species, site conditions, and/or the biotic and abiotic environments remain constant. The law of vegetation dynamics, coined by Pickett and McDonnell (1989), states that if 1. A site becomes available, 2. Species are differentially available on the site, or 3. Species perform differentially at that site; then the composition and/or structure of vegetation will change through time. The reasons behind these changes could include disturbances on a site, higher or lower mortality of particular species due to unfavorable conditions, competitive or facilitative interactions etc. The different possible causes are stated in figure 2.1, a figure by van der Maarel and Franklin (2005).

Apart from an effect of the external environmental factors, availability of species can result from inter or intra-specific interactions of three different net effects - facilitation, tolerance, and competition. The following paragraphs give an overview of these interactions, and their mechanisms of action, which is also described in figure 2.2:

Facilitation

Facilitation includes positive interactions between two individuals that increases fitness, growth or reproduction of one or both individuals (Brooker et al. (2008)). This can happen through either micro-environmental changes such as access to or protection from radiation, protection from pests, or through introduction of beneficial organisms such as mycorrhizae, microfauna, or dispersal agents. Alternatively, it can simply occur because of the elimination of other competitors (see figure 2.2) (Choler et al. (2001); Holmgren et al. (1997)). A common example of facilitation is the occurrence of "nursery plants", which are individuals or species, that in certain stages of their life, provide resources or protection needed by the other plant or species (Liu et al. (2020)). This is often important in early life stages of seedlings as there is a high mortality rate observed in the regeneration process, and may also play a role in driving community dynamics (Padilla and Pugnaire (2006)). There are many examples of such occurrences observed in natural environments. (Kunstler et al. (2006)) exhibited the establishment of *Fagus sylvatica*

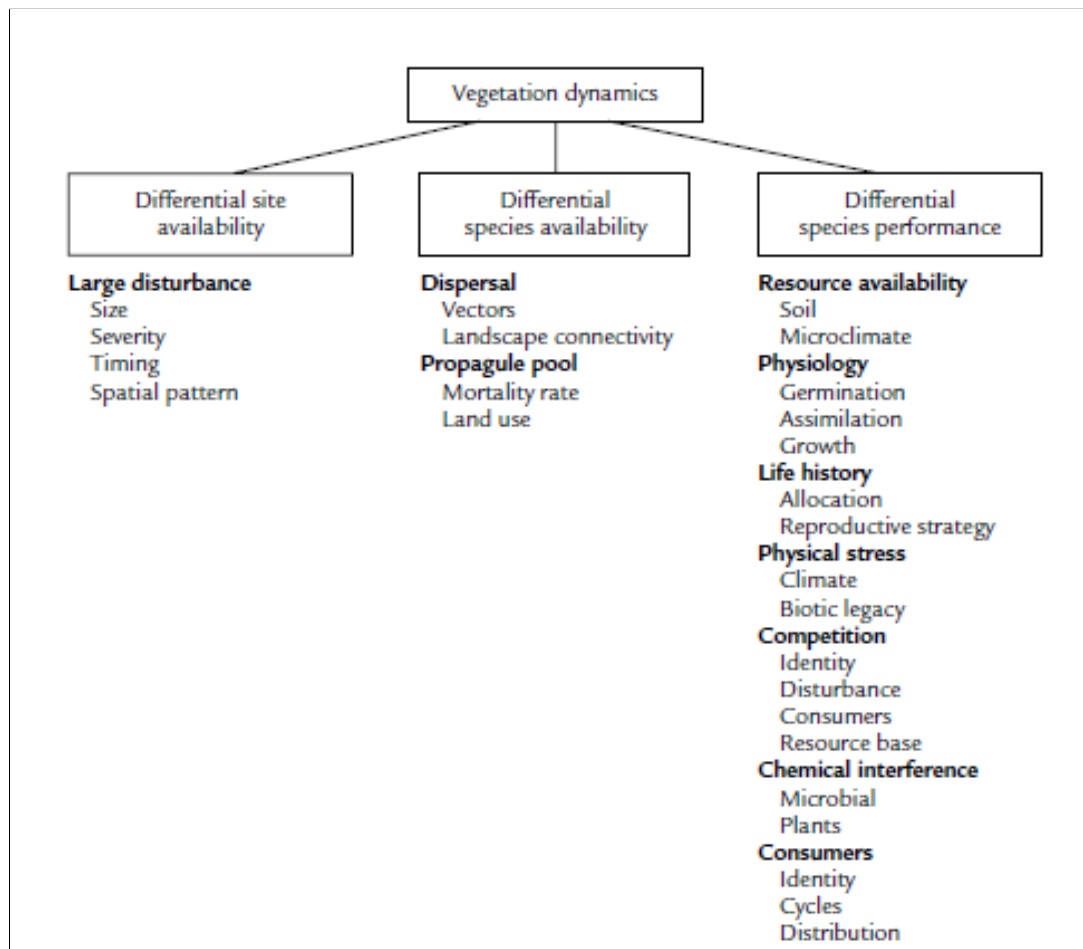


Figure 2.1: Detailed nested hierarchy of successional causes, ranging from the most general phenomenon of community change, through the aggregated processes of site availability, and differentials in species availability and performance, to the detailed interactions, constraints, and resource conditions that govern the outcome of interactions at particular sites. Based on [Pickett and McDonnell \(1989\)](#) and modified by [van der Maarel and Franklin \(2005\)](#).

and *Quercus pubescens* saplings by *Buxus sempervirens* shrubs, through two different mechanisms (shade provision and protection from browsing) in sub-Mediterranean grasslands in France. The last few decades have witnessed a rise in the number of studies carried out to understand the process of facilitation ([Liu et al. \(2020\)](#); [Pretzsch \(2013\)](#); [Jensen et al. \(2012\)](#); [Gómez et al. \(2004\)](#)).

Competition

Competition between individuals or species is a widely studied phenomenon, and contributes greatly to plant community structures, coupled with other environmental factors and interactions. Two very different definitions of competitiveness have been

debated in the literature on plant competition (Grace et al. (2002)). Tilman et al. (1982) proposed a resource-based theory of competition that assigns high competitiveness to individuals or species based on their ability to tolerate low levels of a limiting resource. Grime (1973), on the other hand, had another view based on species ecology, stating that species with greater ability to sequester resources won in competition, as in doing so, they suppress the growth or survival of other individuals or species. There have been attempts to reconcile the two theories, concluding that the two theories can be held complementary, persisting under different resource conditions, with light and nutrient availability determining which theory applies to the situation (Craine (2005); Goldberg and Novoplansky (1997)). Among the forest understory, there is often inter or intra-specific competition for light availability under the overstory cover (Vencurik et al. (2020); Bourdier et al. (2016); Craine and Dybzinski (2013); Ligot et al. (2013); Gaudio et al. (2011b); Balandier et al. (2006a); ?), soil nutrients (?Coll et al. (2004); Daehler (2003)), or water availability and demand (Begović et al. (2020); Simon et al. (2019a); Cavin et al. (2013)). These competitive interactions determine stronger individuals and species that will grow and survive (Grossiord et al. (2014)), and can influence future species compositions (Joy (1992)), or the direction of succession (Thrippleton et al. (2018)).

Tolerance

An individual "tolerates" another individual, when there is no competitive or facilitative interaction between the two individuals.

These concepts can be integrated and generalized as "interactions", and can be direct or indirect, and at different trophic levels (Connell and Slatyer (1977))(figure 2.2). The nature and intensity of these plant-plant interactions is determined by many different biotic and abiotic factors (Jensen (2011)). They can be dependent on resource availability, presence of herbivores (Amrner (1996)), life stage and species identity of both plants (Kunstler et al. (2006)), the life trait that could be potentially affected (De Bello et al. (2012)), or simply the density of other plants surrounding them (Vernay et al. (2018)). These interactions play a huge role in regeneration dynamics, by influencing the growth and survival of plants directly or indirectly (Gratzer and Waagepetersen (2018); Ligot et al. (2013)), and may also prompt changes in forest management strategies in the future (Balandier et al. (2006a)). Pioneered by Callaway and Walker (1997), many studies dealing with facilitation such as Pretzsch (2013); Kunstler et al. (2006); Choler et al. (2001); Holmgren et al. (1997) have emphasized the importance of studying facilitation and competition in synthesis. Competition and facilitation often can go hand in hand depending

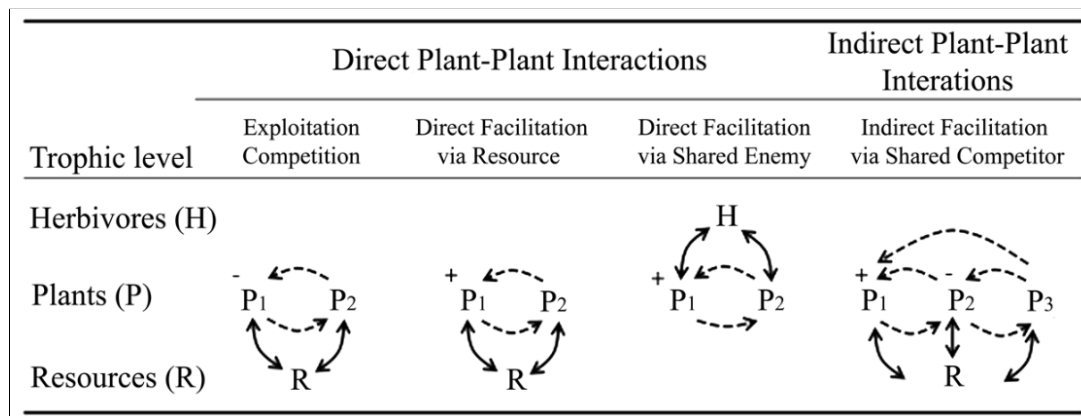


Figure 2.2: Conceptual model for direct and indirect plant-plant interactions across three trophic levels: Herbivores (H), plants (P) and resources (R). Arrows indicate direct interactions (solid lines) and indirect interactions (dashed lines). Negative or positive responses are indicated $-$ or $+$ respectively. This figure is modified from Connell 1990, and adapted from Jensen (2011).

on the life stage of the plants, their physiology, and many direct and indirect interactions. The interactions between species is also known to be determined by site conditions such as regional climate, soil fertility, functional diversity of the species involved, and the developmental stage of the forest (Ammer (2019)). For example, in a Savanna ecosystem in South Africa, the interactions between trees and grasses was determined by precipitation of the year, as tree effects on grasses were facilitative in drier sites, and mildly competitive in the wettest sites (Moustakas et al. (2013)). Closer home, in the French Alps, neighbor removal experiments done in natural alpine plant communities showed differential response of species depending on their elevation and topographical location (Choler et al. (2001)). This particular experiment also revealed signs of natural range shifts, as facilitation appeared to allow species from lower elevations to move up the gradient, but competition at low elevations appeared to restrict species from higher elevations from moving down the gradient.

2.1.2 Succession theory

Succession typically describes vegetation dynamics after the occurrence of a disturbance event of any degree or amplitude (Pickett et al. (2009)). The first theory of vegetative succession was put forth by Clements (1916), describing the sequence of species successively invading a relatively open site after a large perturbation, moving from an empty site to herbaceous vegetation, shrubs, and then trees, finally reaching the stage

of stabilization or climax (Pickett et al. (2009)). Gleason (1927), however, suggested that succession was a much more flexible framework, without a particular direction or completion point. More recently, there are many studies describing changes in other characteristics such as species composition (Hobbs et al. (2007); Connell and Slatyer (1977)), productivity (Mitchell (2013)), diversity (Pretzsch (2013)), niche breadth (Hooper et al. (2005)) or the three dimensional structure of a plant community (Pickett et al. (2005)), during the process of succession.

Occurrence of extreme disturbances on a site, by leading to an empty or open area, followed by appearance of species, is called primary succession. The further progression of vegetation dynamics is termed secondary succession. The progression of these successions is shown in figure 2.3 (adapted from Khanolkar et al. (2020)). The trajectories followed by a species or an ecosystem vary depending on the situation, the main causes behind this being: 1. Differential site availability, 2. Differential species availability, and 3. Differential species performance (fig. 2.1). For instance, (Heydari et al. (2020)) observed post-agricultural secondary succession in Mediterranean semi-arid conditions and found increasing diversity of plant functional groups and soil-based functions progressively after abandonment. As described in section 2.1.1, species interactions can change with changing site conditions, and this can determine the course of succession. In the context of constantly changing climate, and increasing number of disturbances, species interactions and performances are expected to change, leading to potential changes in successional dynamics (Anderson-Teixeira et al. (2013); Didion et al. (2011)). For instance, the continuous, long-term disturbance of deer browsing in old-growth forests in the US has reportedly shifted forests from natural succession to more homogenous woodlands (White (2012)).

2.1.3 Community assembly

The community assembly theory has many similarities with the succession theory, which is discussed in section 2.1.2. Both are based on fundamentals of ecology, including biogeography, trait based theory, evolution and phylogenetics, and therefore have overlapping concepts (Chang and HilleRisLambers (2016)). However, they have some differences in the way they are defined and the processes on which they emphasize. In general, succession deals more with the temporal trajectories of a community after a known disturbance, whereas community assembly is trying to understand the mechanisms behind species patterns in a local environment, without necessarily having the history of a disturbance, or

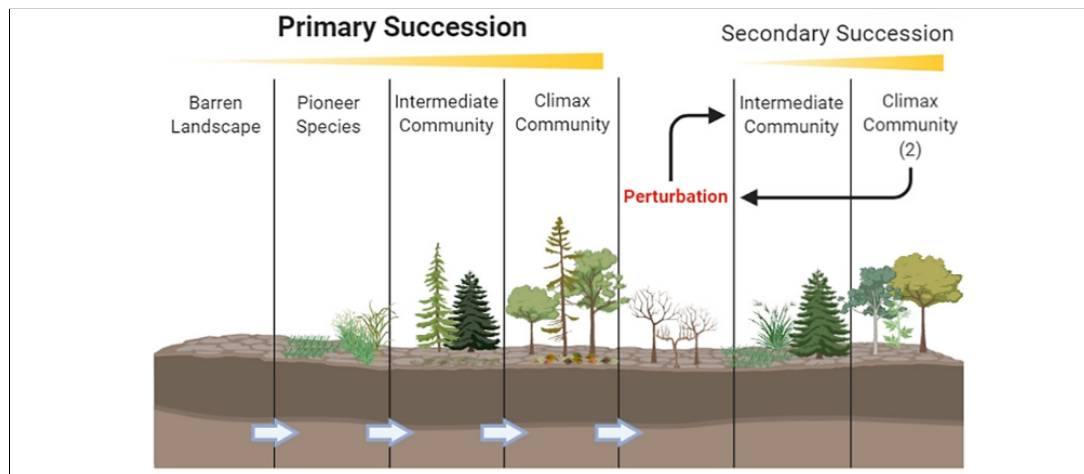


Figure 2.3: Model of ecological succession describing the stages of primary succession (left) that occurs through pioneer species which colonize an initially uninhabited landscape from an environmental reservoir secondary succession (right) that occurs through locally resident species following a perturbation that disrupts the normal steady state and results in the formation of a stable, but different climax community. As the perturbations, however minor, are constantly occurring, even a relatively "steady-state" community is a dynamic state of flux, and moving toward a desired equilibrium, which may never be truly reached. Image taken from [Khanolkar et al. \(2020\)](#).

any knowledge of its history altogether ([Chase \(2003\)](#)). The pattern of community assembly itself has different debated views. One view (pioneered by [Clements \(1916\)](#)) maintains the thought that given similar environmental conditions, and similar species composition, in a given disturbance, the plant community will converge towards a single stable state or climax. [Gleason \(1927\)](#), along with many others ([Lockwood et al. \(1997\)](#); [Samuels and Drake \(1997\)](#)), holds that in similar environmental conditions and species composition, the outcome of community compositions may vary depending on the history of the species or the location or the local physical or physiological plant-plant or plant-animal interactions (see fig 2.4). For example, the mountain forests of Northeastern United States are witnessing species range shifts attributing to climate change. The response of regenerated saplings to climate and land use change is species dependent even in similar site conditions and locations, with some species experiencing range expansion, contraction, or an upward or downward shift. The resulting tree species composition is thus expected to differ depending on specific differences in demographic processes ([Wason and Dovciak \(2017\)](#)).

[Chase \(2003\)](#) supplemented these arguments by suggesting that each of the above-mentioned mechanisms could be true depending on many conditions listed hereafter. For

example, a single equilibrium should exist in similar sites with small species pool, high dispersal levels, low productivity, and high disturbance. However, with similar sites having large species pools, low levels of dispersal, high productivity and low disturbance rates, there could be multiple stable states. These conclusions are influential while carrying out predictive analyses or models that imply future ecosystem or community structures.

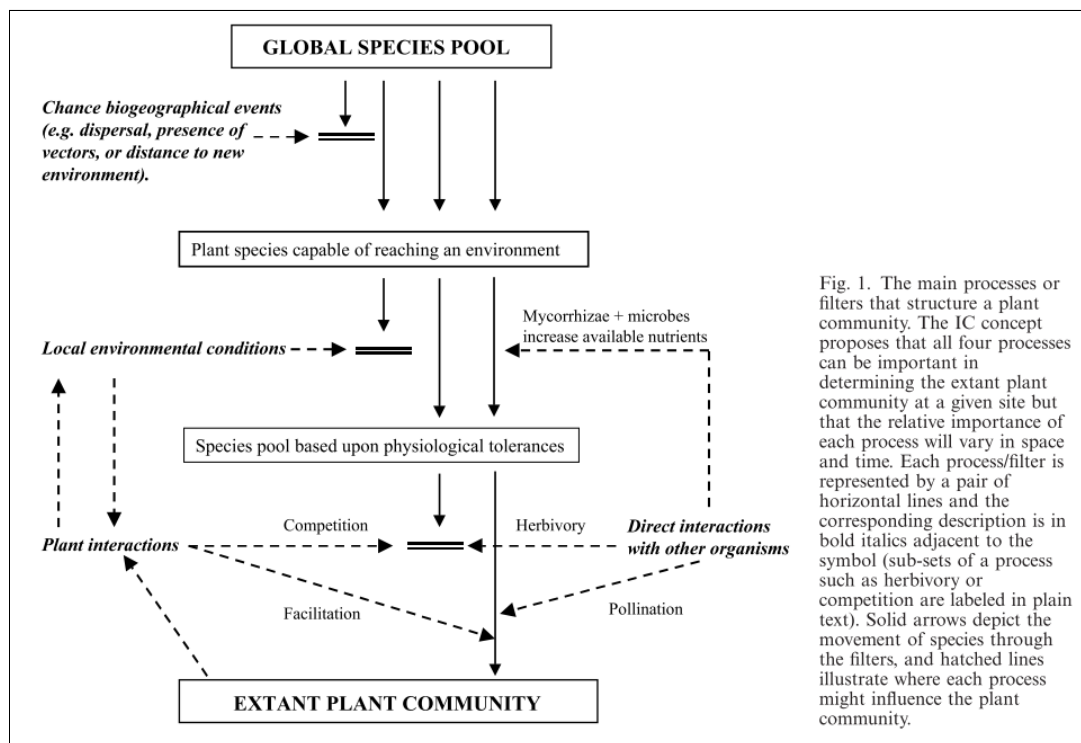


Fig. 1. The main processes or filters that structure a plant community. The IC concept proposes that all four processes can be important in determining the extant plant community at a given site but that the relative importance of each process will vary in space and time. Each process/filter is represented by a pair of horizontal lines and the corresponding description is in bold italics adjacent to the symbol (sub-sets of a process such as herbivory or competition are labeled in plain text). Solid arrows depict the movement of species through the filters, and hatched lines illustrate where each process might influence the plant community.

Figure 2.4: The main processes or filters that structure a plant community. The concept proposes that all four processes can be important in determining the extent plant community at a given site but that the relative importance of each process will vary in space and time. Each process/filter is represented by a pair of horizontal lines and the corresponding description is in bold italics adjacent to the symbol (subsets of a process such as herbivory or competition are labeled in plain text). Solid arrows depict the movement of species through the filters, and hatched lines illustrate where each process might influence the plant community (Lortie et al. (2004)).

2.1.3.1 Environmental filtering

One of the pervasive concepts in community assembly is that of environmental filtering (Kraft et al. (2015)). In every community, abiotic environmental "filters" define the success or failure of species establishment in certain environmental conditions. The environment, thus acts as a selective force for the spatial structure of communities,

where plants may or may not establish at a particular site (Liu et al. (2021); Tuomisto et al. (2003); Wright (2002)). This community assembly rule constraints through environmental filters, which species can occur in the community and which combinations are unsuitable (figure 2.4) (van der Maarel and Franklin (2005)). For example, the persistence of seed banks of a species in the soil is determined by multiple abiotic factors such as soil moisture and nutrients, presence or absence of weeds that will hinder the establishment of seeds, light availability (based on the overstory canopy cover) at the location of the seeds. This concept is frequently observed in forest and regeneration dynamics, specially towards species range limits (Fisichelli et al. (2013)), as filters such as temperature (Bontemps et al. (2012)), water (Senf et al. (2020)) , light (Weisberg et al. (2005)), soil conditions (Pinho et al. (2018)), topography (Szwagrzyk et al. (2021)) are dominant environmental filters in regeneration establishment, and thus species coexistence (Lusk and Laughlin (2017)). For example, the fitness of beech regeneration in its southern climatic limits is at risk due to increasing warm and dry temperatures, which may lead to removal of the species from those particular environments (Silva et al. (2012)).

However, environmental filtering cannot be the only mechanism driving community compositions, as many other biotic factors such as dispersal limitation, competitive and facilitative inter and intra-specific interactions, that are excluded by environmental filtering theory, also play a big role in determining spatial patterns of species abundance (Kraft et al. (2015); Jabot et al. (2008)). This is one of the biggest critiques of the environmental filtering theory, put forth by many such as (Aguilar-Trigueros et al. (2017); Cadotte and Tucker (2017)). However, this theory is a worthy first step in determining if a species can occur in a site, and does not decide all the drivers for species occurrence or abundance in a site (Kraft et al. (2015); Jabot et al. (2008)).

2.1.3.2 Neutral theory

The neutral theory, developed by Hubbell, first in 1879, and then revised in 2001 (Hubbell (2001)), puts forth that all individuals in a community are strictly equivalent regarding their prospects of reproduction and mortality, irrespective of the species they belong to, and they also have limited dispersal abilities, being more likely to disperse in neighboring areas than remote sites (Hubbell (2001)). The theory originally ignores species niche and coexistence theories (Chave (2004)), but later studies demonstrate that niche and neutrality form ends of a continuum from competitive to stochastic exclusion (Gravel et al. (2006)). This theory has surprising capacity to predict empirical patterns of species

abundance (Chave (2004)), but reconciling the theories of niche and neutrality could also show promising results (Laroche et al. (2020); Jabot et al. (2008); Gravel et al. (2006)). Jabot et al. (2008) demonstrated the reconciling of the theories of neutrality and environmental filtering using simulated datasets as well as data from tropical tree plots in Panama to infer the drivers of tree recruitment rates, and discovered a cumulative effect of environmental filtering and dispersal limitation (an assumption of the neutral theory).

2.1.4 Ecological niche

Ecological niche is a fundamental concept of ecology, which is the ecological space representing the range of environmental conditions necessary for the persistence of a species (Polechová and Storch (2018)). Fundamental niche of a species, as defined by Hutchinson (1957) is a multidimensional ‘cloud’ of favorable conditions determined by all environmental (i.e. abiotic and biotic) variables where the species can reproduce and survive (Vandermeer (1972)). The realized niche, which is a subset of the abstract fundamental niche, is where the species can actually persist, given the presence of other species competing for the same resources (Vandermeer (1972)). Thus, a realized niche generally has a narrower extent along respective dimensions; a species that could potentially live in a broad range of humidity conditions, for instance, may occupy a much narrower range of these conditions in an environment with competing species, since its population growth rate decreases to negative values in some conditions (Patten and Auble (1981)). Here onwards, the term “niche” will indicate the realized niche, unless stated otherwise.

A large number of competing species often have overlapping niches, and co-exist in the same community (Kim and Ohr (2020); Courbaud et al. (2012)). They are known to occupy different environmental niche axes, where various gradients of resources such as light, water, soil nutrients are partitioned and shared, for instance, by adjusting root depth of different species (Silvertown (2004)). The partitioning can be temporal (e.g. by the use of resources at different life stages (Scheiner and Willig (2013))), spatial (e.g. by occupying different spaces at the same time (Shurin et al. (2004))) or trait based (e.g. by modifying traits in order to allow co-existence (Pausas (1999))). For example, species like spruce-beech can co-exist by light partitioning (Diaci et al. (2020); Kunstler et al. (2005)), and spruce-beech can also occupy different root depths in order to co-exist (Pretzsch et al. (2014)).

The realized niche and distribution of a species also has an intricate relationship, and can depend on niche size, species dispersal ability, habitat availability and stability. Potentially, a species can be absent in suitable habitat conditions, or present in unsuitable conditions (Pulliam (2000)). Competition for resources or dispersal limitation can lead to local extinctions, rendering suitable habitats empty. For example, peleo-ecological evidence shows that *Abies alba* (silver fir) occupied a much larger range 5000 years ago, than its current distribution (Tinner et al. (2013)). On the other hand, species can occupy unsuitable habitats, called "sink" habitats because of migrations, or excess reproduction.

Even though the existence of niche is not the only determinant of species co-existence and distributions, it has a considerable impact, and a species cannot persist if conditions are not favorable for reproduction and survival. Production of seeds, dispersal, germination and growth of new seedlings, describe the regeneration niche, which is a major component of the global niche concept (Grubb (1977)). As the niche of a species is dynamic, and depends on various environmental factors, it has also shown sensitivity to climate change (Bykova et al. (2012)).

2.1.5 Alternative stable states

As mentioned in section 2.1.2, according to the theory of succession, an ecosystem can follow multiple different paths depending on several environmental factors. The concept of alternative stable states suggests that a community can have more than one final stable state, even under the same environmental conditions and same species pool (figure 2.5). These alternative states can be separated spatially or temporally, with one or more drivers governing a species community. Temporal separation of alternative stable states includes the alternation of grasses and shrubs after instances of fires (Ransijn et al. (2015); D'Odorico et al. (2012); Lett and Knapp (2003); Laycock (1991)). Alternatively, there can be local separation inside the same external environment, for example, the presence or absence of deer in a forest stand can shape community compositions in the same abiotic environment (Côté et al. (2004)). These alternative states may occur gradually, as with the presence of deer in a forest, or abrupt, as with fires in grasslands.

The occurrence of alternative stable states have been widely observed in natural conditions (Wood and Bowman (2012)), as well as experimentally (Schröder et al. (2005)).

They are often driven by a feedback, in terms of disturbances, competition, facilitation, or a change in behavior or extent of a component in the immediate environment (Shurin et al. (2004)). For example, fire regimes in beech forests of Patagonia result in two different steady states depending on the extent and location of the fire (Pausas (2015)). The frequency of disturbances such as fires has increased substantially due to climate change, and hence climate change can indirectly trigger alternative stable states (Wood and Bowman (2012)).

Species compositions, or distributions, often change over time or space, and hence (Fukami and Nakajima (2011)) raise a question of whether they should be called stable states, or transient states, in order to understand and acknowledge the historical contingency of a community. In order to re-evaluate this concept, it is necessary to not only recognize the period of occurrence of each of these final states, but also pay close attention to the identity and magnitude of factors initiating the different states, as in the context of forests (Acevedo et al. (1996)). The presence of white-tailed deer in the eastern United States resulted in at least 3 distinct stable vegetation communities in rangelands, depending on different mechanisms (browsing coupled with clear cutting, browsing coupled with fire, browsing coupled with suppressed regeneration).

2.1.6 Intermediate disturbance hypothesis

The intermediate disturbance hypothesis (IDH) suggests that the peak of species diversity occurs in disturbances with intermediate levels of intensity and frequency (figure 2.6. Wilson (1994) based this hypothesis on the claim that ecological communities are dynamic, and seldom reach an equilibrium in which competitively superior species exclude other species. When disturbances occur, killing or damaging species or individuals, they will potentially open new spaces for less competitive individuals, thus setting back the process of complete exclusion of the competitively weaker species (Roxburgh et al. (2004)). However, this is more likely in patchy and dynamic ecosystems, with trade-offs between the colonizing and competitive ability of species (Roxburgh et al. (2004)). This is particularly the case in forests, when trees of shade tolerant species die, such as beech, the created gap is colonized by regeneration of light demanding species such as oak or pine, that disappear if no disturbance occurs (Packham et al. (2012)).

At one end of the scale, communities with no or low intensity and/or frequency of disturbances exhibit low species richness as they are dominated by the competitively

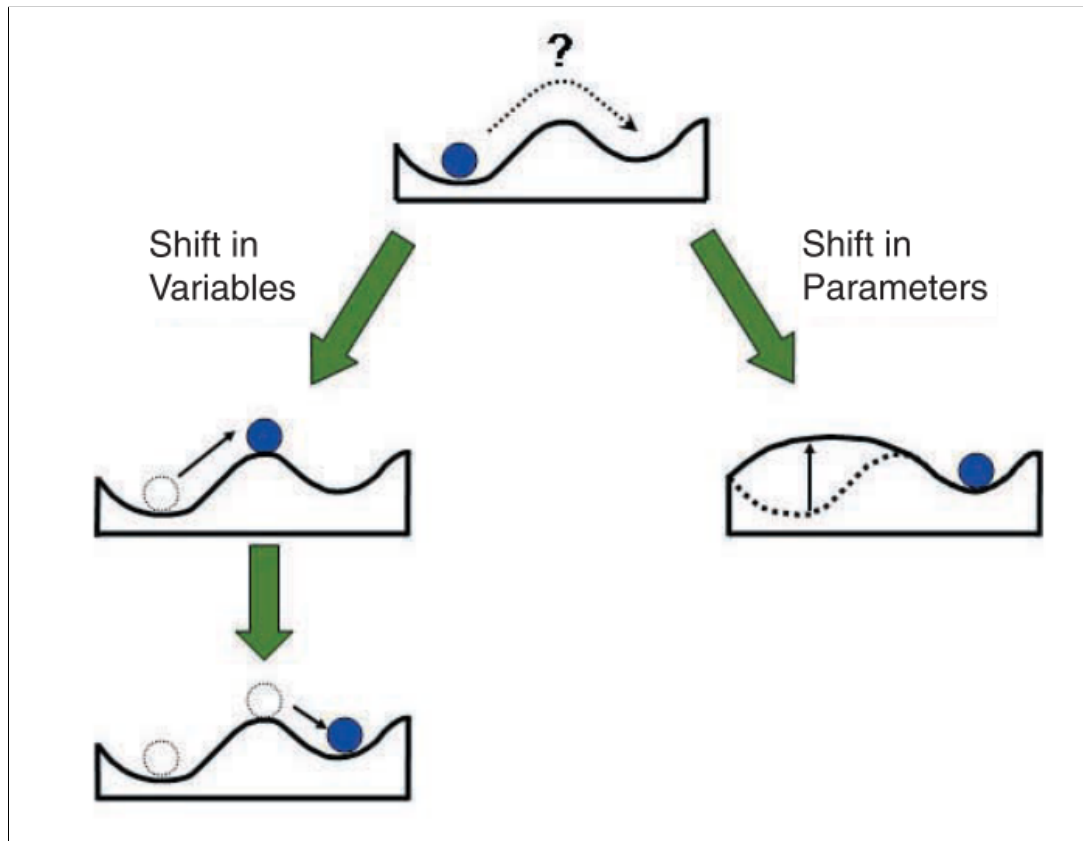


Figure 2.5: Two dimensional ball-in-cup diagrams showing (left) the way in which a shift in state variables causes the ball to move, and (right) the way a shift in parameters causes the landscape itself to change, resulting in the movement of the ball. Adapted from [Beisner et al. \(2003\)](#).

superior species. For example, beech species dominance (*Fagus sylvatica* in Europe, *Fagus grandifolia* in North America, *Fagus crenata* in Japan) is often observed repeatedly with low species richness in forests. On the other extreme, frequently and/or intensely disturbed ecosystems have low species abundances as only a few species can colonize between disturbances, or after a large disturbance. For example, with the establishment of invasive species following recurring disturbances ([Thompson et al. \(2001\)](#)). Hence, species richness is expected to be highest in intermediate levels of disturbances, where both rapid colonizers and competitive species can survive and co-exist. For example, the creation of gaps in beech forests (because of windthrow, or management practice) results in immediate increase in species diversity of the following regeneration ([Von Oheimb et al. \(2007\)](#)).

However, there is criticism and debate about the certainty of the IDH ([Moi et al. \(2020\)](#); [Fox \(2013\)](#)). Fox suggests that it is necessary to consider other mechanisms of species

co-existence to understand factors driving species diversity. (Moi et al. (2020)) does not completely refute the hypothesis, but demonstrates that most articles supporting the IDH are conducted in terrestrial ecosystems (e.g. Bush and Colinvaux (1994); Sheil and Burslem (2003)), whereas many results of the studies carried out in aquatic ecosystems failed to find evidence in support of (e.g. Gerwing et al. (2017); Kubicek and Reuter (2016)). The positive impact of the IDH on species diversity has been repeatedly demonstrated in forest ecosystems (Nagel et al. (2021); Motta et al. (2011); Koniak and Noy-Meir (2009); Roxburgh et al. (2004)). These disturbances include creation of gaps (Franc et al. (2008); Molino and Sabatier (2001)), storms uprooting trees (Meyer et al. (2021)), or fires destroying vegetation (Kolbek and Alves (2008)), and they act in favour of regeneration by creating favourable microsites (Von Oheimb et al. (2007)), reducing competition or increasing dispersal abilities (Sheil and Burslem (2003)). Such seasonal or rarely occurring disturbances have often shown in increased ecological diversity and productivity, thus asserting the validity of this hypothesis in forest ecosystems.

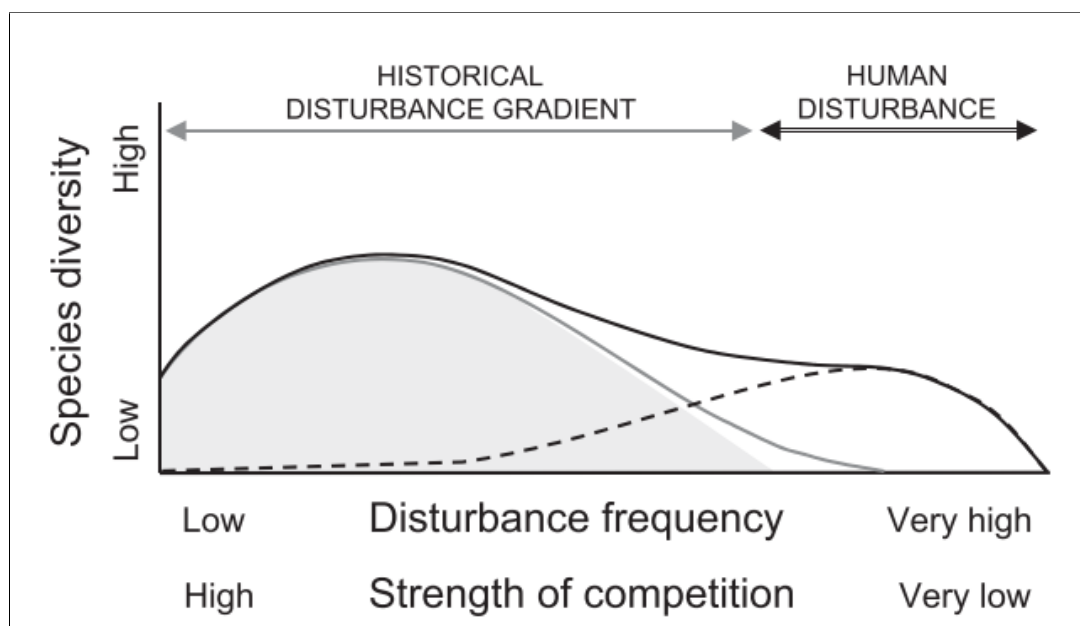


Figure 2.6: In early stages of invasion, the addition of alien species combined with human disturbance extends the IDH curve and augments species richness in high disturbance sites; it does not reduce native diversity. Early stages of invasion focus on colonization and include introduction and naturalization sensu Richardson et al. (2000). Grey shading indicates pre-invasion community species diversity under the historical disturbance regime; lines indicate diversity post-invasion and post- anthropogenic disturbance: solid black line, community diversity; dotted black line, alien diversity; solid grey line, native diversity. Adapted from Catford et al. (2012).

2.2 Role of global changes in ecosystem functioning

Anthropogenic activities in the past couple of centuries has been recognized as the main cause of major environmental changes (Lewis and Maslin (2015)). They include land use changes such as conversion of terrestrial ecosystems into croplands, pastures, deforestation and fragmentation; nutrient eutrophication, especially in aquatic ecosystems, leading to toxic algal blooms among other problems, changes in atmospheric composition, increasing air temperatures accompanied by changes in precipitation regimes, changing seasonal and annual temperature leading to changes in phenology of many species (IPCC (2014); Parmesan and Yohe (2003)). By affecting plant, animal and fungal species differently, global changes have the potential to modify interactions between species from local to global scale, with significant consequences on ecosystem functioning (Tilman et al. (2014); Morris (2010); Hooper et al. (2005)).

2.2.1 Climate change as a disruptor of forest dynamics

Forests cover almost one third of the world's terrestrial habitat, and are estimated to host more than 80 % of the world's terrestrial biodiversity (FAO (2020)). In the absence of human interventions, the functioning of forest dynamics depends on climate, soil and topographical conditions, and disturbances - biotic and abiotic (Ehbrecht et al. (2021)). The interactions between the environment and species, described in section 2.1 play a crucial role in determining community and ecosystem dynamic and composition (Srinivasan et al. (2015); Keddy (1992)). However, the explosion of human activities in the recent past have changed the nature and intensity of these interactions, in turn leading to changing forest dynamics, and structures. Even though forests have a remarkable resilience capacity, and the ability to mitigate disturbance events, the force and intensity of these changes is too large for forest species to resist (Aitken et al. (2008)).

Climate change affects forest ecosystems by modifying the frequency, intensity and duration of extreme climatic events such as extreme heat, fires, droughts, invasions by plants and pests, hurricanes, storms or landslides (Williams et al. (2008)). These changes are bringing about many changes in different forest characteristics. Among them, a few are listed below:

2.2.1.1 Climate impact on species diversity, range and distributions

Biodiversity is a major determinant of ecosystem dynamics and functioning. On the basis of natural history observations and qualitative comparisons across habitats, greater diversity leads to higher ecosystem stability, greater resistance to invasion by exotic species, and lower disease incidence (Tilman et al. (2014)).

Global decrease of species richness and natural abundance of species are attributed to changing climate. (Thuiller et al. (2005)) projected distributions of 1350 European plant species, and predicted that at least half of them could be vulnerable or threatened by 2080, whereas (Thomas et al. (2004)) predict an extinction of 35 % of total global terrestrial species in maximum climate change scenarios by the year 2050. However, local patterns of a change in species richness may be positive or negative (Menéndez et al. (2006)). For example, cool-temperate regions that experience warming and very dry regions that experience increased moisture availability are both expected to exhibit increases in richness (Hawkins et al. (2003)).

The number of species per area, or the species richness, is strongly limited by climatic constraints (Sommer et al. (2010)). Many vascular plants evolve under varied conditions, and need to expand their niche breadth by developing additional adaptations of survival under less-favourable climate conditions (Wiens et al. (2009)). For example, paleo-ecological evidence shows that *Abies alba* has survived in much warmer and drier conditions than its current range. Hence, the potential distribution of species is mostly constrained by their physiological level of tolerance, such as their ability to deal with frost and drought (Currie et al. (2004); Hawkins et al. (2003)). Moreover, biotic interactions influence the realized ranges of species (Raath-Krüger et al. (2019); HilleRisLambers et al. (2013); Wisz et al. (2013)). In addition to climatic controls, topography also affect the species richness of an area (Moura et al. (2016); Yu et al. (2015); Dufour et al. (2006); Kumar et al. (2006)), by acting as as surrogate of habitat or vegetation heterogeneity (Moura et al. (2016)). Different biogeographical regions also determine species richness. For plants, prime examples are winter rainfall regions such as mangroves that have higher richness than expected from their current climate (Osland et al. (2017)). This suggests that regional events as well as long-term climate fluctuations play an additional role in shaping species-richness patterns (Sommer et al. (2010)).

2.2.1.2 Climate induced range shifts

Range shifts are often caused by migration of individuals or a species, or the appearance or disappearance of a species in a region. Although the geographical ranges of species are dynamic and fluctuate over time (Schurr et al. (2012)), the effects of changing climate are leading to a redistribution of species universally (Pecl et al. (2017)). When the climate of a location becomes unfavorable for a plant species, they move to a more favorable location (Pecl et al. (2017)), through spatial preferences for dispersal or establishment.

Increasing temperatures and dry climates impair the establishment and growth of many temperate terrestrial species (Walck et al. (2011)). As the effects of climate are different on different species, key interactions between species in an ecosystem are disrupted and new interactions develop. Cumulative changes in many such interactions can ultimately lead to a large-scale structural shift in the community composition (HilleRisLambers et al. (2013); Van Der Putten (2012)). For example, (Didion et al. (2011)) simulated forest structures of 3 different climatic zones in the Swiss Alps, for 6 different tree species, and observed a significant pole-ward shift of species, along with reduced basal areas, and a resultant change in species composition, which was attributed to a combined effect of climate change, and increased ungulate browsing.

Individuals and species are moving pole-wards or towards higher elevations as warmer extremes become intolerable (Chen et al. (2011); Shoo et al. (2006)). It can contribute to the contraction of species ranges for many of them, especially those which are already at their warmer extremes (Honnay et al. (2002)). This contraction of ranges creates a fear of local as well as global extinctions. Meta-analyses show that, on average, terrestrial taxa move pole-ward by 17 km per decade and marine taxa by 72 km per decade (Chen et al. (2011); Milad et al. (2011)). For plants, this migration is slower than animals, with dispersal and establishment of new generations in more suitable conditions (Renwick and Rocca (2015)), and time lags can be observed, especially in the migration of tree species that have very long lifespans (Bertrand et al. (2011)). As climate change accelerates, these lags will likely increase, potentially threatening the persistence of species lacking the capacity to disperse to new sites or locally adapt (Ash et al. (2017)).

There are efforts of conservationists focused on species susceptible to climate change with the help of "assisted migration" (Gömöry et al. (2020); McLachlan et al. (2007)). This program focuses on taking seeds or seedlings of a species from populations belonging

to southern edges of the species range, thus adapted to climate change, and introducing them to northern habitats where populations may not fare well in climate change scenarios (Sáenz-Romero et al. (2021)). This ensures not only growth of better adapted individuals, but also maintains genetic diversity for an uncertain future (McLachlan et al. (2007)). There have been trials in Canada and Mexico that show improved performances of species after moving them to higher elevations, with risks such as diseases or invasions that need to be mitigated (Sáenz-Romero et al. (2021)), but its policy implications remain to be decided before any implementations (McLachlan et al. (2007)).

2.2.1.3 Phenology changes

Phenology is the study of periodic or seasonal activities carried out by plants or animals, such as animal or bird migrations (Horton et al. (2020)), fruiting or flowering of plants (Morellato et al. (2016)), or timings of development stages of insects or animals (Chuine and Régnière (2017)). As changes in phenology are visibly evident, and thus relatively easy to track (Walther et al. (2002)), there are already evidences of these changes due to changing climate (Iler et al. (2021); Piao et al. (2019); Visser and Both (2005)). For example, (Piao et al. (2019)) found climate induced advancement in leaf unfolding in spring in North America, Europe and China, but this advancement was higher for field sites in China and Europe compared to North America.

A recent review by (Iler et al. (2021)) discusses the different ways in which phenology can modify plant demographic processes of growth, survival or reproduction. It can affect plant populations positively or negatively, depending on the species and process under consideration. Plants can perform better if life-cycle events shift earlier than expected, as they gain time to grow or reproduce, but also could be at a risk of late spring. Alternatively, they could also be exposed to novel environments that can result in negative consequences to the demographic process. For example, in an experimental setup on woody species, all of them displayed variations in leaf phenology (flushing and senescence) consistently and growth over years of temperature increase, but the direction of change varied between species. This is expected to eventually bring about a shift in population dynamics (Vitasse et al. (2009)): Phenological shifts could have population level consequences as reproduction and survival of organisms is at stake (Iler et al. (2021)).

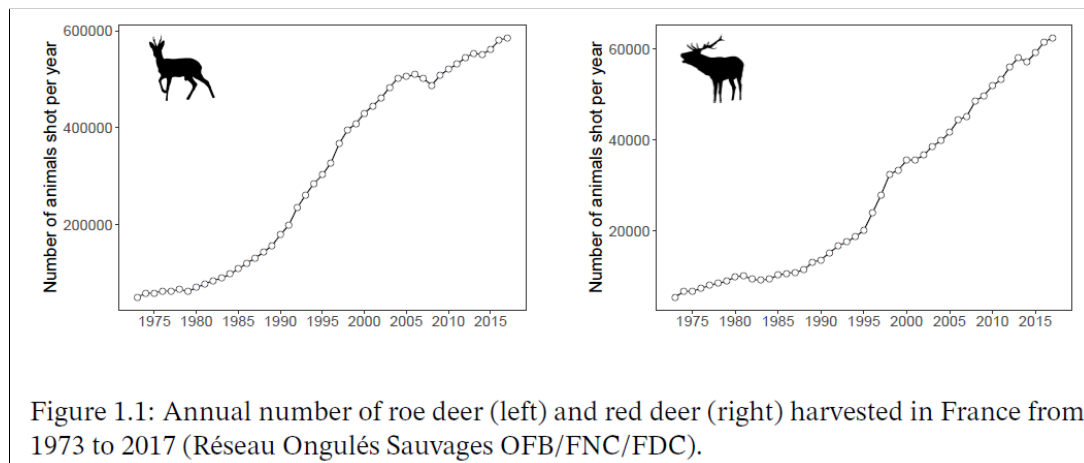


Figure 2.7: Annual number of roe deer (left) and red deer (right) harvested in France from 1973 to 2017 (Réseau Ongulés Sauvages OFB/FNC/FDC). Adapted from [Barrere et al. \(2021\)](#).

2.2.2 Increasing ungulate populations as a global change

There has been a significant increase in the populations of large-herbivores in forests of Europe and North America in the last few decades ([Nuttall et al. \(2014\)](#); [Côté et al. \(2004\)](#); [Adams \(2002\)](#); [Clutton-Brock et al. \(2004\)](#)). This is the effect of several anthropogenic factors, whose intensity and extent varies depending on the location.

Ungulate population trends in Europe have a long history of being driven by human induced activities. As humans transitioned from hunter-gatherers to settlers, there was habitat reduction, resource distribution (sharing with livestock), as well as intensive hunting of deer for food, which resulted in large declines in ungulate populations. The 20th century saw a number of changes, such as restoration initiatives (increasing forest covers, reducing food competition and increasing habitat availability), management practices (such as regulated hunting ([Massei et al. \(2015\)](#)), re-introductions and supplementary feeding), that gradually brought back the populations ([Valente et al. \(2020\)](#)). In addition to these, a decline was observed in natural ungulate predator populations such as the grey wolf (*Canis lupus*) and the Eurasian Lynx (*Lynx lynx*) ([Ripple et al. \(2014\)](#)). Simultaneously, changing climate meant milder winters, which may have promoted ungulate populations, though climate change also has negative effects on ungulates, so this argument is debated ([Gaillard et al. \(2013\)](#)).

A change in the nature of anthropogenic interventions, combined with changing cli-

mate, have led to an explosion in ungulate populations in Europe for nearly all the ungulates present in the continent (Gaillard et al. (2013)) (figure 2.7). However, as there is no way to accurately estimate ungulate populations, different metrics such as harvest rate, or number of deer-vehicle collisions have consistently reported increasing trends (Löf et al. (2021)). In France, over the last 40 years, there has been an eight fold increase in the number of red and roe deer harvests, indicating high populations (Barrere et al. (2021)). This population increase has many consequences for forest ecosystems, by increasing the intensity of plant-herbivore interactions, and limiting forest regeneration.

2.2.2.1 Ungulate browsing affecting regeneration in forests

Ungulates rely on vegetation in forests as a food resource to survive. The direct consumption of seedlings and saplings by ungulates reduces their height growth and survival and can be one of the most influential effect on forest regeneration (Borderieux et al. (2021)). The palatability of ungulates to different species varies, and they selectively consume only certain species favored by them, unless those species are low in density or hard to find, in which case they move on to the next best. Along with grasses and herbs, many tree species such as oak, ash, fir, maple are frequently browsed, threatening seedling and sapling growth and survival, and ultimately their future abundance in the ecosystem (Pettersson et al. (2020); Götmark and Kiffer (2014)). This browsing pressure is concentrated on saplings ranging from 20 to 200 cm, and is negligible on seedlings below 20 cm or above 200 cm in height Löf et al. (2021) (Götmark et al., 2014; Löf et al., 2021). Though the morphological consequences of deer browsing on saplings are well known, the functional consequences of this impact remain largely unknown.

Due to these damages caused by ungulates, there have been efforts to limit their growth and demography. The most common management tool to control ungulate populations in the absence of natural predators is hunting. However, there has been a decrease in the number of hunters, and hunting as a sport, in the last few years. Forests with low ungulate densities are less attractive from the hunter's perspective due to the difficulty of harvesting animals. Consequently, many hunters wish to keep ungulate populations at a sufficiently high level to maintain the attractiveness of the activity. A growing proportion of the public opinion is also in favor of abundant ungulate populations, regardless of silvicultural considerations, and tends to disapprove of regulating these populations through hunting (Peterson (2004)).

Another intuitive and extensively used vegetation-focused approach is to exclude ungulates from the forest stands that need protection by erecting fences around the area (VERCAUTEREN *et al.* (2006)). Though a few negative effects for forest regeneration have been reported inside fences – e.g. shrub proliferation (Ward *et al.* (2018)), or increased seed predation by rodents due to the absence of trampling (Muñoz and Bonal (2007)), a recent meta-analysis showed the efficiency of this method in promoting the height growth, abundance and diversity of saplings inside fences (Bernes *et al.* (2018)). One of the main drawbacks is the financial cost, which can often be prohibitive for forest managers (Löf *et al.* (2021)). Fencing can also have additional repercussions at larger spatial scales, by increasing landscape fragmentation, and heterogeneity in large herbivore spatial distribution, resulting in increased browsing pressure in unfenced areas (Baltzinger *et al.* (2018)). Other means of protection that target specific individual trees exist as well. Mechanic individual protection can be used (plastic or metal grids that surround the tree) to prevent browsing and fraying on specific trees in the stand and to “divert” the browsing pressure towards other, less valuable saplings. Similarly, chemical or natural repellents applied to individual trees are increasingly being used to deter browsing (Stutz *et al.* (2019); Kimball *et al.* (2009)). However, studies investigating the efficiency of these repellents have shown highly contrasted results (Lindmark *et al.* (2020); Elmeros *et al.* (2011)).

2.3 Sustainable forest management

2.3.1 Forest management adaptations to global changes

Europe is the continent with the highest proportion of forests under management plans, with 96 % of its forests being managed (FAO (2020)). There is increasing focus of forest management on sustaining ecological productivity while also maintaining economic goals of harvesting. As seen previously, global changes have a strong impact on forest ecosystems, and contribute to changes in forest communities and structures. The forests that are regenerating now will have to deal with the consequences of future climate (Thuiller *et al.* (2005)), indicating the importance of including and monitoring regeneration processes in forest management strategies. In future conditions, when most species in the world are predicted to be vulnerable to geographical distributions and range shifts, changes in phenology, behavior, or even extinction, there will perhaps be little scope of economic gains, unless these changes are mitigated through forest management (Santopuoli *et al.* (2021)). Hence, it is necessary to shift the focus on

more sustainable management practices by first identifying and anticipating future risks, rather than by reacting to current problems (Messier et al. (2015)). For example, continuous cover forestry has proved to be a promising management strategy, especially in mountain areas where it provides continuous protection against natural hazards and continuous forest landscape (Pretzsch et al. (2021); Coll et al. (2018)), along with maintaining species abundances in the stands (Torresan et al. (2020); Ficko et al. (2016)).

Forest Europe (formerly the Ministerial Conference on the Protection of Forests in Europe, Helsinki Resolution 1 (H1) in 2003) defined Sustainable Forest Management as: the 'stewardship and use of forest lands in a way, and at a rate that maintains their biodiversity, productivity, regeneration capacity, vitality and their potential to fulfil, now and in the future, relevant ecological, economic and social functions, at local, national and global levels and that does not cause damage to other ecosystems'. This 19-year-old definition, even though very detailed, poses multiple challenges to foresters, researchers and policy makers alike, in order to meet its ecological, economical as well as social objectives. Adapting current management practices to changing climate involves understanding the requirements of the ecosystem in the future (Spittlehouse and Stewart (2003)). It could include information about species that will not be suitable in a future environment, but can be planted artificially if economically important (Doust et al. (2006)); increasing deadwood in forests that need more micro-sites to support biodiversity (Marzano et al. (2013)); increasing age limits of trees to be harvested in order to decrease proportions and frequencies of harvests, or even decreasing this age limit to promote genetic adaptation of new cohorts and individuals. (Sousa-Silva et al. (2018)) interviewed more than 1000 forest managers and owners from seven European countries to understand the perceptions about adapting management practices to climate change, and more than half of them agreed and were ready to comply. But most did not practice any adaptations due to lack of knowledge and technical expertise. Choosing a suitable management strategy is a complicated task, depending on various factors such as the dominant species in the forest, the main drivers and threats to the forest dynamics, and its vulnerability to climate change. As this is very technical information, it needs to be investigated well by researchers and implemented into policy guidelines. Nevertheless, the opinions of foresters are essential as they deal with practical aspects of forests regularly. An important step would be to improve communication between different stakeholders, in order for this knowledge and information to reach from academicians to practitioners effectively.

2.3.2 Summarizing silvicultural management measures

As mentioned earlier, choosing management strategies for particular stands or ecosystems can be a daunting task. It certainly makes it easier if there is a clear understanding of the different possibilities. (Oettel and Lapin (2021)) did an important exercise of reviewing and listing the main silvicultural management measures that support biodiversity at the stand and landscape level. In the case of spruce-fir-beech mixed forests, it is important to focus on practices that can help promote and maintain mixtures of these three species. Quoting below, some of the measures summarised by (Oettel and Lapin (2021)) Some are already in practice, and some are recommended ones, in order to fulfill ecological and economic objectives in spruce-fir-beech mixed and uneven-aged stands:

1. Provide horizontal and vertical structural heterogeneity

This is a crucial point, often already the case in uneven aged forests. Nevertheless, it is important to monitor and ensure structural heterogeneity in stands to promote stability and resistance to natural hazards. The structural heterogeneity includes assuring a differentiation in diameter at breast height (dbh), tree height, dimensions and ages, which aides in providing more microsites for sapling establishment, and different light conditions for different species to grow.

2. Adapt tree species composition

In mixtures that are dominated by one or more species, this is an important measure to adjust tree species compositions through harvesting. Desired species are left standing in order to increase their share in favour of other tree species. In doing so, tree species composition can be oriented in a desired direction. Further adaptation can further be achieved by planting and regulating mixed growth.

3. Promote deadwood quantity and quality

Deadwood promotion refers to the purposeful presence of dead trees, either standing or fallen or just stumps as a result of previous harvesting, in forest stands, as a way of promoting microsites. It is useful to promote regeneration of species such as spruce, which require very specific microsites to establish the seedlings.

4. Provide spatial heterogeneity at landscape level

One of the most common management practice carried out to promote spatial heterogeneity is the creation of gaps in forests. This is usually carried out by selecting a group of trees to harvest, creating empty spaces for new individuals to establish. Gaps can be of various sizes, and the size of the gap is determined by requirement of the stand.

5. Reduce understory density

The reduction of the density in the undergrowth can be achieved by reducing stem number and controlling mixed growth. This measure promotes stand stabilization depending on stand conditions, as well as an increase in growth and can promote the tree species mixture.

6. Increase rotation period

The rotation period refers to the age of the stand before harvesting. For uneven-aged forests, it refers to the age of the individual tree. Increasing stand age provides habitats for species that depend on mature forests and allows the provision of large-scale deadwood.

7. Provide uneven-aged forests under continuous forest cover

Adaptation of forest management to ensure uneven forest structures and continuous forest cover is achieved through single tree harvesting. Natural regeneration can occur simultaneously in small gaps and soil disturbances are reduced due to low management intensity.

8. Avoid forest fragmentation and habitat isolation

Forest loss, clear cutting and extensive forest road construction can lead to fragmentation of the forests. This should be avoided in order to maintain the stability of a forest and ensure habitat connectivity.

9. Maintain genetic diversity

Genetic diversity in a stand not just promotes stability, but also accelerates the process of adaptation to climate change. "Assisted migration", or replanting genetic variations that are already accustomed to warmer climates can potentially prevent mass mortality. Another idea is to reduce the DBH at which trees are harvested, in order to rapidly reduce the number of unadapted trees producing seeds.

10. Perform active monitoring

Active monitoring in forests refers to the continuous observation of different species and processes. It forms the basis for detecting changes over time. Forest management can be adapted according to these changes. Monitoring is also used to evaluate the success of adaptation measures.

Not all of these silviculture measures ensure adaptation to climate change or disturbances, but nevertheless, are crucial for the sustainable succession of a forest. For example, promotion of deadwood does not directly aide in mitigating climate change effects, but

does provide suitable microsites for species to regenerate, which is an important step in adapting forests to climate change.

2.4 Study species and their characteristics

2.4.1 Norway spruce (*Picea abies* H.)

Norway spruce, or *Picea abies* H., (hereafter spruce) is a conifer, one of the most important trees in Europe for ecological and economic reasons (Kuuluvainen et al. (1998)), and is widely found all over Europe, as shown in figure 2.8b. It has been cultivated historically for harvesting (Jansson et al. (2013)), and its wood is used for timber constructions, furniture, construction of musical instruments. While spruce stands are planted for controlling erosion, there are also breeding programs to produce better wood quality (Spiecker (2000)).

From a biological point of view, spruce is a long lived species (200-300 years naturally), and generally can grow upto 50-60 m high, with a DBH of up to 150 cm in very large trees. Its current niche extends from lowlands (artificial plantations) to Boreal and subalpine conifer and mixed forests across Europe, upto an altitude of 2400 masl (Jansson et al. (2013)). In the Alps, when it is not in pure stands, it occurs with European larch (*Larix decidua*) and Swiss stone pine (*Pinus cembra*) on higher elevations (1800-2100 m), with European beech (*Fagus sylvatica*) and silver fir (*Abies alba*) under fresh conditions at intermediate altitudes (800-1800 m) and with Scots pine (*Pinus sylvestris*) in drier conditions (Leuschner and Ellenberg (2017)).

Spruce is a secondary colonizer, but can be both a pioneer and a climax species. It shows good yield and quality performance under different conditions, and has been favoured by silviculture over long periods of time (Tinner and Ammann (2005)). It is fairly shade tolerant and can survive under closed canopies, growing better as it grows older and higher (Granhuis et al. (2016); Kneeshaw et al. (2006)). Its growth and survival depends to a large extent on climatic conditions, especially in the high latitude regions (Boucher et al. (2020)). It commonly grows best on acidic soils and prefers deep soil with good nutrient and moisture content, but can survive on most substrates (Dyderski et al. (2018)) except in highly dry or wet environments (Caudullo et al. (2016)).

In the last few decades, spruce forests have shown symptoms of slow decline in moun-



Figure 2.8: The image on the left side (a) is a representative image of branches of a Norway spruce (*Picea abies*) tree, with cones hanging on the branches, and on the right side, (b) is a distribution map of *Picea abies* in Europe. The green part depicts its natural range and isolated populations, whereas orange part depicts its introduced and naturalized (synanthropic) area and isolated population (taken from EUFORGEN).

tainous areas, including yellowing, loss of needles, die-back of branches and reduced growth (Caudullo et al. (2016)). As it prefers cool and moist climates, there is a possibility of this important species to be severely affected due to warming climate (Thurm et al. (2018)). There have been evidences of climatically driven reduction in survival of spruce regeneration as well as adult trees in different parts of its range (Brandl et al. (2020); Schurman et al. (2019); Pretzsch et al. (2014)). This effect is stronger in lower altitudes and latitudes, such as in central Europe, owing to more frequent hot and dry conditions, suggesting a reduction of range in its southern edges (Tremml et al. (2022); Feurdean et al. (2011); Bradshaw and Lindbladh (2005); Kullman and Engelmark (1997)). However, there are also prospects of spruce faring better in higher and northern latitude sites due to its preference for cool climates (Schurman et al. (2019)). In addition to direct effects of climate, there are also some indirect effects that are important to be considered as they reduce growth and wood quality of spruce. They are, increasing frequencies of infestations of threats such as bark beetles (*Ips typographus*) (Seidl et al. (2008)), or root-rot causing fungi, (Orman and Dobrowolska (2017)). In addition to other disturbances such as storms and fires, bark peeling by deer and wild boar can also cause damages to seedlings and young trees, making them more susceptible to pests and fungi (Cukor et al. (2019); Burneviča et al. (2016); Kiffner et al. (2008); Vasiliauskas et al. (1996)).

2.4.2 Silver fir (*Abies alba* Mill L.)

Silver fir, or *Abies alba* Mill L. (hereafter, fir) is another important conifer species present across Europe as shown in figure 2.9b, with both ecological and economical importance. Its wood is used for construction, pulpwood for paper, and its resin to make turpentine and medicinal and cosmetic products. Fir is a slow growing tree, preferring moist habitats and can live up to 500-600 years. It can reach heights above 60 m, making it one of the tallest species of the genus *Abies* in Europe (Leuschner and Ellenberg (2017); Tinner et al. (2013)).

Fir is present in areas with altitudes from 500-2000 masl, and mean yearly precipitation of 700-1800 mm. The known factors limiting its distribution are increase in aridity during the growing season, and severe or frequent winter frosts (Mauri et al. (2016)). Its distribution spans from places such as Pyrénées, Northern Italy, Eastern France, to the Swiss plateau and in south and Eastern Germany as well as in the Czech Republic and Austria (Tinner et al. (2013); Tinner and Ammann (2005)). There are not many plantations of fir outside its natural range, possibly due to higher number of insect infestations in monocultures (Dobrowolska et al. (2017); Klopčič et al. (2017)). It is mostly found in mixtures with Norway Spruce (*Picea abies*) or Scots pine (*Pinus sylvestris*) in higher altitudes, and with Beech (*Fagus sylvatica*) at lower altitudes. It is a highly shade tolerant species and can remain under canopies of larger, older trees for years (Čater and Diaci (2017); Ficko et al. (2016)).

An essential feature of fir is its relatively higher resistance against wind, snow and ice storms than Norway spruce, which increases forest stand mechanical stability (Nagel and Diaci (2006)). However, it has many potential threats due to warming climate and ever increasing human activity (Thurm et al. (2018); Klopčič et al. (2017); Elling et al. (2009)). Fir can be susceptible to frosts, fires, insects, fungi, and most importantly, SO₂ pollution. (Dobrovolny (2016)).

There is an ongoing debate whether the species will shrink or expand in response to global warming. For example, Ruosch et al. (2016); Gazol et al. (2015) suggest a range shift of fir towards higher altitudes and latitudes, and Dobrowolska and Bolibok (2019) predicts a range shrinkage in future climate change scenarios. While paleo-ecological evidence reveals the ability of fir to survive in much warmer and drier climates than its current ranges (Tinner et al. (2013)), the potential of fir to survive in these conditions, in

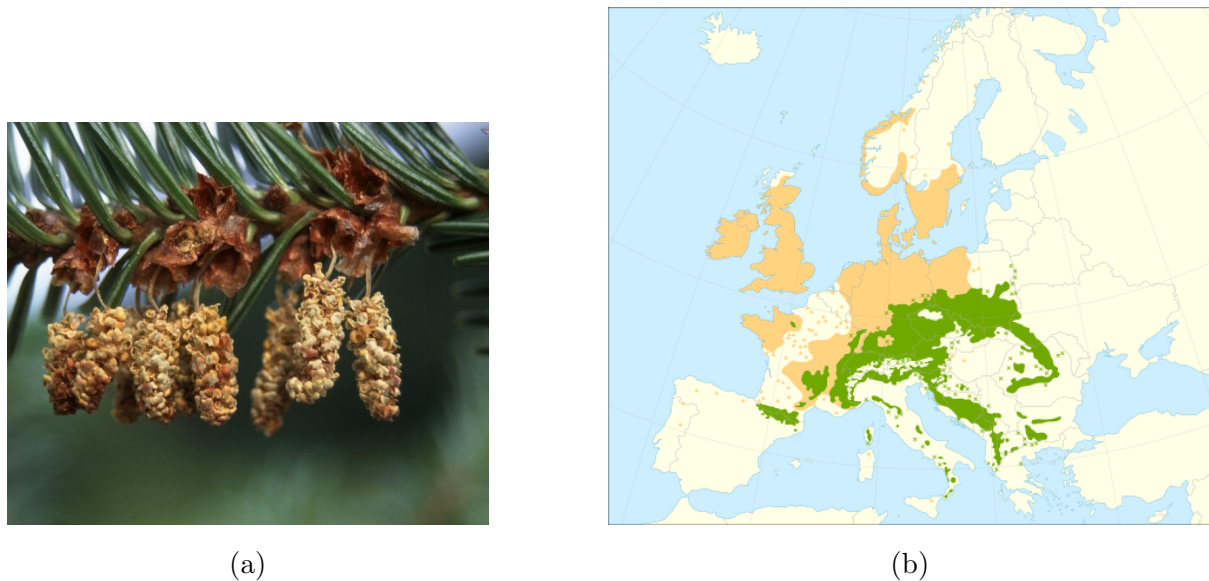


Figure 2.9: The image on the left side (a) is a representative image of branches of a silver fir (*Abies alba*) tree, with cones hanging on the branches, and on the right side, (b) is a distribution map of *Abies alba* in Europe. The green part depicts its natural range and isolated populations, whereas orange part depicts its introduced and naturalized (synanthropic) area and isolated population (taken from EUFORGEN).

the presence of human interventions and other disturbances, and take its realised niche closer to its fundamental niche, is uncertain. Apart from warming, fir is at a high risk from browsing by herbivores, being the most heavily browsed commercially important species in Europe. There is ample evidence of reduced silver fir regeneration and heavy damages to seedlings by ungulates (Nagel et al. (2014); Heuze et al. (2005); Senn and Suter (2003)). Even if there is an agreement on the higher climate resistance of fir compared to Norway spruce and European beech, the exceptionally high threat of ungulate herbivory to fir may compensate this higher fitness (Bernard et al. (2017); Heuze et al. (2005); Senn and Suter (2003)).

2.4.3 European beech (*Fagus sylvatica*)

European beech is one of the most widespread broad-leaved, deciduous species in Europe, spreading from Sicily to south Norway (figure 2.10b). In the southern part of its range in Sicily, it is found at altitudes more than 1000 m as high as 2000 m, but in higher latitudes, it can also be found as low as sea levels (Packham et al. (2012); Fang and Lechowicz (2006)). It can reach up to 30-50 m in height and can typically live 150-300 years.

Beech is a resilient species, tolerating very shady situations (it is the most shade-tolerant broad-leaved tree in its range), so that natural regeneration is possible in silvicultural systems with continuous crown coverage as the seedlings are able to survive and grow below the canopy of established trees (Žemaitis et al. (2019); Ligot et al. (2013); Wagner et al. (2010)). It can grow in most soil conditions, but cannot tolerate sites that are regularly waterlogged, as it prefers well drained soil (Diaci et al. (2020); Hammond and Pokorný (2020); Madsen et al. (1997)).

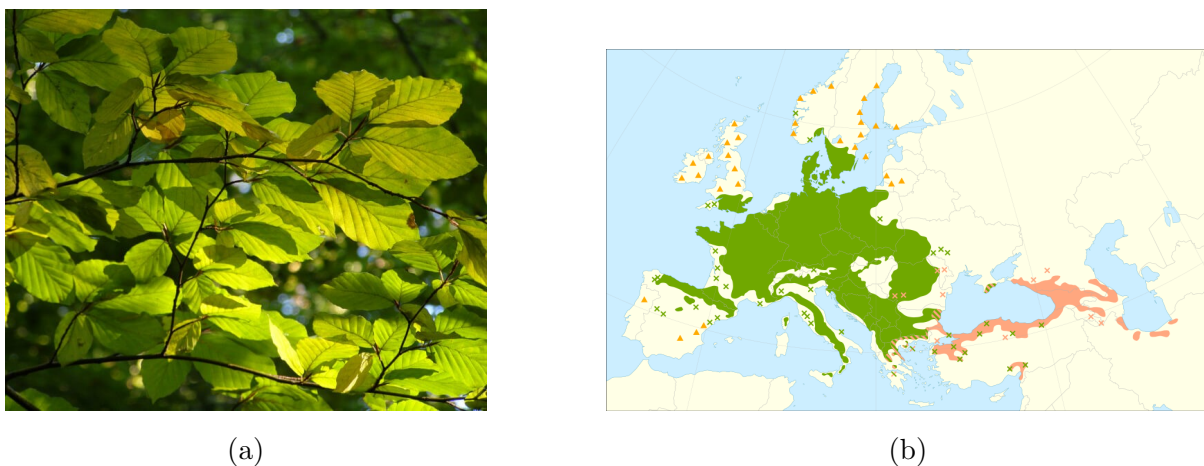


Figure 2.10: The image on the left side (a) is a representative image of branches of a European beech (*Fagus sylvatica*) tree, with cones hanging on the branches, and on the right side, (b) is a distribution map of *Fagus sylvatica* in Europe. The green part depicts its natural range and isolated populations, whereas orange part depicts its introduced and naturalized (synanthropic) area and isolated population (taken from EUFORGEN).

Even though fairly tough, beech has some threats owing to the environment around them. Spring frosts can cause major damages to young trees or flowers during the growing period (Rigo et al. (2016)). Beech is fairly resistant to browsing, and not the most preferred palatable species for deer, among broad-leaved or conifer species. However, in areas with high ungulate population, deer often choose the younger saplings to consume (Fuchs et al. (2021); Parobeková et al. (2018)). Beech trees can be attacked by various root rotting fungi such as *Genoderma applanatum*, other insect pests such as *Phytophthora ramorm*, large pine weevil (*Hyllobius abietis*) (Brunet et al. (2010)). In lower altitudes, there are reports of beech showing high temperature and drought sensitivity (Dulamsuren et al. (2017); Kramer et al. (2010); Jump et al. (2007)), but higher forests in the mountains do not show any strong limitations for beech, whereas, increasing growth and recruitment

rates (Dulamsuren et al. (2017)). This indicates a possibility of range expansion of beech towards higher altitudes.

2.4.4 Co-existence of spruce-fir-beech in mixed uneven-aged forests

Spruce, fir and beech have overlapping geographical niches, as they all occupy mountain forests between the altitude of 400-1600 masl, and often co-exist with each other. However, there is a definite niche partitioning at the level of microsite that allows them to survive in the same stands (Diaci et al. (2020)). This is done through exploitation of resources across space and time. For example, spatial separation is done by having different root lengths. Beech exploits deeper soil horizons than spruce (Jaloviar et al. (2018)). Each of them requires a species specific set of nutrients. Additionally, there is also a temporal or seasonal distinction, as conifers like spruce and fir may assimilate when beech is leafless (Hilmers et al. (2020)). The light tolerances of spruce-fir and beech are also different, allowing them to establish at different locations within the stand.

Few decades ago, many of these mixed forests were very often natural forests with spruce as the dominant species, and this dominance was promoted by forest managers due to the economic importance of spruce. However, the advantages of having mixtures in forests have led to conversion of the majority of these forests to mixed uneven-aged stands (Felton et al. (2010)) through management initiatives (Jaloviar et al. (2018); Mina et al. (2018); Dobrovolny (2016); Pretzsch et al. (2014)). Recently, however, the sensitivities of the three species to changing climate and various disturbances has created unstable forest structures, changing relative species compositions, with threats of range shifts and change in forest structures (Ehbrecht et al. (2021); Allen et al. (2010); Dale et al. (2000)). There are adaptive management techniques underway to prevent the domination of any one species in these mixtures (Bolte et al. (2009)), and more in depth studies about the behaviours of different species in climate change scenarios is necessary.

2.5 Environmental drivers of regeneration in spruce-fir-beech mixed forests

The process of forest regeneration is typically divided into five steps: seed production, seed dispersal, germination, seedling establishment, sapling growth and mortality (until

the sapling reaches the tree recruitment stage)(Dey et al. (2019)). Each of these steps has certain environmental filters (discussed in section 2.1.3) that determine if a species can establish and survive in a particular site, and the fulfillment of these filters allows a species to define its niche (discussed in section 2.1.4). In the same way, these filters also enable removal of individuals or species that are unable to persist.

The reproductive strategy of forest trees is to usually invest in a large amount of seed production with low survival probability (van der Maarel and Franklin (2005)). The number of fruits and seeds produced and dispersed by trees are generally very high, but their probability of successfully turning into a young adult tree is dependent on many stochastic (eg. climate, disturbances) and deterministic (eg. competition, niche) factors. Hence, it is necessary to identify the main factors responsible for successful passing of each step of regeneration, in order to determine appropriate forest management practices after accommodating any constraints (Dey et al. (2019)).

2.5.1 Seed production and dispersal

Seed production and dispersal are key processes in community dynamics, as their spatial and temporal distributions lay the template for subsequent processes (Larson and Funk (2016); de Andrés et al. (2014); Amm et al. (2012); Koniak and Noy-Meir (2009)). Seed production is presumably related to species, age, size and vigor of the parent tree, whereas dispersal and germination of seeds are largely stochastic rather than deterministic processes (Price et al. (2001)).

In many tree species, there is an inter-annual variability in seed production rates among individuals and populations. This phenomenon is called "mast seeding", and is observed in many species in boreal, temperate as well as tropical ecosystems, including spruce (Zamorano et al. (2018)), fir (de Andrés et al. (2014)) and beech (Bogdziewicz et al. (2021)). High temperatures promote large scale flowering in spruce, fir and beech, indicating an advantage to seed production in warmer climates. But this effect is more pronounced with a cool summer followed by a warmer one, and not well studied in cases of constant increase in summer temperatures (Bogdziewicz et al. (2021)). Mastling years are typically synchronized between individuals of a species, but not always between species, nor can be predicted more than a few months in advance (Pesendorfer et al. (2020)). Hence, it is a major constraint for forest managers planning the stand's regeneration phase, which requires several years of preparation (Millar et al. (2015)).

Dispersal of seeds of a tree occurs either biotically (animal mediated) (Monson (2014); Schurr et al. (2012)) or abiotically (wind, gravity mediated) (Löff et al. (2018); Dobrowski et al. (2015)), and can occur over short (under the canopy of mother tree) or long distances (dispersal by birds upto 16 km) (Van Der Putten (2012)). Spruce, fir and beech are largely dispersed by wind. Beech has relatively heavier seeds than spruce and fir, and can be often found in the vicinity of a few meters from the mother tree, whereas spruce seeds have been found to travel the farthest distances with wind (Paluch et al. (2019)).

2.5.2 Seedling germination

Germination and establishment of a seedling is the transition from a seed lying on the ground to a germinated seedling. This phase is highly dependent on favorable "seedbeds" created through microsite conditions of varying dimensions and properties (Hunziker and Brang (2005)). Environmental conditions during the establishment of seedlings do not determine just the number of seedlings germinated, but also their size (Moser et al. (2017)). Small seeded and light demanding trees such as Norway spruce prefer soil humidity, and the presence of decomposing coarse woody debris for its establishment, as it is nutrient rich, allows good seed interception and retention (Diaci et al. (2020)) (see figure 2.11). Fir and beech do not have very specific microsite requirements like spruce, and can well establish on any substrate, provided that forest floor plant competition is not too high, but do better on debris than on forest floors. However, spruce has the best survival rates after growing on debris, with most number of older and taller seedlings, indicating high growth rates (Orman and Szewczyk (2015)). However, other topographical factors such as elevation, or climatic factors like temperature and soil moisture availability also play a major role in determining seedling establishment by limiting growth abilities of seedlings (Moser et al. (2017); Orman and Szewczyk (2015); Jump et al. (2007)).

2.5.3 Sapling growth and survival

Figure 1.3 describes the variables that affect different phases of the forest succession cycle, and many of them are known to drive regeneration growth and survival of saplings. Factors influencing regeneration can be divided into several categories such as light availability and related microsite partitioning, soil characteristics, competition with understory, topographical characteristics, climatic conditions, browsing etc.



Figure 2.11: Picture of a spruce sapling established on the stump of a harvested tree. Spruce prefers micro-sites such as shaded deadwood and stumps to establish its seedlings. Picture credits: Mithila Unkule

Light, in the form of direct or diffused light, or in the form of canopy openness, is an unavoidable factor that affects sapling growth. Even though sapling germination does not require light availability, it is necessary for the growth and survival of the seedlings into older individuals. Among spruce, fir and beech, spruce is the most light tolerant species, and often outcompetes beech and fir growth in open gaps with lots of diffused light (Diaci et al. (2020)). It does not do very well in shady conditions, and hence fir and beech often surpass spruce sapling growth in dense stands with little understory light (Stancioiu and O'hara (2006)). However, saplings often have different requirements at different stages of its life (Kneeshaw et al. (2006)). For example, smaller beech and fir seedlings grow better in lower light or diffused light conditions, but prefer larger gaps and more light for faster growth later in stages of tall saplings (Orman et al. (2021)). Precipitation, or water availability in the form of soil moisture as well as air humidity play a major role in growth and survival of regeneration of all three species, as does

the air temperature. The two factors are often linked, and have a synergetic effect on sapling growth and survival, and are combined to formulate different indices such as climatic water balance, soil water balance, or evapotranspiration (Ehbrecht et al. (2021)).

Beech regeneration occurrence and growth positively correlates to increased soil and air moisture, and it thrives in high water conditions. It can also survive well in warmer and drier environments than spruce and beech (Fang and Lechowicz (2006)). However, fir may have the potential to outcompete beech under warmer climatic conditions if the amount of rainfall is sufficient and there is no soil water deficit (Vitasse et al. (2019); Lebourgeois et al. (2010)). Spruce saplings display drought sensitivity as well (Helenius et al. (2002)), though less than beech regeneration (Diaci et al. (2020)), but do not prefer waterlogged sites. Nevertheless, it has been discovered that these relative sensitivities depend to a large extent on the site specific topographical conditions such as elevation, aspect, slope and site productivity (Collins and Carson (2004)).

The growth and survival of all three species is hindered by competition with other tree saplings, understory species, herbs, grasses etc., as they compete for nutrients and light (Thrippleton et al. (2016)), and is higher in larger gaps (Walters et al. (2016)). Spruce seedlings are generally smaller and slower in growth compared to beech in the presence of other understory vegetation; therefore, regeneration studies often reported their great sensitivity to herb competition (Hunziker and Brang (2005)).

Another crucial factor affecting the growth of regenerated saplings is ungulate browsing. Among the three species, fir is known to be the most browsed, and has reduced growth and densities in regions of high browsing (Bernard et al. (2017); Klopčič et al. (2017); Heuze et al. (2005); Senn and Suter (2003)). Factors that inhibit regeneration often act in synergy and may completely halt gradual conversion; however, with appropriate silvicultural measures, many difficulties can be reduced (Diaci et al. (2020)).

2.6 Computational approaches to understand regeneration

2.6.1 Modelling regeneration

Regeneration in a forest is dependent on a web of complex variables, with multiple demographic processes, and each process depending on potentially different variables. Sometimes, the questions that need to be answered, in order to understand the functioning of regeneration processes, remain beyond the scope of observational or experimental studies due to lack of data, or too many explanatory variables, or a short time scale (Sutherland et al. (2013)). In such situations, it is possible to use computational resources to formulate mechanistic or empirical models that synthesize the data collected, allowing us to address complex patterns and processes (Spiegelberger et al. (2012)). As trees are long-lived organisms, and the growth of regeneration is a long process, the need for regeneration models remains pronounced. In the process of forest dynamics, the understanding of the growth and mortality of overstory trees is well studied experimentally as well as through simulation models (Bianchi et al. (2021); Bugmann et al. (2019); Vanderwel et al. (2013); Diaci et al. (2011); Helenius et al. (2002)). Forest dynamics models are loosely divided into species distribution models (SDMs), individual based models (IDMs) and dynamic global vegetation models (DGVMs), and each of them model different aspects of forests, with different goals (Maréchaux et al. (2021)). Most of the large forest dynamics models simulate many processes, and can sometimes include regeneration as a sub-model (Fisher et al, 2018). However, among many other factors, reducing recruitment rates of adult trees has created a need to understand regeneration processes, and the drivers and limiters for a seed to reach adult stage (Bugmann et al. (2019); Dobrowski et al. (2015)). Literature about regeneration models, with information about the processes involved in transition from sapling establishment to a mature tree remains limited (Vacchiano et al. (2018)). Indeed, modelling this entire process would involve the processes of seed production and dispersal, germination, sapling establishment, growth, mortality rates, until it grows to become a tree. Not just that, it will be crucial to include different biotic and abiotic factors driving or limiting each of these processes. For example, seed production and dispersal are lined to the species, overstory tree densities and species, soil nutrients, as well as climatic factors. Germination of seeds and their establishment are more stochastic processes. And these are just a few of the many processes to be modelled.

There are multiple approaches to model regeneration, such as mechanistic models that simulate different processes, gap models, statistical models that can either work on a stand or size class scale, or base it on individuals, as well as non-parametric models (Miina et al. (2006)). The data acquired for these models either comes from controlled regeneration experiments (in which case it is not spatially or temporally representative), collection of regeneration data as part of a routine forest inventory (in which case it is not very accurate) or specific regeneration surveys (which require time and resources) (Miina et al. (2006)). Each of them have their own advantages and caveats, and usually a mix of multiple model types is used to produce a more comprehensive model, depending on the resources and data availability (Price et al. (2001)).

An example of using experimental plots to determine regeneration was done on Norway spruce by (Weisberg et al. (2005)). Another similar attempt was on European beech by (Axer et al. (2021)), and they managed to predict the occurrence and density of beech regeneration to a high level of precision, but could not predict processes such as dispersal. However, in both mentioned studies, due to small temporal and spatial scale respectively, it was not possible to generalize the results to larger scales. Another example displays the potential of the use of a forest inventory. The National Forest Inventory (NFI) dataset of France contains country-wide information about various forest variables, including regeneration. However, in such inventories, it is often difficult to determine factors such as earlier stand treatment, origin of seedlings, previous disturbances or history of the site. The regeneration dataset in the French NFI is limited to visual regeneration cover, with no real "measurements" of sapling densities, heights or growth. Borderieux et al. (2021) modelled regeneration of *Quercus petraea* by using this dataset, but were unable to model individual processes that explain detailed mechanisms of *Quercus* presence in mixed stands. However, having big, nationwide datasets is very valuable in determining large scale spatial and temporal patterns as shown by (Pettersson et al. (2019); van Oijen et al. (2013); Piedallu et al. (2011)).

Some examples of models that use specific regeneration surveys to model regeneration are Samsara2 (Courbaud et al. (2015)), represented in figure 2.12a and RReshar (Balandier et al. (2020)) represented in figure 2.12b. They are individual based, spatially explicit models that simulate regeneration to generate future forest structure projections based on resource availability (light, competition from understory vegetation) and silvicultural practices carried out in the stand (only Samsara). However, as they rely on

specific input variables, it becomes necessary to design and execute surveys which can be time and resource consuming.

Predictive regeneration models are certainly very time and energy efficient in order to provide information about the future that cannot be obtained easily from observational or experimental methods.

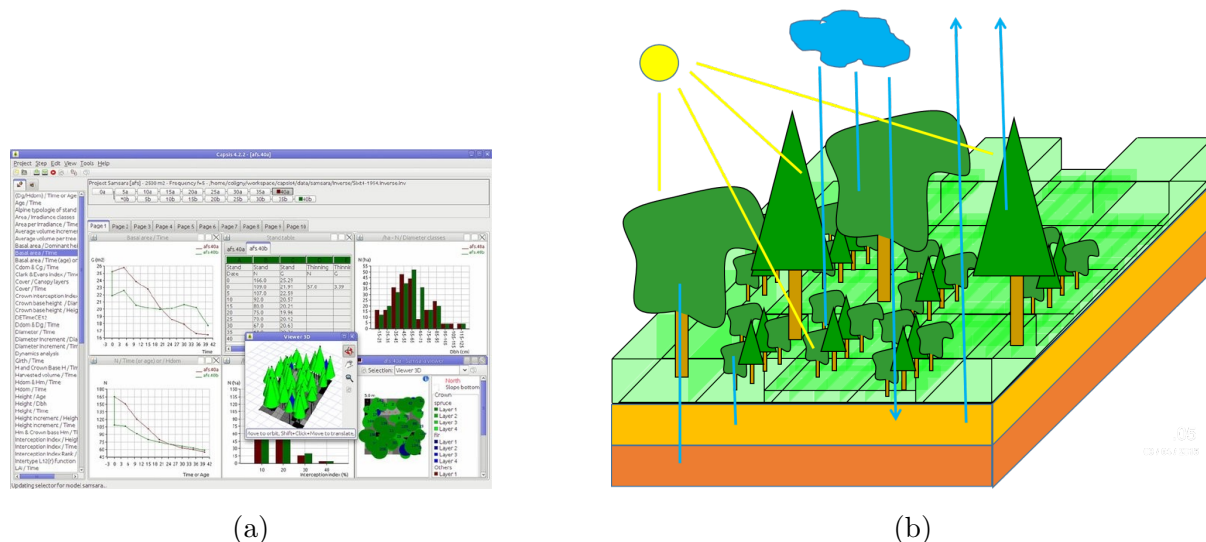


Figure 2.12: The image on the left side (a) is a representative image the model Samsara in the graphical interface of the software Capsis, illustrating the result of different silvicultural measures in stand structure and composition (b) shows a representative diagram describing RReShar, in which regeneration depends on light, water demand and competition with understory vegetation.

2.6.2 Approximate Bayesian Computation (ABC)

Approximate Bayesian Computation (ABC) is a likelihood-free Bayesian method used to perform statistical inferences with Bayesian models that have intractable likelihood functions (Karabatsos and Leisen (2018)). It was first introduced by (Tavare et al. (1997)), and (Pritchard et al. (1999)), and then modified by (Beaumont et al. (2002)), to use in the field of genetics. Since, then, it has been used in very diverse fields, most commonly in various sub-fields of biology, medicine, but also in economics and finance (Karabatsos and Leisen (2018)). It is an emerging method in ecology and evolutionary studies (Beaumont (2010)).

ABC is based on the rejection algorithm, a simple technique to generate samples from probability distribution. This algorithm consists of simulating a large number of datasets under a hypothesized scenario. The parameters of the scenario are not chosen deterministically, but from a probability distribution. The generated data is then reduced to calculated summary statistics, which are variables that effectively represent the sampled dataset. The model is then run for a large number of iterations, and the simulated summary statistics that are closest to the observed values are chosen. The "distance" to be tolerated between observations vs. simulations is provided by the modeler, and the given number of closest simulations are selected. The parameter values corresponding to the selected subset of simulations are the posterior parameter values (Bertorelle et al. (2010); Csilléry et al. (2010)). The method is explained graphically in figure 2.13, as first displayed by Sunnåker et al. (2013).

This method is suitable for modelling complex processes, and specially phenomena where data collection for each process is difficult to obtain. It is a promising method in estimating regeneration parameters here, as it is difficult to measure variables for processes such as seed germination, establishment of saplings, survival of saplings, to name a few.

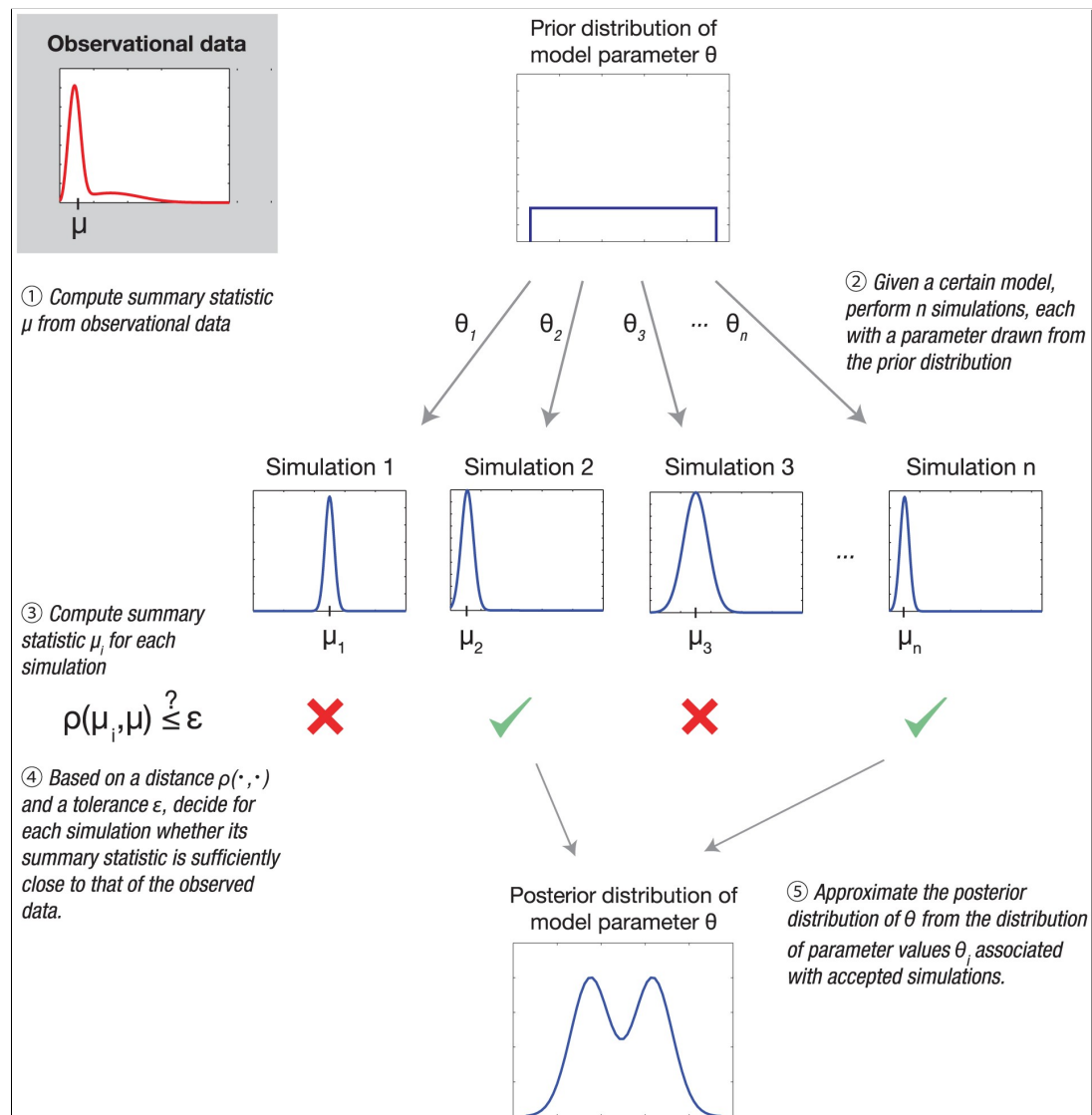


Figure 2.13: A conceptual overview of parameter estimation using Approximate Bayesian Computation (ABC), adapted from [Sunnåker et al. \(2013\)](#).

2.7 Scientific hypotheses

In previous sections of chapter 2, I introduced various theories and concepts based on knowledge gaps in regeneration studies, and questions to be answered. On the basis of this theoretical approach and understanding of the different knowledge gaps mentioned in chapter 1, I will address the following general hypothesis in this thesis:

1. Climate change negatively affects the regeneration rates in spruce-fir-beech forests. An increase in temperature followed by decrease in precipitation will impair one or more of regeneration demographic processes (seedling establishment, growth and

survival). Thus, I anticipate an overall reduction in regeneration densities of spruce, fir and beech in the French Alps and Jura mountains.

2. Light, temperature, water demand, soil water and nutrient conditions will impact growth and survival of saplings, and will differ between species. More shade tolerant species such as beech and fir will be more prone to survive in lower light access than light demanding species like spruce. More water demanding species, such as spruce, will be more sensitive to climate change effects, due to the increase and duration of drought events. Increasing ungulate browsing will also significantly decrease sapling growth and survival rates, especially that of fir. The magnitudes of these effects are expected to be species specific, which will in turn change relative regeneration densities of spruce, fir and beech. These species will adapt and change in response to these new environmental conditions, which could lead to a shift in species composition of future forest stands.
3. Sufficient regeneration flux is necessary for renewal of a forest after harvesting. Current forest management strategies focus on maintaining mixtures and biodiversity of the stand, but lack quantitative estimates of harvest: renewal ratio, which will ensure replenishing the harvested volume of wood. In the context of multiple detrimental environmental factors like climate and ungulate browsing reducing regeneration, I predict insufficient tree recruitment rates in the absence of any change in forest management interventions adapted to climate change.

CHAPTER 3

Climate and ungulate browsing impair
regeneration dynamics in spruce-fir-beech
forests in the French Alps

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3.1 Abstract

Key message: Different components of water balance and temperature reduce density and height growth of saplings of *Picea abies* (L.) H. Karst (Norway spruce), *Abies alba* Mill. (silver fir) and *Fagus sylvatica* L. (European beech) in mixed uneven aged forests in the French Alps and Jura mountains. Ungulate browsing is an additional pressure on fir and beech that could jeopardise the renewal of these species in the future.

Context: The uncertainty in tree recruitment rates raises questions about the factors affecting regeneration processes in forests. Factors such as climate, light, competition, ungulate browsing pressure may play an important role in determining regeneration, forest structures, and thus future forest composition.

Aims: The objective of this study was to quantify sapling densities and height increments of spruce, fir and beech, and to identify dominant environmental variables influencing them in mixed uneven aged forests in the French Alps and Jura mountains.

Methods: Sapling height increment and density were recorded in 152 plots and non linear mixed models were obtained to establish relations between them and environmental factors known to affect regeneration, namely altitude, slope, aspect, canopy openness, soil characteristics, temperature, precipitation and ungulate browsing.

Results: Regeneration density, varying from 0 to 7 saplings per m^2 , decreased with sapling height and was also negatively affected for spruce by PET, but positively for fir by precipitation and for beech by mean annual soil water content. Height increment

reached up to 50 cm annually, increasing with sapling height, canopy openness, and decreasing under high maximum summer temperatures for spruce and beech. The statistical effect of different environmental variables varied slightly among species but trends were quite similar. Additionally, ungulate browsing was high, with fir being the most intensely browsed, followed closely by beech, while spruce was rarely browsed.

Conclusions: All these results suggest that more temperature warming and a decrease in water availability could negatively impact sapling growth and density in the three species, with possible reduction of forest renewal fluxes. The observed increase of ungulate populations leading to increased browsing could be particularly detrimental to fir saplings.

3.2 Introduction

Mixed uneven aged forests of spruce, fir and beech occupy extensive areas in Europe (Brus et al. (2011)), specially in the French Alps (Toigo et al. (2015)). Their presence throughout Europe, in such wide environmental conditions, make them a target of rapidly changing climatic extremes such as increasing frequencies and intensities of droughts (Cailleret et al. (2014); Diaci et al. (2020)) and ever increasing summer temperatures (Schurman et al. (2019); Lombaerde et al. (2020)). The last few decades have also witnessed increasing number of wild ungulates in the Alps, which also puts plants in these forests at a higher risk of being browsed (Heuze et al. (2005); Nagel et al. (2014); Bernard et al. (2017)). Different studies have highlighted changes in plant demography (Gray and Brady (2016)), inconsistent demographic responses to climate at species range edges (Kunstler et al. (2020)), limitation of regeneration and tree recruitment (Silva et al. (2012); Dey et al. (2019); Löf et al. (2019)), stressing a potential risk of reduced forest regeneration. For a species to maintain its range, regeneration must compensate mortality and harvesting in a climate warming context. Several articles document and predict increasing frequency of mortality events because of changing climate (Bodin and Wiman (2007); Allen et al. (2010); Manso et al. (2015)). Natural regeneration in many forests is especially variable and already low (Dey et al. (2019)). If regeneration reduces while mortality increases with climate change, even if harvesting events remain constant, this could jeopardise forest renewal. A diminution of regeneration because of global changes could therefore have a major impact on species distributions and their persistence.

In mountain forests, regeneration processes are especially slow and scarce. Regeneration has often been stressed as a limiting process in mountain forest dynamics (Kräuchi et al. (2000)). To better understand and anticipate degraded regeneration dynamics and potential species resilience or adaptability, it is necessary to identify key drivers of regeneration demographic processes. These include processes such as seed production, germination, and seedling growth, mortality and survival, upto the stage of tree recruitment. Our objective in this study was to quantify sapling densities and height growths of spruce, fir and beech in mountain forests and to identify key environmental factors influencing them. Studies such as Balandier et al. (2006b); Diaci et al. (2020) have shown the role of many different factors in these processes. Stands of spruce, fir and beech are known to largely depend on light availability for their regeneration growths (Dyderski et al. (2018); Diaci et al. (2020); Lombaerde et al. (2020); Gaudio et al. (2017)). The role of soil nutrients and water availability in facilitating regeneration is also well studied (Madsen et al. (1997); Dyderski et al. (2018)). Besides, regeneration depends on a large scale on inter and intra specific competitors. However, the species identity and cover determine if plants can act as facilitators or competition to certain species (Balandier et al. (2006b); Collet and Chenost (2006); Laurent et al. (2017); Thrippleton et al. (2017)). Disturbances such as fires (Dey et al. (2018)), frost (Defosseze et al. (2016)), insect infestations (Dobrovolny (2016)) also affect regeneration processes. In spite of this knowledge, accurate estimation of regeneration demographic rates and precise identification of the effects of climate and other environmental factors on regeneration in mountain forests is difficult. This could be because saplings are scattered in space with high variability among sites, environmental factors could be highly inter-correlated, and saplings are difficult to monitor over successive years because of their small size and low survival rates. We tried to overpass some of these difficulties by analysing sapling densities and height increments by sampling a large environmental gradient in the French Alps and Jura mountains.

In this study, we address the following questions related to the regeneration of spruce, fir and beech in mixed uneven-aged forests:

1. Studies have observed and predicted high variability as well as decreasing regeneration densities and height increments. What are the magnitudes of sapling height increments and densities in the French Alps and Jura mountains?
2. Many factors such as light, temperature, soil conditions and water availability, presence of ungulates are known to affect regeneration. What are the key drivers of sapling height increments and densities of spruce, fir and beech?

We also discuss if there a risk to the current species distribution and forest structures because of regeneration shortage and unreliability.

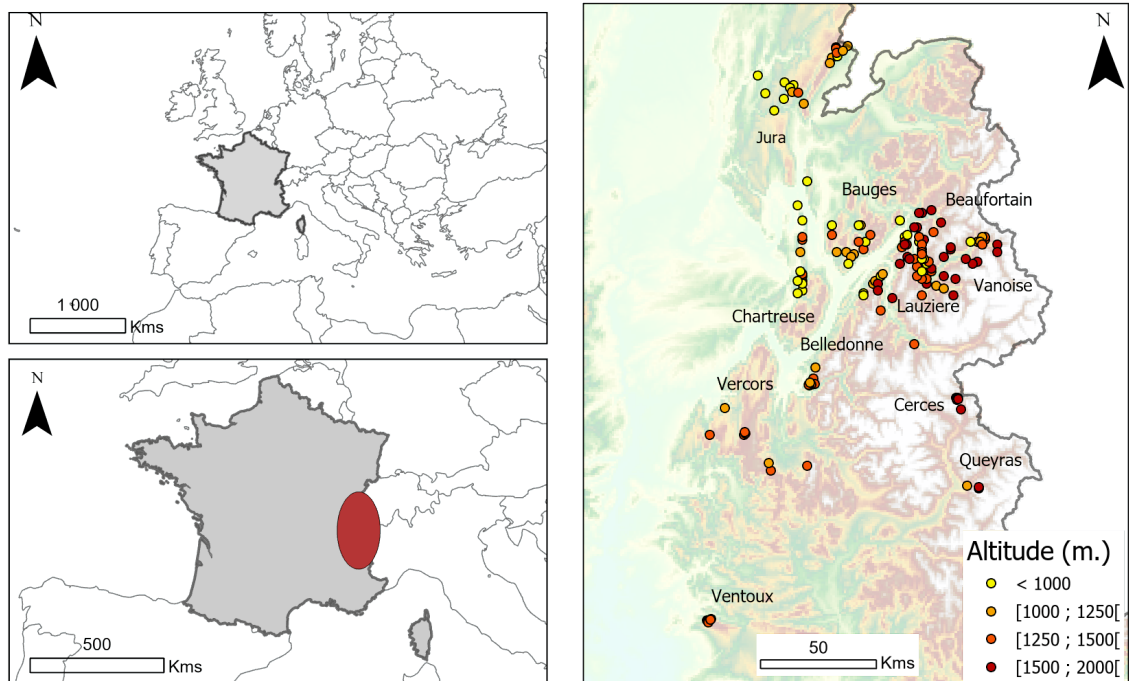


Figure 3.1: Locations of sampled plots and mountain ranges in the French Alps and Jura mountains, with each point representing a sampled plot, and colours of points representing altitude gradients

Mountain range	Altitude (masl)				Summer temp (°C)				Tot. BA (per Ha)				No. of plots
	<i>Min.</i>	<i>Mean</i>	<i>Max.</i>	<i>SD</i>	<i>Min.</i>	<i>Mean</i>	<i>Max.</i>	<i>SD</i>	<i>Min.</i>	<i>Mean</i>	<i>Max.</i>	<i>SD</i>	
Bauges	806	1137	1439	203	9.7	11.8	14.1	1.3	14.8	34.8	50.7	10.2	13
Beaufortain	741	1390	1769	296	8.4	11.0	15.1	1.9	14.1	33.8	64.5	13.3	25
Belledonne	936	1271	1619	208	8.8	11.3	13.1	1.3	19.9	37.9	97.1	16.9	19
Cerces	1303	1666	1765	150	10.1	10.9	11.7	0.5	23.1	36.7	59.3	11.4	8
Chartreuse	515	937	1380	313	9.8	12.7	15.7	2.1	13.4	23.6	36.4	7.7	14
Jura	544	1035	1444	249	9.4	12.0	15.2	1.6	17.8	54.4	133.3	33.5	18
Lauziere	660	1341	1679	298	8.6	11.0	15.4	2.0	12.1	39.6	78.2	19.2	18
Queyras	1029	1512	1774	419	11.3	13.1	16.4	2.8	20.4	23.7	29.7	5.2	3
Vanoise	1001	1448	1796	271	8.9	11.6	14.9	1.8	10.7	33.6	57.8	13.1	16
Ventoux	1010	1219	1357	116	11.3	12.2	13.6	0.7	28.6	36.1	46.3	5.6	9
Vercors	1136	1357	1495	140	10.1	11.1	13.0	1.0	20.4	35.4	73.9	15.7	9

Table 3.1: Site wise distribution of sampled plots, with distributions of altitude, temperature and plot basal area covered.

3.3 Materials and methods

3.3.1 Field sampling

3.3.1.1 Study sites and plot sampling strategies

The study was carried out in the French Alps (44.17°N, 5.23°E to 46.39°N, 6.90°E) in mixed uneven-aged mountain forest stands, with at least one out of spruce (*Picea abies* (L.) H. Karst), fir (*Abies alba* Mill.) and beech (*Fagus sylvatica* L.) as dominant species. Sampled plots were distributed over 11 mountain ranges, to cover a wide range of climates, elevations, and site conditions (fig. 3.1, table 3.1). The sampling locations were determined based on existing networks of permanent plots established by the Office National des Forêts (ONF), France and INRAE, with information of the species tree basal area on the plots. The plots in these networks were first categorized into 24 classes, and then subsets taken to cover various stand structures and environmental conditions in the sampling. The categorisation was based on the following variables:

1. total basal area (BA) of adult trees on the plot (2 classes: higher and lower than the mean of all plots),
2. mean annual air temperature (T°C) of the plot (2 classes: higher and lower than the mean of all plots),
3. annual mean of monthly precipitation (mm) on the plot (2 classes: higher and lower than the mean of all plots),
4. identity of the dominant species on the plot (spruce, fir or beech).

Thus, we covered a wide range of stand structures, tree densities and compositions (BA of the different species as a proxy) for the different climates encountered in the area, including the distribution edges of the species (temperature and precipitation as a proxy). Thus, 24 categories were formed, and up to five plots were chosen by random selection from each category. A total of 152 plots were sampled across all mountain ranges. The observations described in the following sections were carried out by the authors. All data is available here: [Unkule et al. \(2021\)](#).

3.3.1.2 Assessing stand structure

In order to characterize stand structure and composition, two concentric circular plots of radii 10 m and 15 m were marked from the center, to measure the tree basal area (BA) for each species. Diameter at breast height (DBH) of all adult trees above 7.5 cm and 17.5 diameter were measured in the 10 m and 15 m radius circle respectively, using a tape or a caliper, and the species identity noted. This information was used to calculate tree BA per hectare and per species for the plot.

3.3.1.3 Assessing sapling growth, density and browsing rates

The Point Center Quadrat Method (PCQM) was used to estimate sapling density, with a maximum radius of 10 m ([Mitchell \(2015\)](#)). This method was selected after a survey of different regeneration sapling methods ([Brice Carnet \(2018\)](#)). A big advantage of this method is that it makes it possible to adjust the prospected area to sampling density and avoids empty plots due to small plot sizes.

The 10 m radius circular plot was divided into four quadrants, with boundaries in the north, east, south and west directions. Saplings were divided into 4 height classes: 10-50 cm (H1), 51-150 cm (H2), 151-300 cm (H3), and above 300 cm, but below DBH of 7.5 cm (H4). This division was made in order to evaluate, if any, an effect of the sapling height. Across 152 plots, we sampled 2370 individual saplings (plants between height 10 cm, and DBH < 7.5cm), 720 spruce, 891 fir and 759 beech.

In each quadrant (i), the sapling nearest to the plot center, of each species, and in each height class, was selected, and the following measures noted to the smallest count of 0.5 cm: sapling length when held straight (H), mean of annual shoot length increments for the past 3 consecutive years (ΔH), at least when it was possible, and distance (D_i) (in m) of sapling from the center of the plot (figure 3.2). The annual shoot increments were

determined by measuring the length between marks of two bud scars, which are known to be indicators of one growing season. Using this information, the density of saplings of each species and height class was computed as: $(1/((\sum D_i)/(N_0/N_Q))^2) \times CF$ where N_0 is the total number of quadrants (here 4) and N_Q is the number of vacant quadrants. CF is a correction factor obtained from a table developed by [Warde et al. \(1981\)](#) to take into account the presence of vacant quadrants. As the role of wild ungulates on sapling growth and survival is often highlighted, any physical damage to the terminal bud of a sapling was noted as an incident of browsing by an ungulate, in order to quantify the browsing rate for each plant species. The height increment of browsed saplings was considered zero.

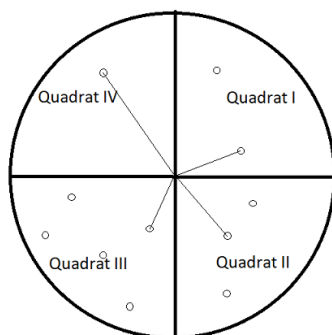


Figure 3.2: Representation of a PCQM plot used for estimating sapling densities: each dot represent the sapling nearest to the plot center in each quadrat, for each height class and species measured (maximum radius=10m)

3.3.1.4 Calculation of competition and browsing pressure indices

A competition index was calculated to quantify competition of spruce, fir or beech with other understory vegetation (all plants less than 150 cm height, either herbaceous or woody species). First, dominant understory plant species were identified. Their cover was estimated by a visual assessment of ground cover occupied by the vertical projection of their foliage onto the soil (GC). The different species were assigned scores (SC) according to their potentially negative competition effect on regenerated saplings. Very strong interfering species such as graminoids and dense ferns were ranked 3, less competitive species such as *Rubus* sp. 2, and tall shrubs and midstorey trees: 1, and other small forbs 0 (SC) ([Balandier et al. \(2006a\)](#)). A competition index was computed for each quadrant as: $\sum GC * SC$, which was then averaged for the plot. Additionally, an approximate percentage of browsed plants on the plot was noted (BP), and the browsing pressure

index was computed as: $(\sum GC * BP) / \sum GC$. These indices were calculated using approximate visual covers of the vegetation.

3.3.1.5 Evaluating canopy openness

Canopy openness (O) of a site influences stand micro-climate and light. In each quadrant, canopy openness was measured in the four cardinal directions at a distance of 4 m from the center, using a convex densiometer (Baudry et al. (2013)).

3.3.2 Laboratory analyses of soil samples

Within a 1 m radius around the plot center, a soil sample was collected, upto 20 cm depth (excluding litter and humus) using a soil auger. This sample was later used in the laboratory to estimate the C:N ratio and pH of the soil.

Soil samples were first air dried in the lab, and were then placed in aluminum trays in a ventilated oven at 40°C. After complete drying, they were manually sieved through a 2 mm mesh (Retsch steel analytical sieve, ISO 3310-1 standard). Next step was to fine grind them with a 0.25 mm mesh for carbon and nitrogen determination (using an ultra centrifugal mill ZM200 Retsch, stainless steel rotor 8 teeth). Carbon and nitrogen were detected on the 0.25 mm sample by a total combustion process, using an elemental analyzer by the company Vario Micro Cube, Elementar, whereas the pH determination was done on the 2 mm sieved samples using a SevenExcellence pH meter from Metler-Toledo, InLab Solids Pro-ISM electrode.

3.3.3 Soil and climate data extracted from digital maps

To complement data from field surveys, soil and climate information was extracted, described during the period from 1985-2010 for each plot, using digital maps belonging to the Digitalis database by Laboratory SILVA, Université de Lorraine-AgroParisTech-INRA (<https://silvae.agroparistech.fr/home/>). Monthly solar radiation calculated using the Helios model (Piedallu and Gégout (2007)), minimum and maximum temperatures modelled and mapped using Meteo France weather stations and Potential EvapoTranspiration (PET) calculated with Turc formula (Turc (1961); Piedallu et al. (2016)) were used to represent available energy.

Precipitation (Prec) and climatic water balance (CWB, Prec minus PET) were used to estimate available water for plants from climatic data. Soil water balance

Category	Variable	Min	Mean	Max	SD
Climate	Mean monthly prec(mm) - Prec	65.67	118.26	190.79	24.07
Climate	Max monthly temp(°C)	8.41	11.56	16.39	1.71
Climate	Mean monthly PET(mm) - PET	31.35	47.27	69.90	6.78
Climate	Max summer temp(°C)	13.76	16.78	20.89	1.70
Climate	Min winter temp(°C)	-7.71	-4.74	-0.96	1.37
Competition	Browsing Index	0.00	12.99	100.00	22.01
Competition	Competition index	0.00	49.54	212.50	53.16
Competition	Spruce browsing rate (0-1)	0.00	0.03	0.21	0.06
Competition	Fir browsing rate (0-1)	0.00	0.15	0.70	0.16
Competition	Beech browsing rate (0-1)	0.00	0.11	0.63	0.16
Soil	Soil water content(mm) - SWC	7.04	107.86	254.15	62.17
Soil	Soil water deficit(mm) - SWD	0.00	12.62	164.97	23.29
Soil	Soil water holding capacity(mm) - SWHC	13.08	46.89	85.83	16.46
Soil	Soil pH	3.95	5.89	8.48	1.30
Soil	Soil C:N	7.64	16.87	42.38	5.42
Stand structure	Canopy openness(%) - O	0.59	13.21	56.29	10.67
Stand structure	Total basal area(m^2 /ha)	10.72	36.65	133.30	18.46
Stand structure	Spruce basal area(m^2 /ha)	0.00	13.40	66.89	13.32
Stand structure	Fir basal area(m^2 /ha)	0.00	12.72	107.07	16.09
Stand structure	Beech basal area(m^2 /ha)	0.00	6.49	64.28	9.62
Topography	Altitude(masl)	515.42	1275.03	1795.79	307.11
Topography	Slope(°)	0.00	26.40	56.00	10.84

Table 3.2: Distribution of important variable values sampled and evaluated in the models

distribution was also estimated, combining monthly climatic variables with Soil Water Holding Capacity maps (SWHC) using the Thornthwaite formula ([Thornthwaite and Mather \(1955\)](#)) with a Geographical Information System. This calculation provided the spatial distribution of mean annual values of Actual EvapoTranspiration (AET), Soil Water Content (SWC) and Soil Water Deficit (SWD) ([Piedallu et al. \(2013\)](#)).

The resolutions of all the digital maps was 50 m, except precipitation and SWHC, which had 1 km resolution. All climatic data were provided as monthly average of the 1985-2010 period, which were later also aggregated into seasonal and annual means.

3.3.4 Data analyses

All data analyses and models were calibrated separately for the three species, spruce, fir and beech, using R software version 3.6.0 and version 4.0.2 ([R Core Team \(2017\)](#)) and figures were produced using the package ggplot2 ([Wickham \(2009\)](#)). Two different

datasets were used for the analyses of densities and growth of saplings. For the density analyses, plot level data were used, with saplings densities for each species and height class pooled at the plot scale (n=152). For the analyses of growth of saplings, each data point consisted of information of a single individual sapling (n=2370). The final models determining annual height increment was formulated using the subset of unbrowsed saplings (n=2128), as the height increment of browsed saplings was assumed to be zero.

3.3.4.1 Analyses strategy

The variables potentially affecting sapling density and growths were grouped into categories described in section 3.3.1: sapling height, climate, soil, topography, competition and stand structure (table 3.2). A systematic approach was used to formulate multivariate non-linear mixed models, testing the progressive addition of variables from a new category. Preliminary exploration indicated that the variable influencing sapling densities and height increments the most was sapling height. We tested then, the addition of stand structure variables such as canopy openness, total and conspecific tree basal area. In the next step, we added climate and soil category variables to the earlier model, such as maximum summer temperature, minimum winter temperature, mean monthly precipitation, annual mean of monthly soil water content, soil water deficit, soil water holding capacity, its CN, pH. The last step was to test the addition of competition (competition index, browsing index), followed by topographical factors (slope, altitude, aspect). The order of these steps was chosen based on the importance of these variables derived from literature, and considering increasing pressure of climate change. When a variable from one category was selected, other variables from the same category were systematically avoided to prevent correlated variables being present in the same model (except topographical factors). The function "nlme" from the R package "nlme" (Pinheiro et al. (2021)) was used to run these models. Evaluation of the models was done by comparing graphical predictions made by different models and their ecological significance, and by comparing the observed vs. predicted values, along with the Akaike Information Criteria (AICs), Mean Square Deviations (MSD), and the distribution of residuals. A p-value of 0.05 was deemed significant. Based on the principle of parsimony, the simplest model with the most accurate predictions was selected. Even though a number of variables were tested, the selected models were relatively simple, with 2 predictive variables for sapling densities and 3 for height increments.

3.3.4.2 Sapling densities

The model that explained sapling densities (N_{ijk}) for height class i of species j on plot k , as a function of sapling height (H_{ijk}) and a climate variable (V_{jk}), when significant, different for each species was:

$$\begin{aligned} N_{ijk} &= a_j \times e^{(b_{jk}H_{ijk})} \times e^{(c_jV_{jk})} + \epsilon_{ijk} \\ b_{jk} &\sim N(0, \tau_j) \\ \epsilon_{ijk} &\sim N(0, \alpha_j) \end{aligned} \tag{3.1}$$

a_j and c_j were species dependent parameters and b_{jk} were parameters depending both on species and plot.

3.3.4.3 Unbrowsed sapling height increments

The other equation was inspired by the formulation of height increment of conifers by [Ligot et al. \(2020b\)](#). A similar approach as earlier was followed for obtaining models explaining annual height increments. The chosen model for sapling height increments (ΔH_{ijk}) for an individual i of species j on plot k , as a function of sapling height (H_{ijk}), canopy openness (O_k) and a climate variable (V_{jk}), different for each species, was:

$$\begin{aligned} \Delta H_{ijk} &= a_j \times H_{ijk}^{(b_{jk}+c_jV_{jk})} \times O_k^{d_j} + \epsilon_{ijk} \\ b_{jk} &\sim N(0, \tau_j) \\ \epsilon_{ijk} &\sim N(0, \alpha_j) \end{aligned} \tag{3.2}$$

Both equations had a random plot effect, which was tested on different parameters.

3.3.4.4 Browsing

Due to the absence of height increment on a browsed sapling, it was not possible to include it as a factor in the earlier models. Hence, a preliminary exploration was carried out to identify the extent of browsing pressure and its possible damage. Browsing proportions of each species, and saplings of different heights were compared using 2 proportion z-tests, in order to estimate similarities and differences between different proportions. A proportion test (R function "prop.test" ([Newcombe \(1998\)](#))) was used to make comparisons, by specifying the alternative hypothesis to find out if the browsed proportions of each category are significantly different from one another.

Species	Ht. class	No. of inds.	Rege densities (per m^2)			Annual Increment (cm)		
			Mean	Max	SD	Mean	Max	SD
Spruce	1	243	0.052	2.195	0.201	1.802	6.670	1.167
	2	228	0.017	0.304	0.037	3.048	16.500	2.441
	3	147	0.007	0.177	0.019	5.656	21.500	4.612
	4	102	0.006	0.154	0.017	10.310	50.000	9.203
Fir	1	326	0.138	2.778	0.383	1.336	5.120	1.026
	2	248	0.022	0.309	0.044	3.242	10.330	2.343
	3	166	0.009	0.130	0.019	6.498	23.000	4.969
	4	151	0.008	0.141	0.017	11.308	36.670	7.641
Beech	1	232	0.130	7.506	0.642	2.570	11.170	2.332
	2	204	0.058	2.041	0.214	4.568	11.890	3.521
	3	166	0.016	0.790	0.067	9.349	37.830	7.203
	4	157	0.011	0.346	0.035	11.181	38.330	9.572

Table 3.3: Distribution of regeneration density and annual height increment values across species and height classes (H1=10cm-50cm, H2: 51cm-150cm, H3: 151cm-300cm, H4: 301cm-DBH 7.5cm)

3.4 Results

3.4.1 Main factors affecting sapling densities

Out of 152 sampled plots, 116 plots (76%) displayed some spruce regeneration, 128 fir regeneration (84%), and 104 beech regeneration (68%). However, the most obvious observation was the overall low regeneration densities (table 3.3). Globally, even though only 3 plots (1.9%) displayed no regeneration, 40 plots (26%) had total sapling densities below 0.1 sapling per m^2 , and only 22 plots (14.4%) displayed total sapling densities above 1 sapling per m^2 . Only 2 plots had total sapling density of more than 3 saplings per m^2 , indicating the low levels of regeneration.

Even though survival rates were not recorded, it was observed that smaller saplings of all three species (< 50 cm height) were much more abundant than taller saplings (fig. 3.3). Density of saplings of height above 50 cm quickly tended towards zero, which suggested the possibility of survival of very few saplings to older ages.

The equations and parameters representing models that best explained sapling densities are shown in table 3.5. The graphic representations shown in fig. 3.3 represent predictions and confidence intervals (95 %) from these models. All the models that were

tested are described in table 3.4.

The selected models showed that densities of saplings in all three species decreased exponentially with increasing height. Additionally, spruce densities decreased exponentially with increasing mean monthly PET (fig. 3.3 a); fir densities increased exponentially with increasing mean monthly precipitation over the year (fig. 3.3 b); and beech densities increased exponentially with increasing annual mean of monthly Soil Water Content (SWC) (3.3 c). Apart from that, a random effect was observed for sapling densities, which could be a result of many other potential plot specific factors that could not be separated and/or quantified. This effect was stronger for spruce, followed by beech, and least for fir (3.3).

Among all climate and soil variables (V) tested in equation 3.1, even though the most significant ones were selected for each species, there were some other models that were significant as well, but did not make sense ecologically. For example, the density model for beech with height and PET had the lowest AIC value, but the model produced negative sapling densities, and had to be discarded. Additionally, some significant models had higher AIC values (table 3.4). For example, spruce sapling densities were more affected by temperature and precipitation variables, but not so much by soil water conditions. Fir and beech however, showed more sensitivity to soil nutrients and soil water conditions. Unfortunately, addition of biotic factors like the competition index and browsing index to the model were not found to be significant. The level of significance of these models also differed, as described in table 3.4.

3.4.2 Main factors affecting unbrowsed sapling height increment

The measured annual height increment of saplings varied from 0 to 50 cm. The increment of unbrowsed saplings was highest for beech, followed by spruce, and fir displayed the lowest annual height increment, specially for saplings taller than 300 cm. The same approach and environmental variables were tested for models explaining height increments, as for sapling densities.

The most significant model showed that the annual height increment of an unbrowsed sapling depended on species, height, canopy openness, and the maximum summer

Category	V* (Density)	Spruce			Fir			Beech		
		AIC	MSD	p-value	AIC	MSD	p-value	AIC	MSD	p-value
Climate	Max montly temp(°C)	-2708.05	0.00	0.01	-2176.43	0.00	0.57	-836.59	0.01	0.81
Climate	Max summer temp(°C)	-2709.64	0.00	0.01	-2176.42	0.00	0.46	-836.59	0.01	0.81
Climate	Mean monthly prec(mm)	-2721.86	0.00	0.00	-2192.21	0.00	0.00	-434.47	0.03	1.00
Climate	Min winter temp(°C)	-2734.95	0.00	0.00	-2176.01	0.00	0.83	-819.25	0.01	0.02
Climate	PET	-2735.27	0.00	0.00	-2175.99	0.00	0.70	-976.68	0.01	0.00
Soil	Soil C:N	-2706.40	0.00	0.01	-2224.78	0.00	0.00	-887.11	0.01	0.00
Soil	Soil pH	-2699.82	0.00	0.10	-2182.65	0.00	0.01	-926.09	0.01	0.00
Soil	Soil water content	-2697.33	0.00	0.23	-2188.04	0.00	0.00	-948.82	0.01	0.00
Soil	Soil water deficit	-2696.23	0.00	0.45	-2178.15	0.00	0.03	-857.57	0.01	0.00
Soil	Soil water holding capacity	-2695.30	0.00	0.84	-2195.53	0.00	0.00	-892.56	0.01	0.00

Table 3.4: AIC, MSD and p-values of NLME models tested for estimating sapling densities of spruce, fir and beech, $V^* = V_{jk}$ from the equation $N_{ijk} = a_j \times e^{(b_{jk}H_{ijk})} \times e^{(c_j V_{jk})} + \epsilon_{ijk}$, where N_{ijk} =sapling densities for height class i of species j on plot k, as a function of sapling height (H_{ijk}) and a climate variable (V_{jk}).

Species (j)	a_j	σ_a	p-value	b_j	σ_b	p-value	c_j	σ_c	p-value	$\sigma(RE)$	Residuals
Spruce	381.07	139.271	0.007	-0.159	0.006	0	-0.115	0.01	0	0.046	0.022
Fir	2.489	0.56	0	-0.256	0.01	0	0.01	0.003	0	0.074	0.031
Beech	0.611	0.055	0	-0.16	0.01	0	0.017	0.001	0	0.071	0.096

Table 3.5: Parameter values for density models of each species. For each of the fixed parameters (a, b, c) are shown the estimates, the SD and p-value, along with the random effect SD and residuals.

temperature observed on the plot (for spruce and beech). The equations and parameters representing models that best explained sapling height increments are shown in table 3.7, whereas the results shown in fig. 3.4 represent predictions and confidence intervals (95 %) from these models.

Among our sampled species and individuals, the annual height increment of an unbrowsed sapling was most importantly limited by the height of the sapling. Smaller saplings typically grew slower, with differences among species. Canopy openness (hereafter, O) also determined the growth levels of saplings. The results of the selected model (explained in 3.3.4) revealed that the growth of all saplings was very low at canopy openness below 10 %, growing rapidly as it increased, following a power function and reaching almost a horizontal curve at canopy openness levels above 40 %. Taller saplings reached this horizontal asymptote at higher canopy openness than smaller saplings.

Category	V (ΔH)	Beech			Spruce			Fir		
		AIC	MSD	<i>p-value</i>	AIC	MSD	<i>p-value</i>	AIC	MSD	<i>p-value</i>
Climate	Max summer temp($^{\circ}\text{C}$)	3492.59	16.45	0.06	3386.98	6.66	0.03	3982.75	9.50	0.69
Climate	Max montly temp($^{\circ}\text{C}$)	3492.89	16.44	0.10	3387.15	6.67	0.04	3982.82	9.50	0.75
Climate	Min winter temp($^{\circ}\text{C}$)	3658.48	15.35	0.09	3387.15	6.67	0.04	3982.90	9.51	0.89
Climate	Mean monthly prec(mm)	3660.58	15.39	0.40	3389.27	6.69	0.07	3982.72	9.51	0.61
Soil	Soil pH	3488.73	16.50	0.15	3389.23	6.70	0.09	3982.29	9.50	0.47
Soil	Soil water holding capacity(mm)	3489.98	16.48	0.16	3389.22	6.66	0.10	3389.22	6.66	0.10
Climate	PET(mm)	3492.80	16.47	0.83	3388.85	6.71	0.10	3982.68	9.50	0.62
Soil	Soil water deficit(mm)	3493.23	16.52	0.24	3390.11	6.72	0.15	3390.11	6.72	0.15
Soil	Soil C:N	3492.53	16.48	0.47	3391.11	6.68	0.23	3391.11	6.68	0.23
Soil	Soil water content(mm)	3492.26	16.47	0.73	3391.00	6.65	0.28	3391.00	6.65	0.28

Table 3.6: AIC, MSD and *p*-values of NLME models tested for estimating sapling annual height increments of spruce, fir and beech, $V^* = V_{jk}$ from the equation $\Delta H_{ijk} = a_j \times H_{ijk}^{(b_{jk}+c_j V_{jk})} \times O_k^{d_j} + \epsilon_{ijk}$, where ΔH_{ijk} =sapling annual height increment for an individual *i* of species *j* on plot *k*, as a function of sapling height (H_{ijk}), canopy openness (O_k) and a climate variable (V_{jk}).

Saplings belonging to different species also displayed different maximum growths. Beech saplings grew most rapidly followed by spruce, while the least height increment was recorded by fir.

Beech and spruce growth was negatively affected by maximum summer temperature (fig. 3.4 a and 3.4 c). Silver fir growth did not directly depend on any other environmental factors that we took into account in our dataset (fig. 3.4 b). Apart from that, plot specific differences were observed in sapling height increments as well, indicating a considerable random effect. This effect was stronger for beech, followed by spruce, and least for fir.

The significance of other tested climate and soil variables was less obvious for height increment of saplings of all species than for densities, based on high *p*-values for other variables (table 3.6). The closest models strengthened the dependence of beech and spruce on temperature, as they included different temperature variables like minimum winter temperatures and maximum monthly temperatures.

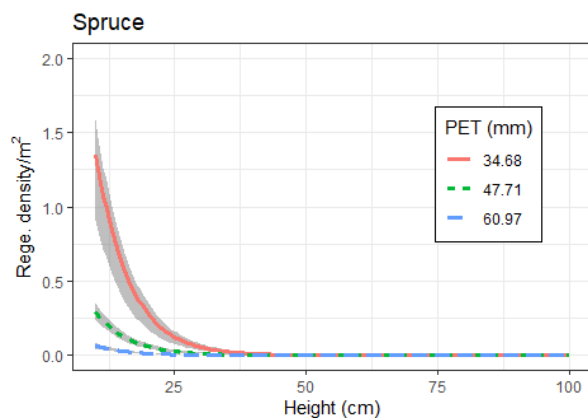
3.4.3 Browsing rates

Out of a total of 2370 saplings that we documented, 242 saplings were browsed or damaged by ungulates at the terminal shoot. This number varied greatly among saplings of different heights and species. Among the different height classes, the most browsed were saplings below 150 cm, which were easily accessible to most browsers. However, within

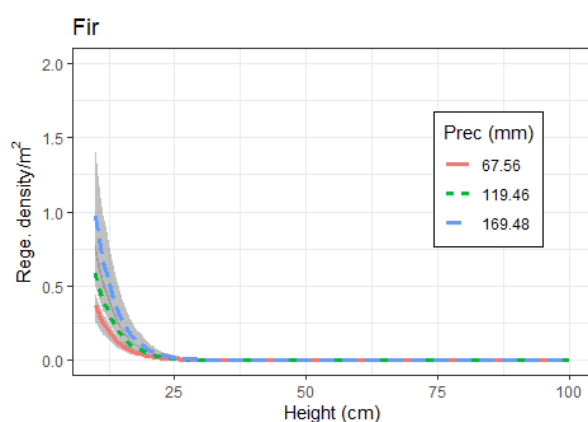
Species (j)	a_j	σ_a	p-value	b_j	σ_b	p-value	c_j	σ_c	p-value	d_j	σ_d	p-value	$\sigma(RE)$	Residuals
Spruce	0.030	0.006	0.000	1.170	0.130	0.000	-0.016	0.007	0.030	0.190	0.030	0.000	0.102	2.727
Fir	0.029	0.006	0.000	0.904	0.037	0.000	0.201	0.030	0.000	-	-	-	0.104	2.733
Beech	0.431	0.072	0.000	0.774	0.133	0.000	-0.015	0.008	0.056	0.077	0.041	0.059	0.094	1.478

Table 3.7: Parameter values for growth models of each species. For each of the fixed parameters (a, b, c, d) are shown the estimates, the SD and p-value, along with the random effect SD and residuals.

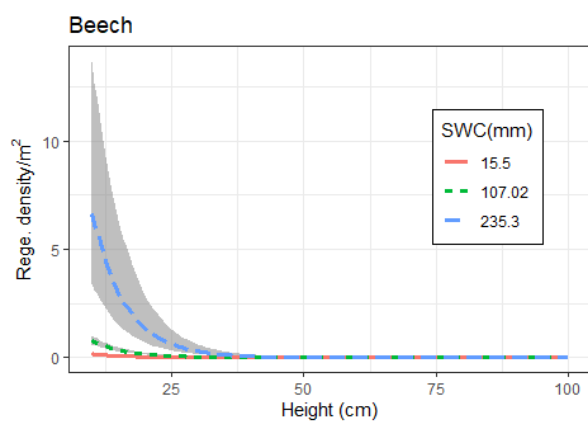
the three species, there was a clear difference in the preference of wild ungulates. As seen in fig. 3.5, and confirmed by the two-proportion z-tests, fir was the most browsed species among the three (14 %), followed by beech (11 %). However, the z-test showed no significant difference between the total browsing proportions of the two species ($p=0.127$). Spruce was the least browsed with 2 % of all the saplings browsed, much less than beech ($p=3.447e-16$) and fir ($p=1.128e-11$).



(a)

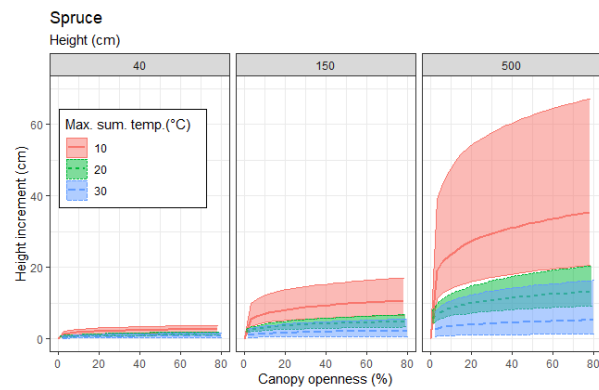


(b)

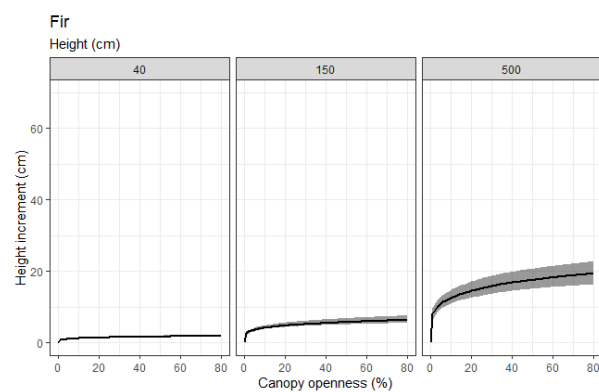


(c)

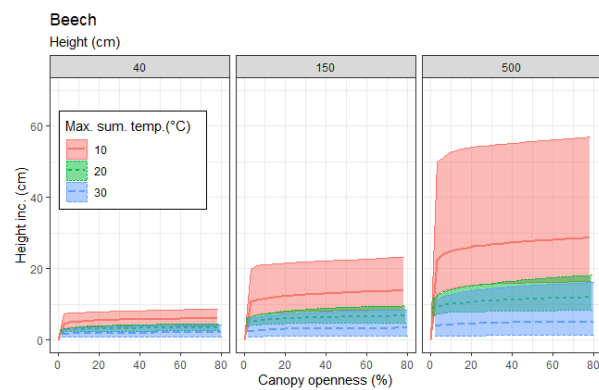
Figure 3.3: Simulation of sapling regeneration densities along sapling height gradients of spruce(a), fir(b) and beech(c) in mixed uneven aged mountain forests. For each species, colored lines represent the sapling density changes with different values of the climate or soil variables selected by the models (PET = Mean monthly Potential EvapoTranspiration (mm), Prec = Annual mean of monthly precipitation (mm), SWC = Annual mean of monthly Soil Water Content (mm)). Values of the variables correspond to first quantile, median and last quantile of the observed values. Warning: Scales differ on y-axis.



(a)



(b)



(c)

Figure 3.4: Prediction of annual sapling height increment of spruce(a), fir(b) and beech(c) along canopy openness (O) gradient, and for 3 sapling heights, 40, 150, and 500 cm, in mixed uneven aged mountain forests. For each species, colored lines represent the height increment changes with different values of the best climate or soil variables selected by the models (Max Sum temp= maximum summer temperature (°C)). Values of the variables correspond to first quantile, median and last quantile of the observed values.

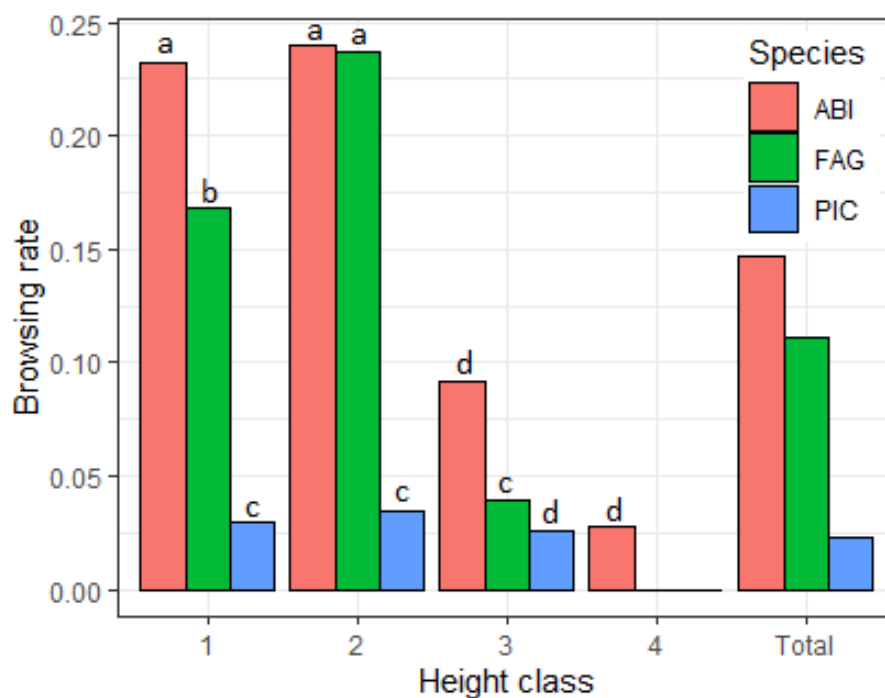


Figure 3.5: Comparative browsing rates of saplings by species (ABI: fir, FAG: beech, PIC: spruce) and height classes (1=10-50cm, 2=51-150cm, 3=151-300 cm, 4=301cm-DBH<7.5cm), as well as mean browsing rates per species. Letters a, b, c, d represent statistically similar and different bars.

3.5 Discussion

3.5.1 Understanding regeneration densities

As observed by forest managers and scientific studies such as [Kräuchi et al. \(2000\)](#); [Lines et al. \(2020\)](#), our study sites had low overall regeneration density of spruce, fir and beech. On an average, all three species had a large number of saplings lower than 50 cm height (table 3.3), with a steep decrease in the number of taller saplings. This suggested that the reason for low total sapling densities was not the limitation of seed rain or germination, but low survival rates ([Simon et al. \(2019b\)](#)). As annual survival rates were not recorded, we relied on diminution of densities across height classes to evaluate survival. Fir densities decreased most rapidly with sapling height, indicating high early mortality, possibly due to high browsing rates of fir. This has also been observed by [Nagel et al. \(2014\)](#) and [Bernard et al. \(2017\)](#). There was no direct effect of browsing observed on sapling densities. However, through its strong effect on growth, browsing maintained saplings at lower heights, and higher mortalities, reducing the density of taller saplings indirectly. Comparison of sapling densities with enclosed experimental plots is necessary to clarify this effect of browsing on density ([Bernard et al. \(2017\)](#)). We, however, identified other key factors affecting sapling densities and height increments.

As stand conditions are often the result of multiple historic events (climate extremes, management, browsing pressure etc), it was impossible to disentangle the different effects, or put in evidence general rules of what is a compromising factor in a given environment ([Benavides et al. \(2016\)](#)). Models were tested to evaluate the effect of light ([Ligot et al. \(2014\)](#); [Orman et al. \(2021\)](#); [Lochhead and Comeau \(2012\)](#)), basal area ([Stancioiu and O'hara \(2006\)](#)), water availability (soil and atmospheric) ([Löf and Welander \(2000\)](#); [Moser et al. \(2017\)](#)), temperature ([Schurman et al. \(2019\)](#); [Lombaerde et al. \(2020\)](#)), competition with other species ([Thrippleton et al. \(2017\)](#)), browsing ([Bernard et al. \(2017\)](#)), and many other variables that are known to affect regeneration densities (table 3.2). We succeeded in identifying the most dominant variables affecting spruce, fir and beech densities, among the ones that we tested. However, the extent and intensity of these effects was species specific [Caron et al. \(2021\)](#). Spruce regeneration densities improved in lower PET (potential evapotranspiration) levels, and significantly declined in higher PET levels, which is supported by [Cienciala et al. \(1992\)](#), who demonstrated high sensitivity of spruce trees to evapotranspiration. Among all the models tested, there were sometimes more than one significant models. In the case of spruce, all significant models

(that were not selected) indicated temperature sensitivity of spruce. None of the models with soil conditions as an explanatory variable (except C:N) showed any significance. This is in contradiction to [Dyderski et al. \(2018\)](#), who showed the importance of soil pH and water logging for spruce regeneration. Beech densities increased with higher SWC. Many studies support this result as soil water availability is known to have an effect on both beech saplings and adults ([Geßler et al. \(2007\)](#); [Diaci et al. \(2020\)](#); [Pröll et al. \(2015\)](#)).

Fir densities relied least on climate factors, though it showed some sensitivity to annual precipitation, requiring higher water input to survive better. Though there are studies that indicate that fir can survive soil water deficits ([Tinner et al. \(2013\)](#)), some also predict that the species will most likely suffer in severe drought conditions [Bottero et al. \(2021\)](#). However, it is interesting to note the detrimental effect of water constraints on the three species, with either limitations in water input, uptake or evaporation. A look at [figure 3.3](#) also suggests that the effects are stronger for spruce and beech, and that they are more climate sensitive than fir. There are multiple studies discussing tree and sapling drought tolerance of the three species which conclude that all three species show signs of drought sensitivity ([Cailleret et al. \(2014\)](#); [Löf et al. \(2005\)](#); [Silva et al. \(2012\)](#)), though there is a debate about their comparative sensitivities ([Diaci et al. \(2020\)](#); [Schall et al. \(2012\)](#); [Zang et al. \(2014\)](#); [Vitali et al. \(2017\)](#)).

We assumed fecundity (or seed rain) of a species to be directly proportional to its conspecific basal area on the stand (similar to [Paluch et al. \(2019\)](#)), and we expected sapling densities be directly proportional to the conspecific BA as well. However, higher BA also reduces light availability, which can hinder regeneration. There was no clear relation between regeneration and BA, perhaps because the two effects could compensate each other, or maybe our plot size was too small for BA to be a good predictor of the local seed rain, or BA was not a good predictor of light at this local scale (the canopy is too heterogeneous). Similar observations have been made by [Comeau et al. \(2006\)](#).

There was high variability in the regeneration data collected both within and between plots. The variability within a plot was probably due to the strong heterogeneity of the environmental factors experienced by individual saplings ([Schurman et al. \(2019\)](#); [Diaci et al. \(2020\)](#)): gaps could make a strong difference below the heterogeneous canopies of these forests, soil was extremely heterogeneous with large rocks, modifying soil depth drastically within distances of a few centimeters. The variability between plots was often difficult to interpret and was translated into high plot effects in our model. These could

be due to many factors difficult to record: past management history, soil conditions, complex climate effects poorly represented in the interpolated climate data to name a few.

3.5.2 Sapling height increments

As discussed in section 3.3.4, height increment models were calibrated only for un-browsed saplings. The maximum annual height increment reached by a sapling was primarily determined by its height, canopy openness of the plot, and maximum summer temperature (for spruce and beech).

The height increment of a sapling was limited by its height, with taller saplings showing higher increments. In comparison with studies like Ligot et al. (2013) carried out in forests in the Belgian Ardennes (40 cm/year increment for 250 cm high beech sapling), sapling height increments in our study were relatively modest (15 to 25 cm/year for a 700 cm high beech sapling), but comparable to other studies such as Dobrovolny (2016) (16 cm for a 200 cm high beech sapling) carried out in mountain forests.

When plotted against canopy openness (O), the shape of height increment curves for saplings of different heights were similar for the three species (fig. 3.4). In particular at low O (< 10 %), the three species presented very low growth, with beech growth slightly above fir and spruce. This finding was in contradiction with those of Stancioiu and O'hara (2006) who reported out-competition of spruce by beech and fir growths, but in agreement with Ligot et al. (2020b), who observed comparable height growths for spruce and fir. Fir is known to be more shade tolerant than spruce (Diaci et al. (2020); Klopčič et al. (2012b)), and is expected to have a low growth rate in shade with a low mortality (Kobe et al. (1995)). However, more recent work showed that sapling size (ontogeny) must also be considered in that tolerance to shade ?. Messier et al. (1999) defined a critical size for a given light level above which the sapling do not survive. This critical size is higher for shade tolerant species. It could also explain why small saplings can easily be found under low canopy openness and that higher saplings are only found under higher canopy openness (Dreyer et al. (2005)).

However, height and canopy openness were not the only factors affecting height increment. Being sensitive to summer temperatures (Schurman et al. (2019)), spruce grew slower in sites with higher maximum summer temperatures. The growth of beech was

also inversely proportional to maximum summer temperatures, as also shown in adult trees by [Seynave et al. \(2008\)](#), which is probably due to its sensitivity to higher temperatures and droughts ([Geßler et al. \(2007\)](#); [Maes et al. \(2018\)](#)). We could not see any direct climate effect on fir, possibly due to multiple interacting effects that could not be caught in our models. There is also a possibility that high browsing rates, and hence a high proportion of saplings with zero increments (which were not included in the model), led to an inconclusive effect of any environmental variable on fir sapling increments. Even though spruce and beech have different niches, and occur more frequently in different altitudes, it is crucial to note that summer temperatures affect the growth of regeneration of both species. This trend seems rather general, and could potentially affect fir as well ([Vitasse et al. \(2019\)](#)).

3.5.3 Browsing

A significant number of saplings (18.6 %) were browsed by wild ungulates such as deer, roe deer, chamois, either at the terminal shoot or at peripheral branches, though the actual impact of these animals on sapling density and growth is difficult to evaluate. However, it does reduce or stunt the growth of a significant number of saplings by chewing off the terminal buds, that is sometimes even fatal for small saplings (picture of a representative sapling shown in [fig. 3.6](#)). Very often, the saplings are also browsed very frequently while they are very young, dying or disappearing even before they are counted for studies like ours. This alters the regeneration composition altogether, and could result in loss of data needed to understand the process. This remains a challenge in regeneration studies attempting to understand the effect of browsing.

Establishing a direct relation of ungulate browsing with sapling densities or height increments was hence, a difficult task, and we did not succeed to include it in the above models. However, the extent of damage by browsing on the field prompted us to explore browsing rates, which turned out to be concerning. Among the three species that we observed, there was a clear and strong preference of browsers towards fir, followed by beech (comparable to fir), and spruce was seldom touched. The affinity of various ungulates to fir is well studied and documented ([Bernard et al. \(2017\)](#); [Heuze et al. \(2005\)](#); ?); [Nagel et al. \(2014\)](#)), with an alarming reduction in fir regeneration in areas of high ungulate population. Beech, however, is not commonly known as one of the popular choices of these animals. This indicates that the browsing pressure was quite high in our field sites, and ungulates were forced to eat beech as there was no fir available anymore. It also

highlights once again, the high vulnerability of fir, and possibly beech in the future, to browsing by ungulates.



Figure 3.6: An old fir sapling, completely browsed every year by animals, thus losing any chance to grow.

3.5.4 Regeneration dynamics and management implications

Saplings of all the three species can grow faster as they grow higher, but their mortality also increases, leading to very few of them reaching a tree recruitment stage. It is not difficult to conclude that these processes could lead to low tree recruitment, and that is exactly what we observed. Only 34 plots out of 152 sampled had trees between the DBH of 7.5-8 cm (assumption is that they have been recruited in the last 5 years), with 5 spruce trees, 45 fir trees and 34 beech trees. Many of them looked evidently old, or unhealthy, thus unlikely that the reported number will survive or grow and contribute to overstory canopy or seed rain. This confirms the concerns of the foresters about limited tree recruits.

It has been well established that the challenge of climate change is already affecting growth and survival of regeneration in forests. The most studied effect is probably that of temperature, as shown in studies all over the world (Schurman et al. (2019)). Higher temperatures affect survival of plants and trees, causing species moving to higher elevations to find optimal temperatures (Munier et al. (2010); Tingstad et al.

(2015); Benavides et al. (2016). However, the direct effect of temperature is often not so obvious, because temperatures are also involved in potential evapotranspiration. We observed a strong plant response to temperature, as well as variables that change water availability to the plant. Increasing temperature and decreasing precipitation is leading to increased frequency and intensity of droughts, and spring and summer droughts, in the growing season of plants could seriously jeopardize regeneration. Additionally, decreasing snow cover could affect water balance. This could be an indicator that mountains are transitioning from temperature to moisture limitation as discussed by Schurman et al. (2019), making predictions even more challenging as this will increase the weight of forest dynamics on local drivers.

All three species are seen to grow better in canopy openness of more than 10 % in the plot, which could be an important management implication, to create big enough gaps to allow saplings to grow fast. At present in our sampling, half sites had canopy openness lower than 9.4 % (median). This has also been studied and reported by others such as Diaci et al. (2020). Reducing BA will also reduce water losses by tree transpiration and could lead to a better water balance, favorable to regeneration (e.g. Bréda et al. (1995); Aussenac (2000)).

Our model predictions point out that among spruce, fir and beech, fir saplings have the highest mortality, and lowest annual height increments. Added to that, the ungulate browsing is the highest in fir. This could create an advantage for spruce and beech regeneration, thus possibly starting a change in species composition of the stands (Dobrowolska and Bolibok (2019); Häslér and Senn (2012); Bernard et al. (2017); Heuze et al. (2005); Diaci (2002); Senn and Suter (2003); Thrippleton et al. (2018); Weisberg et al. (2005); Cretaz et al. (2002)). However, spruce and beech are also more sensitive to climatic changes, specially limited by high temperatures and water availability. This could also reduce their chances of better survival. In spite of all this information, in our dataset, and in spite of being highly browsed, the highest observed tree recruits in the last few years ($7.5\text{cm} < \text{tree DBH} < 8\text{cm}$) belong to fir. ? has also specified a much larger range of fir in the past. This could indicate a lower browsing pressure, and more favourable climatic conditions for fir in the past. However, when comparing it with the other two species, it could also be either that fir is more resilient than spruce to the factors that hinder its growth and spread, or is simply a lag in response by fir, or a lag in detection of this change by us.

3.5.5 Limitations and the way forward

One of the limitations in this study was the uncertainty about the reliability of measured and obtained data. In particular, due to the presence of large rocks, or heterogeneous soil conditions within a plot, soil variables could have been misled. The proxy of canopy openness did not always correspond well to the light available for saplings (Comeau et al. (2006)), often due to the presence of intermediate layers of canopy formed by tall understory vegetation, or sometimes because of a wider-than-expected spread of the overstory canopy. Thus, we see in our data, a possibility of low basal areas, and low light levels occurring in the same plot.

The explored variables related to climate were all modelled, as it was unrealistic to directly measure them on-site for such a large area. Instead we used the platform digitalis to simulate long-term climate on a 50 m spatial grid. This can lead to imprecisions in the climate really prevailing in the different considered sites, in particular in mountainous areas with strong topological effects (Piedallu et. al. 2021 (submitted)). But most importantly the simulated variables give the general climate above tree canopy and not the one experienced by the saplings in the understory, that is to say the micro-climate. Indeed microclimate at the soil level can be very different from the climate depending on stand density and structure (Aussenac (2000)). Of course the first affected variable is radiation we approximated by canopy openness, with some concerns we already debated above. Linked to attenuated radiation, air temperatures are buffered by the tree canopy, with lower maximum and higher minimum (Gaudio et al. (2017)). Tree canopy also intercepts precipitation resulting in less water available in the understory than predicted by incident climate variables and affecting the stand water balance (Barbier et al. (2009)). Therefore, the micro-climate experienced by the sapling has opposite components, in one hand a buffered air temperature limiting extreme events such as frost and heat, and also lowering vapour pressure deficit and PET, and so sapling evapotranspiration and in the other hand a periodic soil water deficit in the upper soil horizons linked to rainfall interception by trees. At the difference of adult trees, as sapling roots cannot reach the deeper soil horizons where water can be still present in drought periods, they are subjected to periodic water constrains not monitored in the simulated general climate variables. All these considerations could explain why we had difficulties to have strong effects of other climate variables on sapling growth and density. Such a lag between the general increase in temperature linked to climate change and the effective shift in understory plant composition (including tree saplings) has already

be reported (e.g. [Dietz et al. \(2020\)](#)). We also highlight the necessity to better monitor and understand the actual water regime experienced by the saplings as suggested by the high number of water-related variables having a significant effect in our models.

The variability in field studies such as this is so high that it questions the reliability of the “space for time” assumption if we want to use our results to predict changes in time. Monitoring of sites would be necessary to have more accurate results, but the very low fluxes of regeneration densities as well as tree recruitment require to do the monitoring on large scales or long duration.

3.6 Conclusions

To our knowledge, this is one of the first studies monitoring the regeneration state of spruce-fir-beech on such a large scale. It gives insights of the likely evolution of forest dynamics and composition in the considered area, with a slightly pessimistic prediction for some areas and species. The three species may be at risk because they respond negatively to factors such as low light conditions, browsing, high temperatures and drought. Spruce and beech suggest a possibility of higher vulnerability in instances of frequent and intense summer heat and drought situations. The strong preference of ungulates for fir puts it in a high risk in case of a rapid increase in ungulate browsing. We could therefore expect a diminution of adult tree recruitment and adult stand density of either species depending on local water and browsing conditions. This real diminution of adult density could lead to an increase of light under canopy beneficial to saplings, which could slow the changes. We could have a kind of resilience mechanism here that could prevent species exclusion. Smaller density would also mean smaller competition between adult trees and the total production could remain moreover the same for a while. However we do not know how far such a mechanism could compensate the effect of recruitment diminution, with a potential risk of changing forest structures, with migration of species at one point.

CHAPTER 4

Spruce and fir tree recruitment at risk:
estimating regeneration processes under
climate change and ungulate browsing in
forests of the Alps

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Manuscript in prep.

4.1 Context and objectives

In this chapter, I build upon the results of chapter 3, in order to formulate a regeneration dynamics model, by explicitly including the processes of fecundity, sapling and survival and browsing pressure on saplings. The aim of this study was to estimate model parameters with a likelihood free approach called Approximate Bayesian Computation (ABC), as the likelihood for processes such as survival was incomputable. Using the estimated parameters for each process and species, I calculated tree recruitment rates in my sampled sites, for current and future projected climate and browsing pressure scenarios. I will present the topic, methods used and results and discussion in this chapter. This is an article manuscript in preparation.

4.2 Introduction

Global environmental changes are affecting tree population demography with potentially significant impacts on species ranges (Renwick and Rocca (2015)) and distributions (Thuiller et al. (2008)), forest biodiversity (Gwitira et al. (2014)) and wood production. Forest tree populations are determined by tree regeneration processes, which include seed production and germination, sapling establishment, growth and survival to the recruitment size (Clark et al. (1999)). Each step of the regeneration process is driven by multiple environmental factors, and involves many biotic and abiotic, facilitative as well as competitive interactions (Henry et al. (2021); Simon et al. (2019a); Tinya et al. (2019); Kunstler et al. (2005)), and changes in regeneration dynamics directly affects forest composition and structure (Paluch et al. (2019); Lafond et al. (2017); Ficko et al.

(2016); [Lochhead and Comeau \(2012\)](#)).

Mixed forests of *Picea abies* (L.) H. Karst (Norway spruce), *Abies alba* Mill. (silver fir) and *Fagus sylvatica* L. (European beech) forests are one of the main forest type in the French Alps, and many other mountains of Europe ([Brus et al. \(2012\)](#)). They are often mixed and uneven-aged, and have been observed to be declined in their habitat suitability ([Vitasse et al. \(2019\)](#); [Dyderski et al. \(2018\)](#)). They have socio-economic importance through wood production, protection against natural hazards, as a central element of mountain landscapes, and as biodiversity reservoir ([Condés et al. \(2022\)](#); [Torresan et al. \(2020\)](#); [Hilmers et al. \(2020\)](#); [Lagarrigues et al. \(2017\)](#)). Sustainable management of these forests requires a continuous flux of new tree recruits that replace dying or harvested larger trees ([Bolte et al. \(2009\)](#)), which depends on the regeneration processes that precede ([Klopčič et al. \(2014\)](#)). There are strong evidences of spruce, fir and beech regeneration sensitivities to changing climate and increasing ungulate pressure separately (eg: [Bottero et al. \(2021\)](#); [Brandl et al. \(2020\)](#); [Diaci et al. \(2020\)](#); [Paluch et al. \(2019\)](#); [Vitasse et al. \(2019\)](#); [Heuze et al. \(2005\)](#)). Both of these factors can potentially jeopardize regeneration dynamics, and hence the sustainability of forest management. However, the extent of damage caused by the two factors combined is not well reported, except by very few studies ([Peringer et al. \(2013\)](#); [Brodie et al. \(2012\)](#); [Didion et al. \(2011\)](#)). Many of these studies, carried out in Central European forests ([Vacek et al. \(2019a\)](#); [Cailleret et al. \(2014\)](#)) reported debatable responses of spruce and beech, but fir is always at the biggest disadvantage due to its cumulative vulnerability to climate change and browsing by ungulates.

Identifying environmental factors that drive regeneration on field is difficult on a large temporal or spatial scale. Understanding climate effects requires the sampling of large environmental gradients, which is indeed difficult to combine with intensive plot re-measurement over multiple years. National forest inventories give snapshots of sapling densities or sapling cover at one or several dates ([Hasenauer and Kindermann \(2002\)](#)), whereas processes that play a role in changing sapling densities are difficult to separate without identification or follow-up of individual saplings ([Defossez et al. \(2016\)](#)). Several studies have analyzed sapling growth of different species, although often for a short duration, or on a small spatial scale (e.g. [Vencurik et al. \(2020\)](#); [Schurman et al. \(2019\)](#); [Ligot et al. \(2013\)](#); [Gaudio et al. \(2011b,a\)](#)). Furthermore, the harm done by ungulate browsing to regenerated saplings have been mainly focused on specific species, such as fir ([Bernard et al. \(2017\)](#); [Heuze et al. \(2005\)](#); [Senn and Suter \(2003\)](#)). But measurements

and estimations of regeneration survival or mortality is a more complicated task, that has been mainly explored in controlled conditions or small experimental field plots (Chang-Yang et al. (2021); Munier et al. (2010); Beckage et al. (2005)). There is little historical long-term data about sapling densities of different sizes or ages, or information about individual sapling mortality, and even fewer studies that use this data to explore regeneration patterns (Beckage et al. (2005, 2000); Steven (1994)). As a result, it is quite challenging to estimate altogether, the processes involved in tree recruitment and to predict their relative magnitude in natural field conditions (Diaci et al. (2020); Beckage et al. (2005)).

An alternative solution to study relations and understand pattern in forest dynamics is to model these processes computationally using forest dynamics models. Forest dynamics models are useful to address questions that cannot be answered solely by experimental or observational studies, from understanding current mechanisms (Wyse et al. (2018); Klopčič et al. (2012b); Acevedo et al. (1996)), to predicting long-term dynamics (Shifley et al. (2017); Klopčič et al. (2010)). Modelling forest dynamics is difficult due to the inherent complexity and interdependence of processes involved. However, there are many modelling approaches that attempt to understand forest dynamics better, such as gap models, individual based or process based models. In these models, each demographic process is described mathematically, with its dependencies explicitly stated. Depending on the type of model, the progression of an individual, or stand or a larger landscape is then simulated to obtain more information about the evolution of the respective forest scale.

The calibration of such model can be done in a variety of ways, among which, an emerging method is Approximate Bayesian Computation (ABC). ABC is a likelihood free statistical method developed for the calibration of complex simulation models, that could help to overcome some of the encountered difficulties such as unavailability of complete or accurate datasets, or complications in calculating likelihood functions of processes Bertorelle et al. (2010). This method is mainly used for parameter inference and model selection for sophisticated models (Csilléry et al. (2010)). ABC has been used widely since the past few years in genetics and evolutionary studies involving large but incomplete or imprecise datasets (Lopes and Beaumont (2010)), and is now emerging rapidly in the field of ecology (Lenormand et al. (2013); Beaumont (2010)).

The ABC parameters estimation process is based on the realization of many simula-

tions of a model, sampling the parameter space by drawing vectors of parameter values in parameter prior distributions. The fraction of simulations, best predicting a set of statistics summarizing the data is then selected and the corresponding parameter values are used to build a joint posterior distribution of parameters (Lenormand et al. (2013); Beaumont (2010); Csilléry et al. (2010)). ABC is convenient for the calibration of simulation models producing outputs depending on several processes in combination because it does not require the explicit calculation of model likelihood. It is also a method that makes possible to estimate elementary processes for which direct observations are missing, through their influence on the global output of the simulation model (Lines et al. (2020)).

As mentioned earlier, simulating regeneration dynamics would require accounting for fecundity, seed germination, sapling growth, and sapling survival, in order to estimate tree recruitment rates. The challenge is to infer the respective magnitude of the different demographic processes from a limited set of on field records such as sapling growth and density at a given time. A few attempts have been already made to use ABC to estimate adult tree growth, mortality and recruitment from a succession of forest inventories, however regeneration was highly simplified in these models (Lagarrigues et al. (2015); Hartig et al. (2014)). More recently, ABC approach was used to quantify the effects of climate and density dependence on regeneration of 13 tree species using re-measured plots of two successive Spanish forest inventories (Lines et al. (2020)), highlighting the potential of the approach. Unfortunately, very few of the European national forest inventories provide measurement of sapling growth or densities, usually providing a rough estimate of sapling cover, without any true regeneration measures (Brus et al. (2012)). Understanding climate effects requires the sampling of large environmental gradients, which is indeed difficult to combine with intensive plot re-measurement over multiple years. A method based on a single inventory would therefore be very valuable in this context.

The objective of this study was to explore and parametrize different demographic processes related to sapling regeneration and tree recruitment along a climatic gradient in the French Alps. We did this using a single field inventory, and used ABC to calibrate the processes. The model was then used to analyze the potential effect of climate change and ungulate pressure projected for the year 2100 on the recruitment of Norway spruce (*Picea abies* (L.) H. Karst), Silver fir (*Abies alba* Mill.) and European beech (*Fagus sylvatica* L.) in the French Alps and Jura mountains. We used data from a specific field sampling combining a single time observation of sapling density and sapling height

increments (Unkule et al. (2021)). Our ecological hypothesis was that ongoing climate change and increasing ungulate browsing would likely reduce tree recruitment rates of spruce, fir and beech, in mountain forests in the Alps, and this reduction would be higher for fir, considering the well-known susceptibility of fir regeneration to ungulate browsing. This could create a risk of change in current forest compositions. ABC would also make it possible to estimate parameters of demographic processes combining observations of sapling densities to observations, using stationary populations.

4.3 Materials and methods

4.3.1 Data acquisition

The data set combined measurements of individual saplings, surrounding adult trees and environmental variables over 152 field circular plots of 10 m radius, sampled across the French Alps (44.17N, 5.23E to 46.39N, 6.90E), in mixed, uneven-aged forests dominated by Norway spruce (*Picea abies* (L.) H. Karst), silver fir (*Abies alba* Mill.), and common beech (*Fagus sylvatica* L.). The sites were distributed over 11 mountain ranges, across a wide gradient of elevations (1400 – 2000m) and thus conditions of temperature, precipitation, light availability and the relative proportion of tree species. In order to characterize stand structure, we measured diameter at breast height (DBH) of each tree above 7.5 cm of diameter, and calculated the total and conspecific tree basal area on the plots for our three species. We estimated regenerated sapling density for each of the three species split into four height classes (H1: 10-50cm, H2: 51-150cm, H3: 151-300cm, H4: 301cm-7.5cm DBH). We used the Point Center Quadrat Method (Mitchell (2010)) to estimate densities from the distance of the closest individual to the plot center in each species and height category, and on each of four quadrats per plot. We also measured the annual height increment of each sampled sapling. We noted any physical damage to the terminal bud of a sapling as an incident of browsing by a wild ungulate (yes/no). We considered that the height increment of the last vegetation season was zero for any sapling with a browsed terminal shoot. We also estimated canopy openness, as a substitute for light, on each plot using a densiometer (Baudry et al. (2013)). Lastly, we obtained climate variables on each plot such as monthly and annual temperatures, precipitation and Potential Evapotranspiration (PET), from the period between 1985-2010, with a 50 m resolution, from the Digitalis database (Piedallu and Claude Gégout (2008)). More details about the data are presented in (Unkule et al. 2022, or chapter 3), and the dataset is available here: (Unkule et al. (2021)).

4.3.2 Simulation model of regeneration dynamics

4.3.2.1 General structure of the model

We built an individual-based model of regeneration dynamics where each sapling on a plot was monitored from its establishment (height 10 cm) to its tree recruitment size (7.5 cm DBH). Each year, new saplings were produced based on tree fecundity; they then grew in annual time steps, and survived with a given probability. We counted and eliminated saplings from the population when they were dead or reached adult size. Considering that we studied uneven-aged stands where a permanent cover is a management objective, and we expect the total canopy to remain somewhat constant, we assumed that the distribution of adult tree sizes was at equilibrium (due to compensating effects of recruitment, growth and death). Following this assumption, we fixed the adult tree canopy in the plots over time. We also assumed that climatic conditions remained constant during the simulation. According to these assumptions, when simulating the dynamic processes of seed germination, sapling growth, mortality, and recruitment as an adult over one century, the number of saplings stabilized progressively in each size class. We simulated the dynamics of sapling populations separately for each species. As the ABC estimation process requires intensive computing, we selected a-priori the environment covariates used in the different sub-models, based on the results of Unkule et al., (2022). After some trials, the only climate variable used in the process equations was the annual monthly mean of potential evapotranspiration (PET) (mm), as it is an integrative variable of the climatic demand for water integrating the effect of higher temperatures in the future. Within this model, we used four functions to represent the different demographic processes:

Sapling production

In the model, for the purpose of simplicity, the fecundity per se (seed production, viability and germination) was not considered. Instead we used the probability for a sapling of 10 cm height to establish as proportional to basal area of the considered species (Courbaud et al. (2015)). N_{jk} , the number of saplings of a species (j), on a plot (k) of area P, follows a Poisson distribution of parameter (λ_j) proportional to species basal area (Gsp_j):

$$N_{jk} \sim Poisson(\lambda_j) \tag{4.1}$$

with $\lambda_j = a_j \times Gsp_j$

The parameter a was restricted to strictly positive values to ensure that the number of saplings produced was greater than 0.

Sapling survival

The equation determining the annual probability of survival of a sapling was based on models by Courbaud et al. (2015) and Unkule et al. (2022). For each sapling, the stochastic event of surviving a given year S_{ijk} , taking the value 0 or 1, was the result of a random draw in the Bernoulli distribution of parameter p_{ijk} . p_{ijk} was a logistic function of a linear combination of plot potential evapotranspiration (PET_k) and sapling height H_{ijk}

$$\begin{aligned} S_{ijk} &\sim \text{Bernoulli}(p_{ijk}) \\ p_{ijk} &= 1/(1 + e^{(-z_{ijk})}) \\ z_{ijk} &= b1_j + b2_j \times PET_k + b3_j \times H_{ijk} \end{aligned} \tag{4.2}$$

Annual height increment

Growth of a sapling was measured in terms of annual height growth. The equation for this process was inspired from Ligot et al. (2013) and Unkule et al. (2022). The annual height increment of a sapling i of species j on plot k , ΔH_{ijk} , was drawn in a Normal distribution of mean I_{ijk} and standard deviation σ_j . Sapling height increment depended on its initial height (H_{ijk}), canopy openness on the plot (O_k), the potential evapotranspiration (PET) on the plot (PET_k), and four species parameters to estimate.

$$\begin{aligned} \Delta H_{ijk} &\sim N(I_{ijk}, \sigma_j) \\ I_{ijk} &= c1_j \times H_{ijk}^{(c2_j + c3_j \times PET_k)} \times O_k^{c4_j} \end{aligned} \tag{4.3}$$

Height increment increased as a power function of canopy openness (mainly a light effect) and with sapling height class, taller sapling having higher increment, but limited by high PET (see supplementary material).

Probability of browsing

Each sapling had an annual probability q_{ijk} of having its terminal shoot being browsed by an ungulate, with a logistic function of its height (H_{ijk}). For each sapling, the stochastic event of being browsed B_{ijk} at the terminal shoot, taking the value 0 or 1, was the result of a random draw in the Bernoulli distribution of parameter q_{ijk} .

$$\begin{aligned}
B_{ijk} &\sim \text{Bernouilli}(q_{ijk}) \\
\text{with } q_{ijk} &= 1/(1 + e^{z_{ijk}}) \\
z_{ijk} &= d1_j + d2_j \times H_{ijk}
\end{aligned} \tag{4.4}$$

Both parameters $d1_j$ and $d2_j$ were allowed to take only strictly negative values in order to have a decreased probability of browsing for taller saplings [Bernard et al. \(2017\)](#). In case a sapling was browsed, its annual height increment was set to zero.

Height of recruitment

The height of recruitment HR_j was calculated using the following allometric equation ([Courbaud et al. \(2015\)](#)):

$$HR_j = e^{(K_j - (K_j - \log(1,3)))} \times e^{(-R_j * Dr)} \tag{4.5}$$

Where K_j and R_j were parameters specific to each species (Table in supplementary material), and Dr was the recruitment diameter set at 7.5 cm, which is the same as used by the ONF, France (French Forest National Office).

4.3.2.2 Parameter estimation using Approximate Bayesian Computation

The model was executed in R version 4.1.2. The model calibration and parameter estimation was done for each species independently. Combining all the processes, we had 10 parameters to estimate for each species. We ran the simulation to let the simulated stand evolve for 100 years, and this process was carried out for 152 plots and 3 species, with the plot specific variables of species basal area, canopy openness and PET.

We chose an independent uniform prior distribution for each parameter. For certain parameters, (a, b1, b3, c1, c2, c4) we chose to restrict the parameter space to only positive values, whereas the others (b2, c3, d1, d2) based on the expected sign of the effect of related variables on demographic processes. Based on some exploratory simulations, and trials and errors, we ensured that the range of values sampled for each parameter was large enough to cover the full parameter space leading to realistic simulations ([Table 4.1](#)). We decided to construct summary statistics based on average variables combining the different plots. Similar to the structure of field data, we divided saplings into four height classes. In order to illuminate the effect of environmental co-variables on regeneration processes and resulting sapling population, we also grouped plots into categories based on

canopy openness (Ok) and PET_k, split into 2 categories- higher (CO₂, PET₂ respectively) and lower (CO₁, PET₁ respectively) than the mean of the observed values. We calculated 20 summary statistics: mean sapling density per height class (4 statistics), mean sapling densities per canopy openness class (2 statistics), mean sapling density per PET class (2 statistics), mean annual height increment per height class (4 statistics), mean annual height increment per light class (2 statistics), mean annual height increment per PET class (2 statistics), mean browsing rate per height class (4 statistics). We hypothesized that these summary statistics represent well the regeneration data that we collected on field and calculated, and that we can predict the equation parameters with the help of these summary statistics. For some combinations of parameters, the simulations produced plots with a density of zero, making the calculation of increments and browsing rate impossible. In order to avoid the elimination of all these plots from the summary statistics, we calculated in those cases the expected increment and browsing probability of a virtual sapling of height corresponding to the mean of each height class. We used the sequential ABC algorithm of [Lenormand et al. \(2013\)](#) with default settings.

4.3.2.3 Model application to predict tree recruitments in the future

The last step was to use vectors of parameter values from the joint posterior distribution estimated from ABC to predict sapling populations and tree recruitment rates in current and future climate and browsing scenarios. We obtained the potential change in PET values in the year 2100 under three climate scenarios projected by the IPCC ([IPCC \(2014\)](#)), using the Turc's formula ([Turc \(1961\)](#)). In the optimistic scenario (RCP2.6), the PET is projected to increase by 4.7 %, by 10.3 % in the intermediate scenario (RCP4.5), and by 17 % in the pessimistic scenario (RCP8.5). In addition to that, as literature on browsing rates does not have consensus about the direction in which ungulate browsing may change, we used values of browsing rates remaining constant, increasing, or decreasing by 20 % of current values. Using the estimated parameter values, and different climate and browsing conditions, we re-ran the simulation model described in section 3.2 to calculate sapling populations and tree recruitment rates of each species over the last 20 years of the 100-year simulation on every plot.

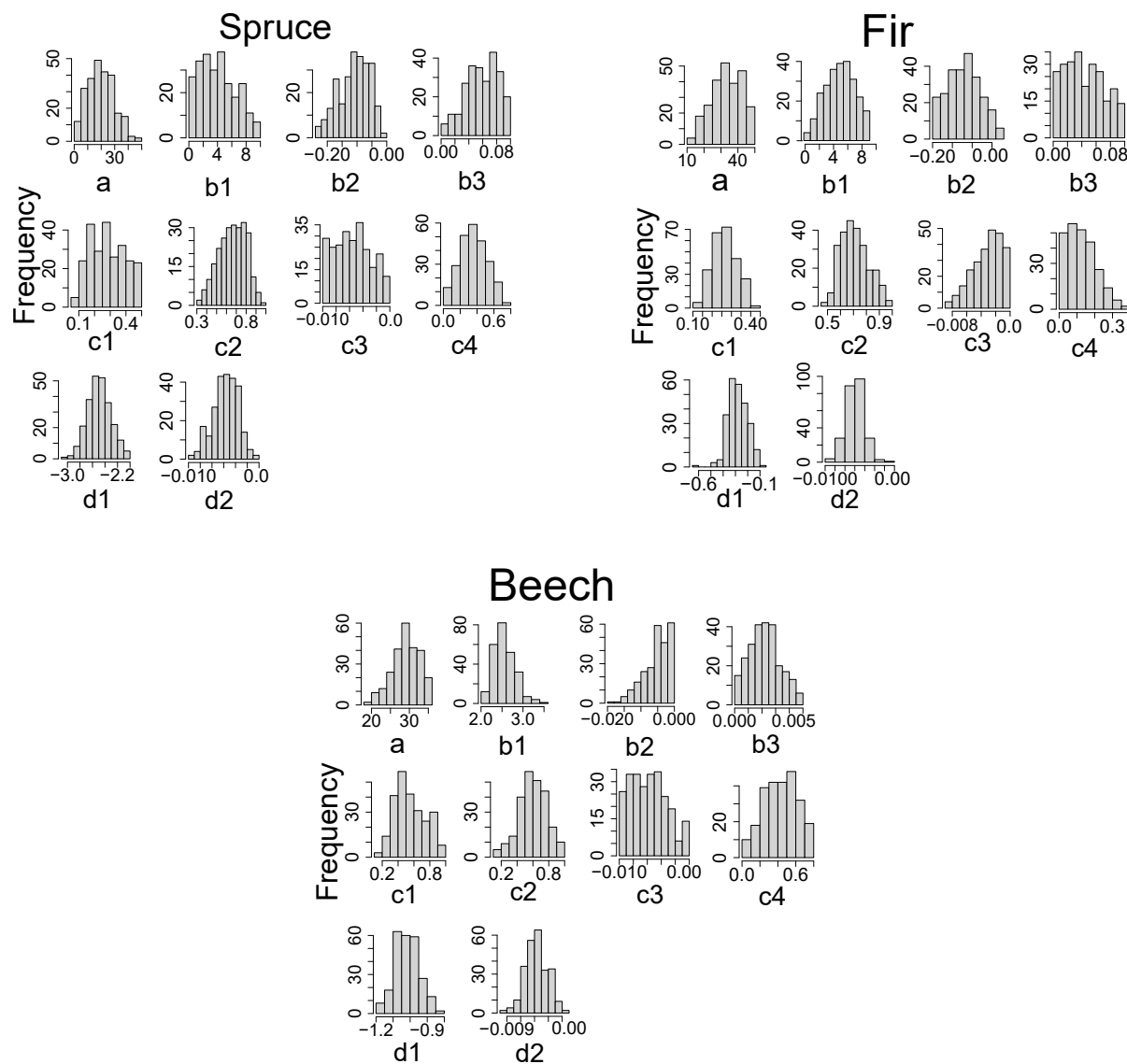


Figure 4.1: Posterior distributions of parameter estimates for the 10 parameters involved in different sub-models of the regeneration model, and for each species. Parameter a corresponds to the fecundity sub-model, parameters b1, b2, b3 to the survival sub-model, c1, c2, c3, c4 to the growth sub-model and d1, d2 to the browsing rates sub-model. Details of prior and posterior ranges and posterior means of each parameter are specified in table 1.

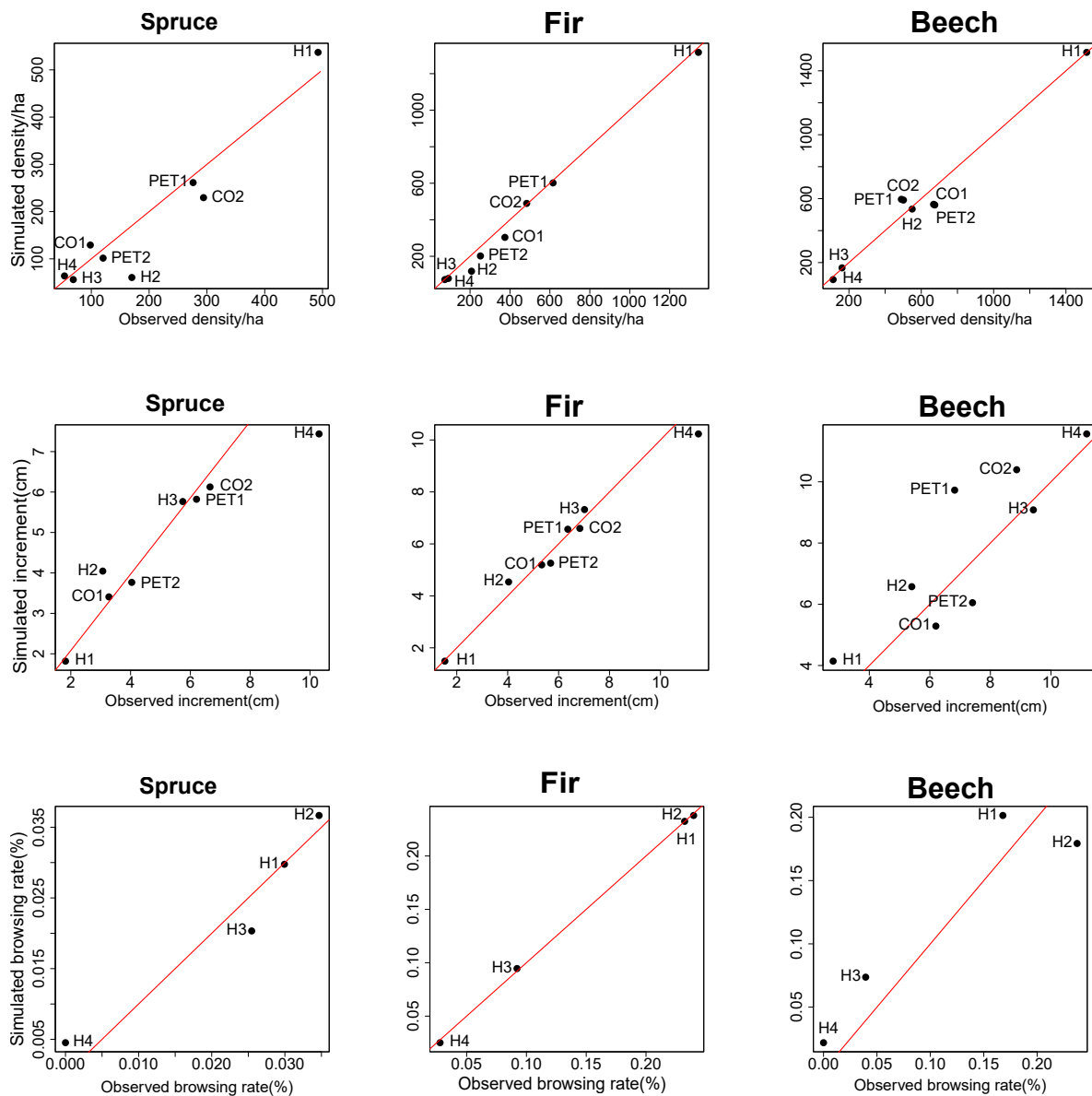


Figure 4.3: Simulated (y-axis) vs observed (x-axis) summary statistics (SS) for each species (corresponding to rows), with different graphs for different categories of SS (densities, height increments, browsing rates - corresponding to columns). SS include mean values of sapling densities and height increments for height, light and PET classes, and browsing rates for height classes. Height classes: H1 = Sapling height 10–50cm, H2 = Sapling height 51–150 cm, H3 = Sapling height 151–300cm, H4= Sapling height 301cm – DBH=7.5cm, PET classes: PET1= plots with PET < mean observed (47.5mm, annual monthly mean), PET2 = plots with PET > mean observed (47.5mm), Canopy openness classes: CO1 = plots with canopy openness < mean observed (10.66%), CO2 = plots with canopy openness > mean observed (10.66%). The red line represents $y=x$.

4.4 Results

4.4.1 Posterior parameter estimation

The ABC simulations predicted parameter values for regeneration processes of fecundity, growth, survival and browsing rates for each species in the model. The histograms for all parameters (except b2 for beech) followed smooth bell shaped curves, indicating that the posterior distribution of the parameters covered the full range of values leading to precise simulations (figure 4.1). Truncations at zero corresponded to limits we fixed in the prior distributions to force parameters to be either positive or negative, based on biological knowledge, as seen in the posterior distribution in b2 for beech (fig. 4.1). The means of predicted parameter values are specified in table 4.1. Each of the parameter for every species is well predicted in the range of priors entered as input, as the construction of the model does not allow parameter values to go beyond the prior range.

4.4.2 Validating accuracy of predictions through summary statistics for current climate and browsing conditions

The graphical comparison of observed vs. simulated statistics for all species revealed a minimum deviation of the points from the 1:1 line with no particular bias, indicating good model predictions (figure 4.3). The different summary statistics are distributed as expected, for example for height increment, $H4 > H3 > H2 > H1$, $CO2 > CO1$, $PET1 > PET2$ meaning that the model correctly reflects observed data. We see that the mean density values for beech in CO1, CO2, PET1 and PET2 categories are not very far from each other, indicated low dependence of beech density on canopy openness and PET compared to spruce and fir (fig.4.3, row 1). Parameters are fitted differently according to the species, leading to much higher browsing rate for fir than for spruce, and to a lesser extent beech (figure 4.3, row 3).

The predicted parameters confirm a significant species difference for the different processes (table 4.1). The number of saplings established at height 10 cm responded less to basal area (parameter a) for spruce than for beech and fir, indicating a smaller number of established spruce saplings at 10 cm for a given basal area. However, sapling survival was higher for spruce and beech than for fir. The magnitude of sapling growth did not differ much between spruce, fir or beech, and were well predicted, except beech height increment for low PET values (PET1), which was over-estimated in model predictions.

Process	Parameter	Spruce			Fir			Beech		
		Prior range	Posterior range	Posterior mean	Prior range	Posterior range	Posterior mean	Prior range	Posterior range	Posterior mean
Fecundity	a	0 to 50	2.354 to 48.644	17.82	0 to 50	12.910 to 49.949	29.007	0 to 50	1.821 to 34.781	26.103
Survival	b1	0 to 10	0.026 to 9.948	4.155	0 to 10	0.021 to 9.749	2.575	2 to 4	2.038 to 3.568	5.277
Survival	b2	-0.3 to 0	-0.239 to -0.012	-0.101	-0.2 to 0	-0.199 to -0.021	-0.005	-0.02 to 0	-0.019 to -2.23e-05	-0.103
Survival	b3	0 to 0.1	0.002 to 0.100	0.05	0 to 0.1	2.16e-04 to 0.099	0.002	0 to 0.005	5.57e-05 to 4.97e-03	0.036
Growth	c1	0 to 0.5	0.073 to 0.496	0.262	0 to 0.6	0.123 to 0.445	0.545	0 to 1	0.162 to 0.999	0.244
Growth	c2	0 to 1	0.322 to 0.951	0.659	0 to 1	0.492 to 0.987	0.627	0 to 1	0.122 to 0.944	0.673
Growth	c3	-0.01 to 0	-0.01 to -3.56e-05	-0.005	-0.01 to 0	-0.008 to -9.56e-06	-0.005	-0.01 to 0	-0.01 to -4.94e-05	-0.001
Growth	c4	0 to 1	0.013 to 0.727	0.359	0 to 0.5	2.63e-03 to 0.392	0.358	0 to 1	2.88e-03 to 0.797	0.104
Browsing	d1	-4 to 0	-3.026 to -2.036	-2.656	-1 to 0	-0.632 to -0.083	-1.006	-1.2 to 0	-1.165 to -0.844	-0.511
Browsing	d2	-0.05 to 0	-0.01 to -0.004	-0.009	-0.1 to 0	-9.65e-03 to -6.57e-03	-0.007	-0.01 to 0	-9.34e-03 to -4.71e-03	-0.01

Table 4.1: Prior and posterior ranges, and the mean of the predicted parameters, for each species and each process.

Browsing was lowest for spruce, followed by beech and the highest browsed species was fir.

4.4.3 Predicted tree recruitment rates for future

Beech had the highest simulated mean current tree recruitment rates over the study plots, with an average of 11 trees recruited per year per hectare, and some sites predicted to have up to 40 recruits per hectare and year in the best scenario (figure 4.5). Fir and spruce have comparatively low tree recruitment rates in current climate and browsing scenario, with means of 4 and 5, and a maximum of 11 and 24 tree recruits per year per hectare respectively. Increasing PET values in different climate scenarios for 2100 negatively affected tree recruitment rates for all three species, but the recruitment rates reduced for fir, spruce and beech in decreasing order. Increased browsing rates reduced tree recruitment of fir the most, and beech to a lesser extent, and decreasing browsing rates led to increased recruits in fir and beech, but there was no significant effect of browsing on spruce. The cumulative effects of climate and browsing affected fir the most, followed by spruce, and least of all, beech. Despite a negative effect of an increase in PET and browsing in the most pessimistic scenario for the year 2100, the average recruitment rate never diminished below 5 recruits per year per hectare, with some plots still having more than 20 recruits. In all of the climate and browsing conditions, all the sites had at least one beech recruit per year and hectare (averaged over last 20 years of the simulation). In the worst climate scenario, and with the strongest pressure of browsing, fir was estimated to have close to 1 tree recruit per hectare only once in every 3 years (or 0.3 trees per year per hectare), whereas spruce was expected to have on an average one recruit per year per hectare. Some plots could continue to sustain a higher number of recruits, but much lower than those of today. If we count the number of plots predicted to have no tree recruitments for the last 20 years (Figure 4.7), out of 152 plots, beech currently has 46 such plots, followed by spruce (112) and fir (91). These numbers are estimated to be 77, 132 and 134 (out of 152) in the year 2100 in the worst-case climate and browsing scenario, with at least 50 % of the plots having no tree recruitment for at least 20 years.

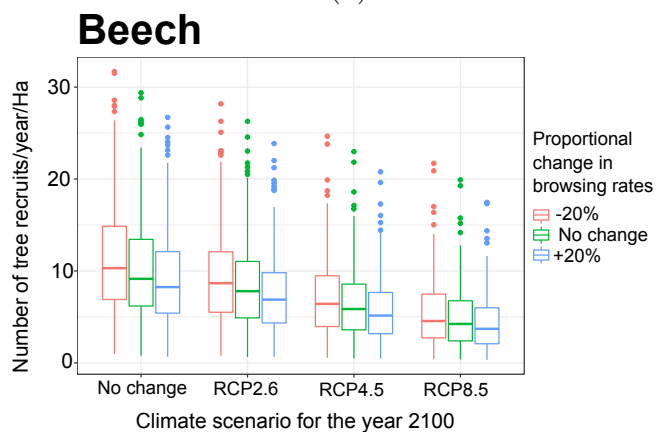
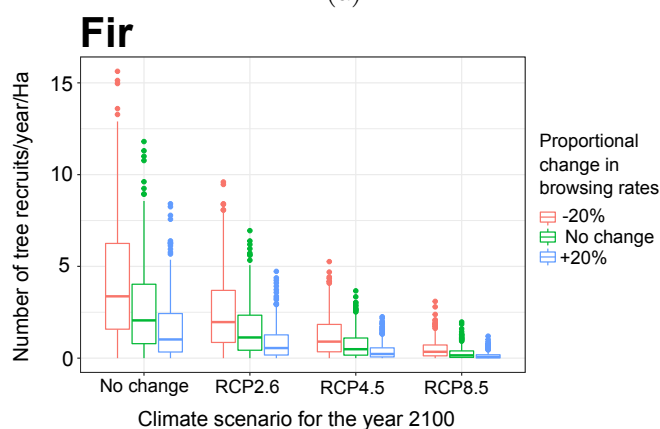
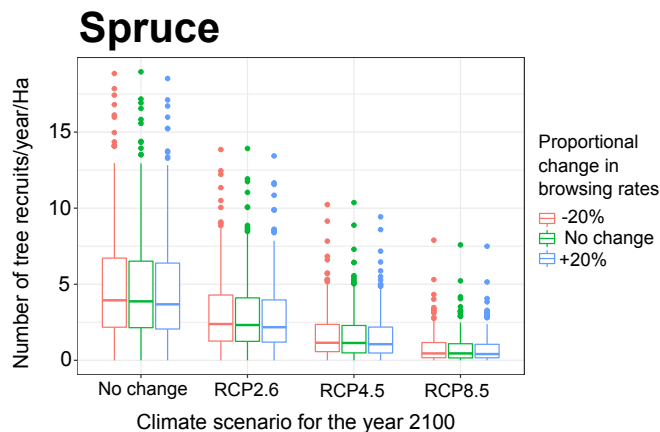


Figure 4.5: Boxplots for tree recruitment rates per year and hectare for different climate and ungulate pressure scenarios, for spruce, fir and beech, across 250 parameter vectors predicted by ABC simulations. The x-axis corresponds to the different climate scenarios in the year 2100 (optimistic-RCP2.6, intermediate-RCP4.5 and pessimistic-RCP8.5) and the colors correspond to different browsing rates (20% decrease, current rates, 20% increase). The horizontal bold lines in each box represent the median, while the lower and upper hinges represent 25th and 75th percentile. Points are outliers.

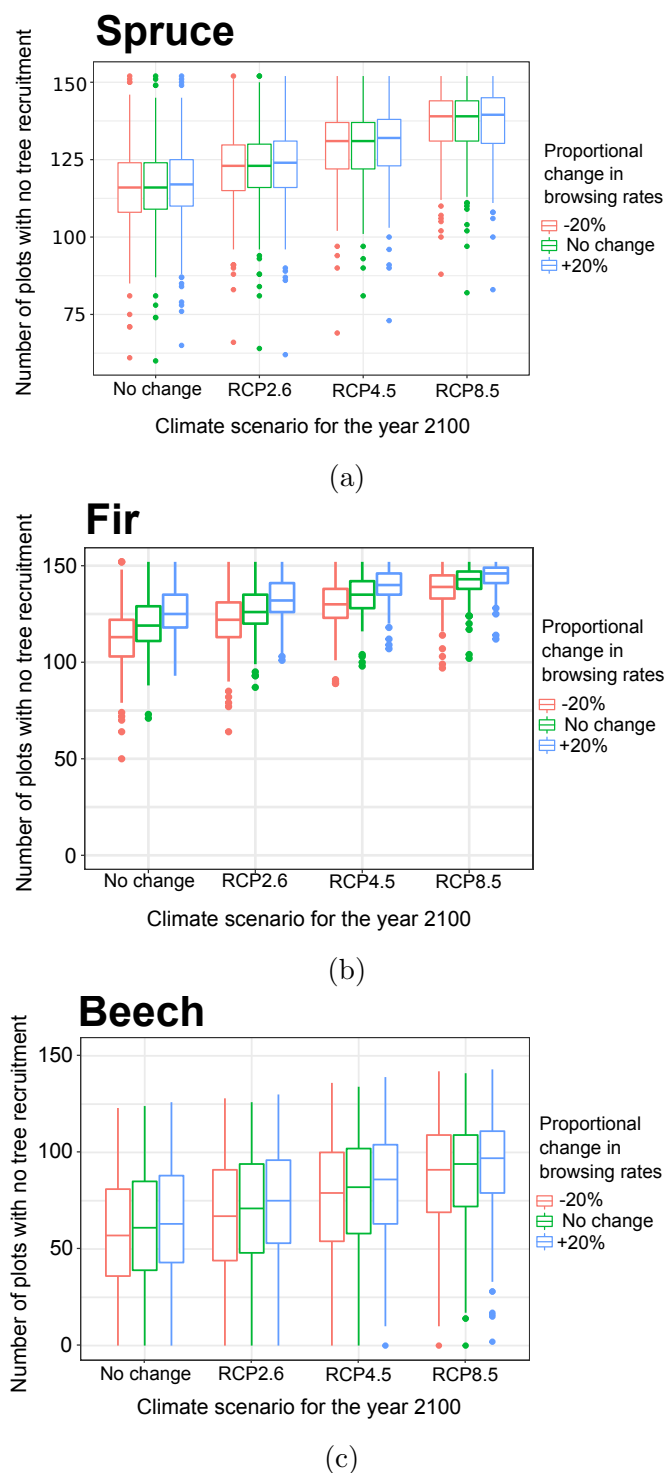


Figure 4.7: Boxplots for spruce, fir and beech, representing the number of plots (out of 152) that are predicted to have zero tree recruitment for the last 20 years out of 100 years of simulations for different climate and ungulate pressure scenarios. The x-axis corresponds to different climate scenarios in the year 2100 (optimistic-RCP2.6, intermediate-RCP4.5 and pessimistic-RCP8.5) and the colors correspond to different browsing rates (20% decrease, current rates, 20% increase). The horizontal bold lines in each box represent the median, while the lower and upper hinges represent 25th and 75th percentile.

4.5 Discussion

Climate change and browsing can have a strong impact on regeneration processes and overall forest dynamics that will shape future communities. Here we found for spruce fir and beech, that at least 50 % of the plots we sampled will not have sufficient tree recruitment by the year 2100. Among the 3 species, both climate and browsing leads to maximum detrimental effects on fir, spruce is negatively affected mostly by climate, and even though both factors affected beech regeneration as well, the effects are comparatively modest. Using the ABC approach, we were able to parametrize several demographic processes and estimate tree recruitments. Both climate change and biotic pressure will impact sapling and tree recruitment dynamics and our study showed that forest management practices are needed to maintain sufficient forest regeneration fluxes.

4.5.1 ABC as a promising methodology

Our study is among the first few attempts to quantify parameters for multiple demographic processes in a complex regeneration model using Approximate Bayesian Computation (ABC). Recently, by using single-census sapling count data of 13 Mediterranean and conifer species from the Spanish Forest Inventory dataset, [Lines et al. \(2020\)](#) used ABC to quantify annual tree recruits and juvenile dynamics using ABC ([Lines et al. \(2020\)](#)). They established climate dependences on the probability of occurrence of a species, while the growth and mortality of an individual depended on conspecific tree basal area and light competition, and tree recruitments were estimated using 2 summary statistics ([Lines et al. \(2020\)](#)). ABC has previously been used for different ecological studies such as understanding population dynamics ([Lamonica et al. \(2021\)](#); [Sirén et al. \(2018\)](#); [Chen et al. \(2017\)](#)), community assembly ([Ruffley et al. \(2019\)](#); [Jabot and Chave \(2011\)](#)), estimating parameters for various individual and process based models ([Lagarrigues et al. \(2015\)](#); [Vaart et al. \(2015\)](#); [Hartig et al. \(2014\)](#)). Many of these ecological approaches are relatively simple, predicting only a few parameters for 1 or 2 processes. However, ABC has the potential of being applied in much more complex problems ([Stumpf \(2014\)](#)), as used very often in genetics and evolutionary studies.

There are no robust methods to compare results of an ABC, or to ensure goodness of fit. Hence, we followed a pragmatic approach of visual and graphical confirmation to make sure the summary statistics and parameter values were well predicted ([Lemaire et al. \(2016\)](#)).

We initially did trials with the ABC rejection method, but the main shortcoming was the computational expense and the speed of simulations, which was 5-10 times slower than the sequential method. We later moved to a sequential ABC method, formulated by Lenormand (Lenormand et al. (2013)), which significantly increased the speed of processing, making the simulations more than 10 times faster, but still had high computational costs. The run time for simulations of each species varied between 7-10 days. This computing time points a limit of ABC for model selection strategies, in which the calibration and comparison of many different models is required.

We were able to estimate all 10 parameters for the demographic processes of sapling establishment, growth, survival, and browsing rates, for spruce, fir and beech, using 20 summary statistics. This demonstrates the potential of estimating processes with partial availability of data. In our case, there was no field data available about the annual rates of new sapling establishment and sapling survival, for any of the species. However, the variables that we were able to observe on the field (sapling densities, height increments and browsing rates), associated to the hypothesis of stationary sapling populations, provided sufficient indirect evidences to estimate the unobserved demographic processes. Height increment is usually not measured in forest regeneration inventories, however it was crucial in our analysis as a flux variable as it provided information about the speed of the processes through time, complementary to the state variable represented by density. Repeated measures of densities on permanent plots is another way to track changes over time. However, it is quite difficult to separate the effects of growth and survival in this data, especially when the time between two observations is long. In any case, the addition of measures of sapling grow in regeneration inventories would significantly improve the possibilities of demographic analyses.

In addition to choosing field data variables carefully, it is crucial to summarize the data into optimal summary statistics in order to calibrate a model (Barnes et al. (2012)). However, identifying the sufficiency of summary statistics is challenging and data specific (Marin et al. (2014); Nunes and Balding (2010)). Here, we calculated summary statistics corresponding to different levels of the co-variables expected to have an effect on demographic processes (sapling height, plot canopy openness, plot PET). The variations of the different observables (densities, increments, browsing rates) between levels of co-variables detected the underlying effects of these co-variables on demographic processes (Barnes et al. (2012)).

4.5.2 Sensitivities and future of spruce-fir-beech forests

We found that there was a significant difference among species in their fecundity, growth and survival patterns, and unsurprisingly, in the tree recruitment rates. Among the three species, the overall seedling establishment was highest for fir, followed closely by beech, and lowest for spruce, even though spruce produced many small seeds and had the highest sampled tree basal area among the three (supplementary material). This could be due to limitations with seed viability (Paluch et al. (2019); Diaci (2002)), or absence of suitable microsites for spruce seedling establishment (Simon et al. (2019a)), or a more complicated relation with basal area as competition for resources in producing seeds. However, by the time the saplings reach tree recruitment, fir displayed the lowest number of tree recruits among the three (figure 4.5), indicating that fir saplings have the lowest survival rates, as supported by (Čater et al. (2014)). There are other studies that suggested high mortality of young spruce saplings due to insect pests (Luoranen et al., 2017) or root fungal diseases (Lilja and Rikala (2000)). Even though fir and beech saplings fare better in low light conditions than spruce (Orman et al. (2021); Lombaerde et al. (2020); Vencurik et al. (2020); Simon et al. (2019a); Čater and Diaci (2017); Orman and Szewczyk (2015)), ungulate browsing damage could possibly pose a greater threat to fir saplings (Fuchs et al. (2021); Vencurik et al. (2020); Paluch et al. (2019); Bernard et al. (2017); Häsler and Senn (2012); Heuze et al. (2005); Senn and Suter (2003); Seagle and Liang (2001)) than the advantage of shade tolerance.

We quantified the influence of climate (summed up by PET) and ungulate browsing on different demographic processes involved in regeneration, along with predicting tree recruitment rates in current and projected future scenarios. We used the PET of a site as the climatic variable affecting sapling growth and survival, as suggested by Unkule et al 2022. PET is influenced by both temperature and water deficit, both of which shape regeneration and forest tree compositions (Schurman et al. (2019); Tingstad et al. (2015); ?). Using PET as the climatic variable in our model also served the advantage of considering the climatic water demand as affected by increasing temperatures in the future as a combined effect on demographic processes. Even though it is more common to use the soil or climatic water balance to establish such relations (Helluy et al. (2021); Moser et al. (2017); Granier et al. (1999)), we found more significant results with PET than other climatic water variables in initial simulations.

Overall, tree recruitments for beech were the highest in current as well as future

climatic projections (figure 3). Beech has been reported to respond negatively to droughts and higher temperatures in lower altitudes (Klopcic et al. (2012b); Silva et al. (2012)), where it is warm and dry. The higher altitude mountains may become a much more suitable habitat for beech 80 years from now, encouraging higher recruitments and movement of these trees to high altitudes (Muffler et al. (2021)). Spruce tree recruitment is not expected to be affected by a change in browsing rates, but is severely reduced in pessimistic climate scenario for 2100 (Cailleret et al. (2014)) (figure 4.5). Our plots cover optimal conditions for spruce today, which means less favorable conditions with climate changes. In contrast, our plots represent the current colder edge of the conditions favorable to beech. Hence, as temperatures rise, conditions in its higher edge become closer to the optimum for beech, posing a considerable chance of a shift in forest composition that can be dominated by beech (Muffler et al. (2020)). It is also the indicator of substantial economic losses, as spruce and fir are conifers, economically more important than beech, which is usually of low quality in mountain conditions (Thurm et al. (2018)).

In a balanced uneven-aged forest stand, the number of small trees recruited annually must equal the number of trees harvested or dying annually; and the commercial volume of harvested or dead trees must correspond to the commercial volume produced annually. In the forests of the Alps considered here, production is between 3 and 10 m³/ha/year depending on the soil and climate. Harvested trees usually have a commercial volume between 0.5 and 1 m³ for thinned trees and between 1 and 2 m³ for mature trees. Maintaining a balanced uneven-aged stand requires therefore the recruitment of about 3 to 20 trees/ha/year. Our predictions show that such a flux of recruits will be difficult to reach in many areas, and that the proportion of conifers among the recruits obtained will likely be very low.

4.5.3 Forest management implications

Our results suggest a risk of insufficient recruitment of new trees, and even in some cases no recruitment at all of fir and spruce by the year 2100 (figure 4.7).

Among the processes that we studied, one of the factors limiting tree recruitment was survival rates, as there was high mortality observed in smaller saplings of all three species. This points to the unavailability of suitable site conditions for optimal growth and development of saplings (Chang-Yang et al. (2021); Holeksa et al. (2021); Kunstler

et al. (2005)). However, obtaining specific optimal conditions for saplings is a challenge. For example, young spruce saplings prefer medium sized gaps when very young, but requires more diffused light as it grows (*Diaci et al.* (2020)).

The first way to reduce sapling mortality and increase sapling growth is to reduce canopy cover and increase light availability. This can be done by reducing the density and size of mature trees, i.e. harvesting more trees and smaller trees. However if it is done homogeneously in space, it increases more diffused light than direct light on the ground, which can be beneficial to certain species to create favorable microsites, but can also increase competition with the understory. Another, more popular strategy that can be used is the creation of gaps of various sizes, by cutting down trees in a clustered fashion, which improves direct light on the ground. However, it also brings heat to the ground, which increases PET, and is not favorable for saplings (*Diaci et al.* (2020); *De Montigny and Smith* (2017); *Bolte et al.* (2009); *Diaci* (2002); *Price et al.* (2001)). Gap creation also makes way for other understory growth such as ferns and shrubs, which act as competition to the saplings, as well as gives larger physical spaces for ungulates to access feed such as fir saplings (*Vandenberghe et al.* (2006)). Managing the size of the gap can turn these negative interactions into positive ones, as shrubs act as barriers for ungulates to reach saplings, thus nursing their growth (*Walters et al.* (2016)). However, *Walters et al.* (2016) also suggests that in the long run, irrespective of the gap size, lesser browsed species areas bound to do better and recruit successfully as opposed to those preferred by browsers.

Along with managing the size of gaps, it is also necessary to consider the individual characteristics of the trees that are being harvested, and the role they play in the current forest structure (*Li and Lo* (2014)). One possibility is to increase the minimum DBH at which trees can be harvested. With bigger trees, a same canopy cover corresponds to a smaller number of trees and a smaller number of recruits is required to replace harvested trees. Moreover, large trees create a heterogeneity within a stand and favor the uneven-aged structure. Maintaining a balanced uneven-aged stand structure is indeed usually easier when a few trees of good quality are allowed to reach large sizes. However, this decreases genetic adaptations to newer environmental conditions as we maintain old trees unadapted to current climate.

If tree harvesting has to continue at current rates, or there are no other solutions to ensure forest renewal, there could be a need to plant smaller saplings in complement

to natural regeneration. There are instances in which forests have been successfully renewed in such adaptive management regimes after disturbances (Buma and Wessman (2013); Löff et al. (2004)). Assisted migration, the anticipation of natural migration by planting saplings of local species with the genetic characters of populations coming from hotter locations or by planting sapling of new species is under debate (McLachlan et al. (2007)). Some experimental trials done to test the potential of assisted migrations reveal promising results for improved survival potential and growth of trees in new climatic conditions (Sáenz-Romero et al. (2021)). However, we lack experiments to analyze the effective success, the risks of genetic pollution and the cost of such strategies (Gömöry et al. (2020)). We do not recommend large plantations or monocultures, especially in mountain areas, because of their negative impact on the protection role of mountain forests against natural hazards, mountain landscapes and biodiversity, and because of the economic risk, such plantations represent (Spiecker (2000)).

In any case, the explosion of ungulate populations has become a problem in the process of forest renewal, and to maintain a biodiversity balance. Another management suggestion would be to make stricter policies to regulate hunting, through conversations between different stakeholders such as researchers, foresters and hunters. Hunters can be giving more returns, there can be use of specific strategies such as "hunting for fear" (Cromsigt et al. (2013)). It is also possible to create large enclosures that will keep away ungulates, which has shown in increase in growth of saplings (Barrere et al. (2021); Löff et al. (2021); Petersson et al. (2020); Diaci (2002)), but sometimes, also an increase in understory vegetation which would otherwise be consumed by herbivores (Laurent et al. (2017)). Additionally, ungulates may play a role in dispersal of seeds, and so large enclosures may also limit the dispersal of seeds for forest renewal (Bogdziewicz et al. (2020)).

There is also a gap in communication about management strategies, between different stakeholders such as foresters, researchers and policy makers, leading to inconsistencies in policies and actual plans (Sousa-Silva et al. (2018)). In addition, there is an absence of integrated action based forest management plans, and specific recommendations for foresters who are meant to implement these plans (Tudoran et al. (2021); Hagerman and Pelai (2018); Beguin et al. (2016); Lindner et al. (2014); Heller and Zavaleta (2009)). However, forest management plans are meant to be site specific, depending on the forest compositions and structure, climate and other site-specific conditions, as well as the intensity of browsing in the region. A better alternative is to involve different stakeholders while making specific management plans for forest stands or landscapes, and to revisit

the plans every few years to adapt them to changing conditions.

CHAPTER 5

Discussion and perspectives

5.1 Synthesis of results

Many recent studies have recognized substantial impacts of different global pressures such as rising temperatures, increasing number of disturbances such as storms, droughts, fires, explosion of herbivore populations, land use change and fragmentation of landscapes etc. on forest ecosystems. Due to these anthropogenic changes, there is a distinctly observed shift in the drivers and limiters of forest and regeneration dynamics. It is necessary to not just identify empirically, but also quantify the effects of most important biotic and abiotic environmental factors governing the different demographic processes involved in forest dynamics. The objectives of this thesis were to identify these factors, and quantify their role in determining tree recruitment fluxes of spruce, fir and beech in the French Alps and Jura mountains in France. In order to fulfil these objectives, the thesis is divided into 4 main parts: a field study to acquire regeneration data (chapter 3), data exploration and identification of main factors affecting regeneration (chapter 3), model building and parameter estimation based on the results of chapter 3 (chapter 4), and predictions of recruitment rates in projected future conditions (chapter 4).

The results confirmed that sapling size, canopy openness, and browsing pressure, in addition to climate, are the major driving force in regeneration processes. I tested the effects of a number of climate variables on sapling growth and survival, some of them being mean annual and monthly temperatures, precipitation, soil water content and demand. I identified an effect of high temperatures and water stress on regeneration demographic processes, and among the variables tested, potential evapotranspiration (PET) proved to be the most significant candidate that summarized the climatic water balance, and integrated the effect of increase in temperatures. Hence, I chose this as the main climatic variable to be included as a predictor of sapling growth and survival processes. Sapling growth reacted positively to higher canopy openness on the plot, whereas survival was not directly affected. Even though there was no direct correlation, growth and survival processes indirectly affected each other, as growth and survival rates were consistently higher for taller saplings. So, if a sapling grew faster, its chances of survival also increased. However, growth, and as a result survival, was negatively affected by the browsing pressure on the plot. Each species reacted to these environmental variables to different extents. For example, fir regeneration (< 150 cm high) was severely compromised by high levels of damage due to browsing by ungulates, followed closely by beech. Spruce was most sensitive to PET, followed by fir and beech was least sensitive, while shade tolerance of beech was highest, followed by fir and spruce was least tolerant

to shade. We suspect many other factors such as soil variables, competition with other understory species, or topography playing a role in regeneration processes, but the the most significant ones were chosen.

A model representing the main regeneration processes was parametrized using Approximate Bayesian Computation (ABC), which helped to estimate tree recruitment rates of these species in the present and projected future climate conditions. Mean current recruitment rate predictions (per year and hectare) of spruce (5) and fir (3) were significantly lower than beech (10) . By the year 2100, in the most optimistic and pessimistic climate and browsing scenarios, I predict average recruitment rates (per hectare and year) to diminish for all three species, but to different extents (optimistic: spruce (3), fir (2), beech (10), pessimistic: spruce (0.7), fir (0.1), beech (4)). The variability of predicted recruitment rates was high, with some plots keeping a high a recruitment rate, whereas others had no recruitment at all. This variability also invites to be prudent in the degree of confidence of these results. Within the range of conditions experienced by our sampled plots, these results indicate a potentially higher fitness of beech in changing climate and browsing conditions compared to spruce and fir.

This thesis highlights the role of regeneration processes in determining future forest compositions, and advocates the inclusion of these processes in forest dynamic studies.

5.2 Discussion and perspectives

5.2.1 What factors contribute to tree recruitment?

The structure and composition of a community at a given time is the result of multiple processes, and multiple environmental factors acting synchronously to influence these processes (Lortie et al. (2004)). Regeneration is composed of the processes of fecundity, seedling establishment, sapling growth and survival until they reach the stage of an adult tree. The fact that a tree is recruited at a moment is dependent on an individual going through multiple environmental filters, as well as intra and inter-specific interactions of competitive or facilitative nature. In this section, I elaborate on the significance of each process in regeneration dynamics, and the role of different biotic and abiotic factors in different processes.

5.2.1.1 Demographic processes in regeneration dynamics

Fecundity and seedling establishment

Fecundity, i.e. the number of viable seeds produced by a plant, is highly species-specific and determined by the life history and adaptive strategy of the species, along with biotic and abiotic factors such as meteorology, pests, predators etc. Thus, many environmental filters act on the seed source before the seed is produced, dispersed or established as a seedling (Szwagrzyk et al. (2021)). Many species, including spruce (Hacket-Pain et al. (2019)), fir (de Andrés et al. (2014)) and beech (Övergaard et al. (2007)), show large inter-annual variabilities of fecundities, called masting, with particular years of high seed production marked as masting years of particular species (Hacket-Pain and Bogdziewicz (2021); Sachser et al. (2021); Pesendorfer et al. (2020); Zamorano et al. (2018); Bisi et al. (2016)). In addition, certain focal individuals of the species are more likely to produce most of the seeds of the year (Gratzer et al. (2021); Walck et al. (2011)). As I had no quantitative measure of seed production, or of the number of very small established seedlings (< 10cm high) as a proxy of seed production, I assumed a linear relation between the number of established seedlings and species tree basal area in the plot, and assumed that it remained constant through the years of the simulation (chapter 4). However, (Qiu et al. (2021)) reveal a bell-shaped relation between fecundity and DBH, indicating lower fecundity for large trees with high DBH. Hence, I could have over-estimated the fecundity, but on an average, I assume that it compensates the variability during masting and non-masting years. I did not test a

direct impact of climate on fecundity or seedling establishment. However, many recent studies carried out in the Alps indicate low sensitivity to rising temperature of seed production of conifers such as spruce and fir, as well as broadleaved species such as beech (Bogdziewicz et al. (2021); Hackett-Pain et al. (2019); Bisi et al. (2016); de Andrés et al. (2014)).

My results show that spruce had the lowest seedling establishment, followed by beech, and fir seedling numbers (10cm high) were the highest. However, there are reports of spruce having the highest comparative seed production among spruce, fir and beech (Diaci (2002)). One possible explanation is that small seedling mortality of spruce could be extremely high in the very first stages, perhaps because spruce requires specific conditions and microsites for establishment, leading to low seedling establishment rates. Even then, the values between the species are comparable, indicating that there is adequate seed production and establishment occurring in current conditions.

Growth and survival

The next demographic processes that I considered were sapling growth and survival. I observed a great variation in densities (0-7 saplings/ m^2) as well as growth of saplings (0-56 cm), which was species and site specific, and depended on many environmental factors. However, the problem lied in identifying multiple interacting drivers and limiters acting on these sites. In many circumstances, I was unable to correctly measure certain variables. For example, there was too much heterogeneity in physical characteristics of soil such as depth, stoniness even within a plot, to take correct measurements. Secondly, the different factors form a complicated web of interactions that could not be easily separated to include in models.

I only had a screenshot of data on the field, and there was no measure of sapling survival rates, which was later estimated using ABC. Survival of a sapling is a result of a dynamic combination of the annual growth of saplings, and change of sapling densities with time. This means that I assumed that if a sapling does not grow, or grows very slowly, over time, its chances of survival decrease and it might die. Thus, I predict that densities of saplings will remain low if saplings don't grow well. Using this approach, I was able to model and predict sapling survival probabilities, as well as estimate tree recruitment rates with density and growth measures. In typical forest inventories, regeneration measures include information about saplings densities or cover, but the

data about sapling growths is rarely included. This thesis demonstrated the importance of including additional informative variables such as sapling growth in forest inventory protocols.

I discovered that sapling growth and survival varied with sapling height, and saplings could grow faster and were more likely to survive as they grew older. Smaller saplings were the most vulnerable, with very high mortality rates, as they required specific conditions to survive (Holeksa et al. (2021); Simon et al. (2019a)). They need to establish, and in particular, to root deep in the soil for easier access to water (Curt and Prévosto (2003)). So the first year is often critical, and this is the reason why often a high number of 1-year-old seedlings are recorded, and no older ones (Diaci et al. (2020)). As saplings grow a little older (20-150 cm), in addition to other abiotic limiters, they can also be damaged or eaten by ungulates, decreasing their chance of survival (Kienast et al. (1999)). Hence, once a species reaches 150-200 cm or above, it can be considered a critical height after which its survival changes increase considerably, as it becomes more resilient to surrounding disturbances such as competition (Chang-Yang et al. (2021); Hansson and Karlman (1997)), or browsing, compared to smaller saplings.

Tree recruitment

Tree recruitment rates are a cumulative result of different regeneration processes (Dobrowski et al. (2015)), and the success of a sapling to reach recruitment stage is a result of many interacting environmental filters (Lusk and Laughlin (2017)). The limitation of either or all of the process leads to a detrimental impact on recruitment rates (Clark et al. (1999)). I elucidated some of these filters in this thesis, but probably missed others, as there were practical difficulties in the investigation of the interplay between them. For example, my model estimated higher fecundity of fir than spruce and beech in current climatic conditions. However, due to limiting factors such as browsing, in survival of fir saplings, it is overtaken by beech, as beech has the highest number of tree recruits. The tree recruitments tend to get fewer in number over years of accumulating environmental changes, as I predict close to no tree recruits for fir, and very few for spruce in the year 2100, but other competitive interactions between species at different life stages, that I was not able to account for, could have an even higher negative impact on the tree recruitment rates. However, it is also possible, due to facilitative interactions, or presence of favorable microsites, and species co-existence becomes easier. This dynamic shift between the number of new tree recruits, or more extreme, the persistence of disappearance of a species from a site after

going through all the environmental filters, will determine the realized niche of the species.

Ensuring a regeneration flux is necessary, not just to maintain forest structures, but also keep up with harvesting rates for economic purposes. According to current harvest practices, about 3-20 new recruits/year/ha are required for maintaining a balanced uneven-aged structure, which is higher than my mean projections for the year 2100 for spruce or fir, which are commercially important species. However, there is high variability in the number of tree recruits predicted on a plot, as recruits are abundant in some sites, but absent in others. I did not detect any specific site characteristics that contributes to this variability, but as indicated in previous sections, one of the shortcomings of this study was the inability to measure and quantify more environmental variables accurately. Additionally, I assume a constant annual fructification rate in our model, which overlooks any temporal variability, that could compensate for missing tree recruits in my model.

Thus, in order to sustain a flux of tree recruitments, it is crucial to manage forests such that there is ample regeneration with scope to grow into trees.

5.2.1.2 Abiotic drivers of spruce, fir and beech regeneration: which species fares better?

I found an increase in observed sapling densities and sapling growths with increasing light availability on the field, and the modelled growth and survival rates displayed the similar patterns. In general, smaller saplings could survive in shade, but they needed more and more light as they grew. This can, in part, explain why saplings are numerous when small, but much lesser in higher height class if light is limited (Balandier et al. (2007)). Light availability, in the form of either direct (Čater et al. (2014)), diffused light (Diaci et al. (2020)) or canopy openness (Barrere et al. (2021); Gaudio et al. (2011b)), is one of the most commonly known drivers of regeneration dynamics (Lombaerde et al. (2020); Simon et al. (2019a); Tinya et al. (2019)). The light availability in turn depends (not necessarily linearly) on the canopy cover on the plot, which could depend on basal area of each species. Hence, in order to accelerate growth and survival of saplings, it is necessary to ensure enough light availability in the plot, which is often done through various management interventions such as creation of gaps by harvesting trees (Walters et al. (2016); Muscolo et al. (2014)). I discuss this management intervention in more detail in section 5.2.2.2.

Among the climate variables that I tested, the results (shown in chapter 4) indicated that high summer temperatures, and overall low climatic balance variables affected regeneration processes. Among the different variables that I considered in the models, potential evapotranspiration (PET), which is an indicator of both temperature and climatic water demand, was the most significant determinant of sapling densities, their growth and survival rates. Hence, the sensitivity of spruce, fir and beech regeneration to PET points toward decreased fitness of saplings in climate change scenarios of warming temperatures and low climatic water availability. Among the three species, spruce is adapted to cold and wet conditions, thus most affected due to warming and droughts, followed by fir; beech is most resilient to warm and dry conditions. Beech has been reported to have low sensitivities (Dulamsuren et al. (2017); Silva et al. (2012); Fang and Lechowicz (2006)), or even positive responses (Muffler et al. (2020)) to increasing temperatures, specially in higher elevations or in the northern part of its range. The opposite is seen in the Mediterranean, which is a much drier region, and beech is much more sensitive to increasing temperatures in that area (Hackett-Pain et al. (2016); Silva et al. (2012)). On the other hand, the worst faring of spruce among the three species is also reported or predicted in future conditions (Begović et al. (2020); Vacek et al. (2019a); Vitasse et al. (2019)) due to its susceptibility to high temperatures and droughts. Along with warming, which is also problematic for fir, the potentially bigger challenge is the damage done by ungulates on fir (Szwagrzyk et al. (2020); Vitasse et al. (2019); Bernard et al. (2017); Vacek et al. (2014); Tinner et al. (2013); Häsler and Senn (2012); Heuze et al. (2005); Senn and Suter (2003)), which is discussed in more detail in section 5.2.1.3. In addition to all these quantified effects, I noticed high variability in observed and well as modelled data that could not be attributed to the variables included in my models, This could be due to site specific effects such as elevation, slope, soil substrate conditions that were not considered. This occurrence is supported by the environmental filtering theory, which suggests that the environment of a species can potentially act as a filter to determine the presence of a species on a site (Lusk and Laughlin (2017)). The community assembly is the result of various environmental filters like light, climate, disturbances such as competition, herbivory and site conditions such as topography. Overall, I predict the tree species composition to shift more in the favour of beech, with the sensitivity to climate change of spruce, and that to climate and browsing of fir. However, in the presence of disturbances, according to the theory of succession, plant community composition can vary significantly, reaching alternative stable states (Chase (2003)). Thus, I expect stands to evolve depending on stand characteristics. For example, high ungulate herbivory could

impair fir regeneration growth and survival in some stands, reducing their presence, while other sites, more protected from herbivores could have flourishing fir populations. Fir and beech are usually strong competitors, but in particular sites at high elevations, in cold climate, spruce could out-compete them and establish its dominance. Thus, not just site conditions, but also the performance of others species will determine the realized niche of each species. This realized niche may be further affected by the possibility of genetic adaptations that allow species to show resilience and mitigate the effects of changing climate (Bradshaw (2004)).

5.2.1.3 Role of ungulate herbivory in regeneration dynamics

Ungulate browsing is known to affect regeneration by disturbing growth and survival of individuals. In the model (described in chapter 4), I assumed for each species, that a browsing event directly affects the growth of an individual, and indirectly affects its survival, as the sapling remains shorter for longer, and hence remains more susceptible to mortality. Taller saplings can potentially have higher tolerance to browsing events as the apical shoot of saplings higher than 150 cm is physically difficult for ungulates to reach. This finding is consistent with other studies that show that older and taller saplings tend to be browsed less often.

As mentioned briefly in the previous section, ungulate herbivory affects fir regeneration much more than beech and spruce, as seen from the results in chapter 3. A decreased fitness at the regeneration stage can thus prevent saplings from reaching adult tree stages. Although the vitality of fir trees has increased since the 1990s in many stands in central and western Europe (Büntgen et al. 2014), fir populations have also locally declined in other areas such as the northern Carpathians, Slovenia and Croatia, mainly due to increasing ungulate browsing (Ficko et al. (2016); Vrška et al. (2009)). In old growth spruce-fir-beech forests in the Western Carpathians, there was no change detected in fir tree basal area of already existing trees in the upper canopy layer. However, there is a limitation in the new tree recruits, indicating a limitation in the stages of growth and survival of saplings, which is attributed to browsing intensities (Parobeková et al. (2018)). We also report a large effect of browsing on the growth and survival of fir saplings, predicting very low number of tree recruits, to the extent that this species may disappear from certain sites by the year 2100. The explosion of ungulate numbers in Europe have affected not only fir, but also many other species such as oak (Barrere et al. (2021); Petersson et al. (2020)), rowan, sycamore maple and goat willow

(Szwagrzyk et al. (2020)) or shrubs such as bramble (Laurent et al. (2017)). However, the effect is most widely reported for fir, indicating greatest threats to fir.

Although I did not study the effect of surrounding vegetation on browsing, it is another factor involved in the selective browsing of a species. For example, in mixed stands of oak-hornbeam, (Barrere et al. (2021)) observed decreased browsing damage to oak, compared to oak-beech stands, as hornbeam is a more palatable species for deer than hornbeam. Saplings of trees such as hornbeam not only added another palatable species for ungulates, but also acted as a physical barrier between oak and the animals. This is an important factor to consider while undertaking management practices such as removal of shrubs and other understory vegetation. The explosion of ungulate populations has led to many negative effects on regeneration, nevertheless, evaluation of damages by ungulates is not a true measure of the ungulate population (Cailleret et al. (2014)). The pressure exerted by ungulates depends on the range occupied by the animals, species favored by the animals, their foraging ability, palatable species availability, which in turn depends on density of ungulates, their age, size, seasonal variations in eating habits etc. forests (White (2012); Morellet et al. (2001)). Hence, the predictions and trends of ungulate populations cannot accurately represent the extent of damage to regeneration.

5.2.2 Predicting forest compositions and adaptation of forest management to environmental changes

5.2.2.1 Estimates of tree recruitment rate in the future

Tree recruitment approximations for current climate and browsing conditions are truncated towards beech, with spruce and fir already at less than an average of 5 tree recruits per year and hectare as indicated in chapter 4. All three species show some sensitivity to both climate and browsing (except spruce, which is not affected by browsing). As the climate sensitivity is higher for spruce and fir, and fir is highly vulnerable to browsing, future predictions suggest the biggest disadvantage to fir, followed by spruce and then beech. Due to this differential species performance in scenarios of climate and ungulate pressure, according to the theory of succession, there are possibilities of changes in vegetation dynamics that could follow different trajectories. Many studies have reported changes in biodiversity (Thom et al. (2017)), species compositions (Czortek et al. (2018)), and species ranges (Wason and Dovciak (2017)) as a result of disturbances such as warmer temperatures, frequent droughts,

change in land use, in different landscapes and ecosystems around the globe. Closer to home, (Didion et al. (2011)) already observed a change in species composition and succession to new stand types, as a result of climate change and ungulate herbivory in the Swiss Alps, and attributed it to altered competition patterns and selective browsing. Similar to my results, (Cailleret et al. (2014)) predicted a complete replacement of spruce and fir by beech in the next 100 years. My results support those of (Cailleret et al. (2014)) that even though spruce is not as susceptible to browsing by ungulates, it's higher sensitivity to climate compared to beech puts it at a disadvantage. This result is partially contradicted by (Klopčič et al. (2017)), with decreasing fir populations, but no projections of changes in spruce populations. Although, this study was carried out on spruce-fir stands and there was no way to understand the role of beech in these dynamics. However, in the absence of fir, and in areas with high ungulate densities, beech is also reported to be severely damaged by ungulates (Fuchs et al. (2021)), thus increasing vulnerability of beech to ungulate browsing as well. This raises questions of what would be the future of beech dominated stands, in high herbivory situations, in the absence of fir.

All these insights in the context of my results suggest the possibility of multiple paths of succession, leading to prospects of alternative stable states depending on environmental conditions. In addition to climatic filters and browsing disturbances, there are also other factors that could possibly determine the community assembly such as site history (Löf et al. (2019)), topography (Moura et al. (2016)), soil and stand characteristics (Piedallu et al. (2019)), competitive and facilitative interactions between and within species (Bosela et al. (2015)). There is also a possibility of phenotypic or genetic adaptations which help species to build resilience to changing environmental conditions (Jump and Peñuelas (2005)).

Having said that, I predict a shift in species composition in spruce-fir-beech forests in general, with an increasing dominance of beech. It may be followed by either establishment of other broad-leaved species, or conifers that can tolerate droughts. Some candidates of species that commonly co-occur with beech, and have potentials of range shifts in the future include chestnut (*Castanea sativa*), European ash (*Fraxinus excelsior* L.), sycamore maple (*Acer pseudoplatanus* L.) (Žemaitis et al. (2019)), oak (*Quercus petraea* (Matt.))(Bontemps et al. (2012)), hornbeam (*Carpinus betulus* (L.)) (Žemaitis et al. (2019)), Scots pine (*Pinus sylvestris* L.) (Pretzsch et al. (2016)) or other pines. Nevertheless, how many of these mixtures survive and persist remains to be studied. However, owing to species variabilities and site heterogeneities, we could imagine that in

a close future, we will still find spruce and fir in the higher elevations, or in some aspects, beech at medium elevation and a colonization with more thermophile vegetation a lower elevations.

5.2.2.2 Forest management implications and adaptive management

My results, indicated in chapter 4, imply a significant impact of climatic conditions in the form of temperature availability and water demand, environmental conditions such as light availability, and disturbances such as browsing pressure on the regeneration of forests that I studied. This impact remained visible in growth and survival of saplings, and is thus expected to modify future tree compositions.

I did not directly test the consequences of applying different management strategies to the forest stands. However, the results show a clear bias of forest compositions towards dominance of beech over spruce and fir in future climate and browsing conditions. Based on these results and the effects of climate and browsing on regeneration of the three species, I can review and discuss a few forest management strategies and their implications, especially in the context of climate change and increasing ungulate browsing. As there is a lag in the response of forests to climate, forests regenerated today will have to cope with the future climate conditions of at least several decades, often even more than 100 years, and hence forest management strategies need to anticipate this future response while being adapted to these changes before implementation (Lindner et al. (2014)).

Adaptive forest management aims to preserve and develop the functionality of forests as a prerequisite for fulfilling the future need for forest ecosystem services, through continuous monitoring and necessary modifications of effects and treatments being used, to ensure that objectives are being met (Bolte et al. (2009)). I, however, restrict here adaptive management in terms of adaptation to climate change.

As climate conditions are becoming increasingly extreme, it is necessary to understand the future needs of a forest and formulate management strategies accordingly. Adaptation could be achieved by either conserving or changing forest compositions and structures, actively or passively (Bolte et al. (2009)). This can depend on the intensity and frequency of disturbance events, susceptibility or resilience of the ecosystem in the face of environmental changes, adaptability of present species composition to new

conditions etc. In our case, the economic importance of spruce and fir makes it a priority to conserve current forest compositions with silvicultural interventions that improve stability and vitality of the stand (Bolte et al. (2009)). However, natural colonization by other conifer species, or even assisted migration can be promoted.

As mentioned in section 2.1, an important environmental factor promoting regeneration establishment, growth and survival is light. An easy way of increasing light availability on a plot is to create gaps by harvesting one or more trees. The DBH at which trees are harvested can be controlled. Increasing the threshold of DBH will result in increasing of tree lifespan, an increase of light conditions heterogeneity on the forest floor, and a decrease of necessary recruitment. However, a drawback is that it increases the risk of natural tree mortality before harvesting, and prevents genetic diversity, which ensures faster adaptability of species to novel conditions. Having said that, just as light availability facilitates the growth and survival of tree species, it also does so with herbaceous species and other understory vegetation, which contributes to competition with tree saplings (Barrere et al. (2021); Helluy et al. (2021); Lombaerde et al. (2020); Laurent et al. (2017)). Hence, maintaining an optimal gap size is an important management intervention to ensure maximum regeneration of tree saplings (Walters et al. (2016); Muscolo et al. (2014)). (Parobeková et al. (2018)), who also observed a takeover of beech over fir and spruce, recommend selected single tree cutting to provide small gaps for regeneration of shade tolerant species such as fir (Ficko et al. (2016); Klopčič et al. (2012a)), and group-selection of trees to cut, creating larger gaps (100-150 m²) in order to supplement regeneration of shade intolerant species like spruce (Klopčič and Boncina (2012)). However, both these strategies also facilitate regeneration of beech, which grows and establishes well in both light and shade conditions (Janík et al. (2014); Ligot et al. (2014)), which could possibly outdo spruce and fir once again.

In the adaptations of forest management to climate change some studies propose to reduce stand density in order to reduce water consumption, among other reasons. Moreover, to increase regeneration, in many situations it is prescribed to reduce canopy cover. So there is a canopy cover to find that makes possible a balance between recruitment and adult tree disappearance by natural mortality and harvesting. An essential criteria of tree selection for harvesting is to remove weak trees before they die. Harvesting therefore replaces partially natural mortality. The balance can be shifted in managed stands compared to natural stands towards lower canopy cover and fewer large trees in order to increase harvesting of leaving trees (much higher value of “fresh

wood” than of dead trees). However the possibility of balance shift is limited and forest managers have to be very cautious not to go beyond the resilience capacity of the forest stand, otherwise long time periods of reduced regeneration can occur with consequences in forest structure, species composition and ecosystem service provision.

Unfortunately, the growth of species like fir, which are susceptible to damage by ungulates, remains compromised even in the availability of light, as they can be severely browsed. The effect of browsing pressure on regeneration is discussed in more detail in section 2.1.3, and it is clear that measures need to be taken in order to control ungulate populations. One of the most discussed management measure is building fences to prevent access of ungulates to saplings until they grow to a height of 200 cm, at which ungulates can no longer easily access the terminal buds. However, fencing is not enough by itself to facilitate regeneration, and needs to be combined with other management practices such as shrub removal, to remove competition in the presence of a fence, or creation of gaps to allow light availability for regeneration growth (Petersen and Malm (2006); Simon et al. (2019b); Jensen et al. (2012); Bergquist et al. (2009)). Building enclosures has also shown promising results of higher growth of saplings (Löf et al. (2021)). However, implementation of such practices is often expensive, complicated, and requires constant monitoring, so is not very suitable to carry out at large scales or in remotely located forests. The other management practice used to control ungulate populations, rather than browsing pressure, is regulated hunting of ungulates, which can potentially remove the pressure on fir saplings, ensuring their faster growth and better survival (Vacek et al. (2017); Diaci et al. (2011)). Thus, maintaining particular ratios of species through management initiatives is a complicated task, and hence the focus should be more on retaining mixtures with set management strategies like gap creation and controlling ungulate populations, rather than relative ratios of different species. (Vacek et al. (2019b)) face a similar dilemma, but recommend retaining mixtures rather than focus on the ratio of each species presence.

In addition to preserving structural diversity, a much spoken about topic is the maintenance of genetic diversity of species. In rapidly changing environmental conditions, it is often impossible for tree species to achieve this diversity sufficiently rapidly by natural selection (Gömöry et al. (2020)). In order to speed up the processes of stand regeneration, and to favor genetic renewal of species, it is sometimes recommended to reduce the threshold of DBH at which trees can be harvested, and harvest all older trees that are not adapted to current conditions, in order to increase the ecological opportunity

for better adapted genotypes (Alberto et al. (2013)). Assisted migration is a frequently suggested mechanism, which includes assisted gene flow i.e. intentional translocation of individuals within the natural range of species, or assisted colonization i.e. translocation of individuals outside the range, which is a way to change species composition at target sites (through active adaptation) (Buma and Wessman (2013); Aitken et al. (2008)). It has its share of limitations and challenges, such as determining appropriate choices of individuals, sites of translocation, experiments based on provenance, but has been shown to have increased species performances in experiments in Canada and Mexico (Sáenz-Romero et al. (2021)).

I suggest an integrative adaptive management approach, which will depend on specific site conditions, keeping in mind that beech is a strong competitor (Mina et al. (2018)), and has the capacity to dominate mixed stands with fir and spruce. In order to choose the correct kind of management approaches, it is a good idea to have long term monitoring of regeneration on a network of sites, as well as strong communication between researchers and practitioners for the part of development of a management strategy and monitoring it (Lindner et al. (2014)).

5.2.3 Modelling forest dynamics

5.2.3.1 Approximate Bayesian Computation as a tool to calibrate regeneration dynamics

Approximate Bayesian Computation (ABC) is a likelihood free approach to estimate parameters for processes with incomplete or inaccurate datasets. As described in chapter 4, I used ABC to estimate parameters for different regeneration demographic processes: fecundity, sapling growth, sapling survival and sapling browsing rate, and further used these parameter values to estimate tree recruitment rates in current and projected future conditions. There are not many ecological studies that have used Approximate Bayesian Computation (ABC) to estimate estimated tree recruitments using regeneration data (Lines et al. (2020)). However, this is an increasingly popular method to estimate tree population and forest dynamics through both individual and process based models (Lamonica et al. (2021); Lagarrigues et al. (2015); Courbaud et al. (2015); Hartig et al. (2014)). Many of them managed to calibrate complex models with more than 20 parameters (Lamonica et al. (2021); Lines et al. (2020)), demonstrating the ability of this method to optimally converge multiple processes without the use of likelihood approximations.

In most model-based statistical inference studies, the likelihood function is of central importance, since it expresses the probability of the observed data under a particular statistical model, and thus quantifies the support data lend to particular values of parameters and to choices among different models (Hartig et al. (2011)). For simple models, an analytical formula for the likelihood function can typically be derived. However, for more complex models, an analytical formula might be indescribable or the likelihood function might be computationally very costly to evaluate (Hartig et al. (2012)). ABC methods bypass the evaluation of the likelihood function (Sunnåker et al. (2013)), and allows the use of aggregated data to derive posterior distributions of parameters to be estimated (Hartig et al. (2014)). In this way, ABC methods widen the realm of models for which statistical inference can be considered. Another difference is that ABC uses summary statistics. It focuses therefore on global patterns in the data represented by these statistics. The choice of summary statistics conditions the patterns taken into account in the model estimation.

In my case, observations consisted of individual sapling height increments and browsing probability, and sapling densities per plot and height class. The browsing and growth equations were able to produce predictions for each individual sapling. The full simulation model was able to produce a prediction of density for each plot and height class. However, each simulation consisted only one stochastic realization of the combination of these processes. Because of high non-linearity and stochasticity, the average result of this combination of processes was difficult to anticipate. It was therefore impossible to follow a classical Bayesian estimation approach, based on the explicit calculation of the likelihood of the model given the data.

With this study, I not only demonstrated the potential of ABC to estimate demographic processes with incomplete and aggregated datasets, but also drew ecological conclusions about the effect of changing climate on tree recruitment rates. With the help of ABC, I was able to predict parameters for processes with no data availability. However, in such situations, it is important to have information about some crucial processes that can be representative of the absent data (Lamonica et al. (2021)). For example, in this thesis, I had information about regeneration densities and height increment of saplings, which aided the prediction of sapling establishment rates and survival rates. With data on annual growth of saplings, even if taken at a single time point, one can reconstruct growth trajectories, and understand past conditions of

saplings, that can help to infer regeneration dynamics (Lamonica et al. (2021)). The process of fecundity would need better estimation, and I suspect that some delays in data convergence could be due to uninformed prior ranges of fecundity, but this requires further investigation and could be improved in the next step of this project.

National forest inventories often have access to forests across the country, which capacities of collecting large-scale data. The ability of ABC to estimate past and futures of forest communities and populations with just one time point of data is an appealing application of such large datasets being put to use. However, it is necessary to choose the correct variables to measure, as certain data variables can be more informative about particular processes than others (Lamonica et al. (2021)). I could estimate the different processes only as a result of the specific variables we measured. Without any information of browsing rates, I could not have established effects of browsing on regeneration, or without density and height increment data, it would not be possible to estimate survival. I strongly suggest including variables such as height increments and information about browsing in addition to sapling densities as much as possible. If not in large national inventories due to logistic constraints, this is certainly possible in more local surveys of regional forests. In addition to choice of data variables to be collected, the choice of summary statistics is another important practice while carrying out ABC, as explained in chapter 4 (Marin et al. (2014); Barnes et al. (2012); Nunes and Balding (2010)). Constructing optimal statistical summaries of the entire dataset is a complicated task. It is important to have summary statistics values that influence the different processes to be predicted (Barnes et al. (2012)). The strategy used in this thesis was to first select important predictor and response variables, and calculate means across categories of these variables (low and high). This allowed us to have representation of the entire dataset in a few values. The use of aggregated data, or summary statistics in ABC also helps to identify global indicators of patterns in data.

5.2.3.2 Combining different modelling approaches

As explained in chapters 3 and 4, this thesis involved combining 2 different statistical approaches to predict regeneration dynamics. In chapter 3, I first used non-linear mixed models (NLME) to identify patterns in the collected data. ABC was then used in chapter 4 to parametrize the model with dynamic regeneration processes, which were obtained from the patterns observed in the data using NLMEs (for example, survival process derived from regeneration density measures). As ABC can be

computationally expensive to run multiple exploratory models, NLME served as an initial platform to do an exploratory analysis of the data, before computing dynamic processes using ABC. Specifically, the NLMEs provided important equations and parameter values to be used for sub-models, which were then used to determine priors of some processes used in ABC for estimation of the complete regeneration dynamics model.

The combining of multiple methods to obtain optimal results in terms of computational time, accuracy of predictions, is also demonstrated by (Lamonica et al. (2021)), who combined the use of likelihood based Bayesian inference with Approximate Bayesian Computation (ABC) in order to derive tree population dynamics.

5.2.3.3 Simulation models to test future scenarios and build management alternatives

After parameter estimation of models comprising of multiple sub-models and species, it is exciting to go beyond computing regeneration dynamics, and apply the results to understand future forest structures and compositions as a result of different environmental changes, or following different management practices. In this thesis, the next step after the predictions of recruitment I did in chapter 4 could be to simulate variations of canopy cover along time because of tree growth and harvesting, and also take into account the retro-action effect of tree recruitment on canopy cover and indirectly on sapling development. This can be done using a forest dynamics model that can also simulate silvicultural practices.

However, building a software for a specific forest dynamics model can be expensive, time consuming, and requires extensive computer science training. Developing models in R is appealing since programming is relatively simple in R and it is easy to share packages with other developers. Moreover, complementary tools like the software shiny make now possible to develop graphical user interfaces for R scripts. However, computing time is quite long with this language. CAPSIS, written in java, is another development platform devoted to forest dynamic simulation models, that makes possible to share many forest oriented objects De Coligny (2002). It solves the above mentioned problems, by allowing scientists and researchers to formulate forest dynamics models and incorporate them on capsis with the help of computer scientists. This permits researchers and practitioners alike to simulate forest dynamics and to explore various silvicultural scenarios and forest simulation results. It also has an interactive interface that lets one visualize the spatial 3

dimensional structures in these simulated forests (Dufour-Kowalski et al. (2012)). Example of models hosted in CAPSIS include, Salem (a stand level model that simulates climate effect on tree stands) (Aussenac et al. (2021)), WallTree (a generic tree growth model to simulate forest evolution) , Organon (tree growth, yield and harvesting simulations), but most of them include dynamics of only adult trees (Coligny et al. (2009)). Other models like RReShar and Samsara include regeneration processes along with simulating adult tree stands. Samsara2 is an individual based, spatially explicit forest dynamics model that has been incorporated in the Capsis software that simulates regeneration processes as well as silvicultural measures. The regeneration in Samsara2 depends on light availability, and stand evolution can take place in the presence of different light conditions and silvicultural measures (Courbaud et al. (2015); Dufour-Kowalski et al. (2012)). Another individual based spatially explicit forest dynamics model in Capsis is called RReShar, in which factors driving regeneration dynamics include light, water and understory vegetative competition (Balandier et al. (2020)). These two models are calibrated for specific tree species such as oak-pine stands for RReShar and different species including spruce-fir-beech stands for Samsara2. The next step in this project is to take into account the results of this study to improve the representation of regeneration processes in Samsara and RReShar, especially considering the effect of climate and browsing, and construct a more comprehensive model. This will not only give a more comprehensive view of the estimated regeneration processes, but also help in understanding the future of forest stand structures after various management practices. The multi-criteria algorithm of tree cutting in Samsara is especially appropriate to test the effect of tree selection for harvesting and thinning, based on tree species, size, quality, growth, spatial distribution, and presence of saplings around a tree.

CHAPTER 6

General conclusion

The objectives of this thesis were to (a) identify and quantify the effect of various environmental factors on different tree regeneration processes, (b) estimate the tree recruitment rates as a result of different demographic processes, and (c) quantify tree recruitment rates in current and future environmental conditions. In order to fulfill these objectives, I used multiple methodologies (field survey, exploratory statistical analyses, statistical modelling) to estimate various demographic processes. I showed that processes of fecundity (seed production) and survival of saplings can be calibrated without the availability of data corresponding to direct observation of these processes, using Approximate Bayesian Computation (ABC). This not just lead to ecological consequences, but also confirmed the use of ABC in complex ecological studies when only coarse data is available. Moving on to the regeneration processes, I established dependencies of sapling growth and survival on climatic conditions, with potential evapotranspiration (PET) negatively affecting both growth and survival of spruce, fir and beech, even though to different extents. I also presented that saplings grow better in higher light availability, although fir is most shade tolerant, followed by beech, and spruce requires most light to grow well. The growth of saplings, especially fir, was also compromised by the damage caused due to herbivory by species such as roe deer, red deer and chamois. This indirectly affected survival of saplings, as higher saplings grew faster, but saplings eaten by herbivores remain short for a longer period of time. I also showed that with increasing PET (as a results of increasing temperatures and changing water availability) and browsing rates, by the year 2100, most sites will witness close to no new tree recruits of fir, and very few of spruce, resulting in possible changes in stand compositions in favour of beech in the absence of any changes or adaptations in management practices.

In addition to these ecological results, I also established some methodological results. I confirmed the capacity of Approximate Bayesian Computation as a method to estimate parameters for a regeneration dynamics model, based on limited data variables. This also lead to the inference that it might be essential to re-think the variables measured in forest surveys that collect regeneration data to include variables such as sapling growths or fecundity estimates, along with densities. Due to time constraints in the thesis, there was no scope during this project to couple the regeneration model with an adult tree dynamic model, and hence it was impossible to understand the spatial structure of stands, or to implement silvicultural practices on the stands. However, I believe that I have laid the foundation of a comprehensive model, with climate and browsing pressure dependencies, which can be merged into Samsara to give a bet-

ter understanding of forest dynamics and stand structures and compositions in the future.

I started this manuscript to highlight how changing environmental conditions can disturb the balance between tree regeneration, establishment of new tree recruits and tree harvests. The results confirm that this is indeed true, as human induced changes have caused a change in climate and ungulate populations, which in turn disrupts regeneration and tree recruitment processes. The requirements of humans of harvesting these trees create a larger problem as natural renewal of forests cannot be matched to the harvesting rates. Nevertheless, many management initiatives are being carried out for forest stands to better adapt to climate change, with innovative opportunities that use new scientific advancements and technology. These findings illustrate that even though the origin of the disruption of forest dynamics is anthropogenic, humans could also be the key to restore this balance through appropriate forest management.

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Abstract

Global environmental changes are affecting tree population demography with potentially significant impacts on forest biodiversity and wood industry. Forest regeneration processes include seed production and dispersal, seedling establishment, growth and survival of saplings till they reach adulthood, at which point, they become part of the adult tree stand. Changes in regeneration dynamics, thus, directly affect forest composition and structure and can jeopardize the sustainability of forest management. This is especially the case in mountain forests where environmental gradients are strong and where forests are often uneven-aged, i.e. combining trees of all ages in a single stand. Regeneration processes are difficult to monitor at large spatial or temporal scales. There is also often, absence of large scale historical datasets that can help recognize patterns of regeneration processes in different environmental conditions. In this thesis, I quantified the effects of different biotic and abiotic factors on regeneration dynamics of Norway spruce (*Picea abies*), silver fir (*Abies alba*) and European beech (*Fagus sylvatica*) in the French Alps and Jura mountains. I also predicted changes in tree recruitment fluxes in these forests for different climate change situations projected by the IPCC, and different ungulate browsing pressures.

I carried out field sampling in which I recorded sapling densities and height increments of spruce, fir and beech, along with potential environmental drivers of regeneration, such as altitude, slope, aspect, light availability, soil characteristics, ungulate browsing pressure, temperature, precipitation evapotranspiration and many more climatic variables, in 152 plots across the French Alps and Jura mountains. I then established patterns of the effects of these biotic and abiotic factors on sapling density and growth using non-linear mixed models. I showed that temperature and water demand, in the form of potential evapotranspiration has a negative effect on sapling density and height increments, and height increments are also affected positively by canopy openness, in addition to climate variables. Browsing of the terminal shoot by ungulates, which prevents sapling height growth and reduces survival, is especially frequently observed on fir.

Using these established patterns, I calibrated a more comprehensive model of regeneration dynamics, representing the processes of new seedling production, sapling growth, browsing and survival of saplings, and finally their recruitment into adult trees.

I estimated parameters for these processes in combination, using Approximate Bayesian Computation (ABC), based on the field data collected earlier. The results imply that with frequent and intense heat and drought events, by the year 2100, sapling growth and survival of the three species will be highly impaired, with a substantial reduction of forest renewal fluxes, with species specific differences. An increase of ungulate populations leading to increased browsing could be especially damaging for fir saplings, and beech saplings to a lesser extent. Within the range of climate sampled by me, the cumulative effect of rising temperatures and browsing intensities is most detrimental for fir, followed by spruce, whereas beech fares comparatively better in future climate conditions, indicating the possibility of a shift in forest species compositions in these stands in the absence of forest management strategies adapted to mitigate the effects of these disturbances.

In addition to establishing the susceptibility of regeneration to climate and browsing pressure, this study confirms the potential of Approximate Bayesian Computation (ABC) to estimate dynamic regeneration and tree recruitment processes based on a screenshot of field conditions. It also highlights the importance of regeneration processes in determining forest dynamics and tree species compositions. I conclude that future forest regeneration is vulnerable to temperature, water demand and ungulate presence, urging researchers and forest managers alike to take management measures that align with anticipated future conditions in the mountain forests.

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