Modelling **Forest** Regeneration in Europe

Louis A. König

Propositions

1. The regeneration phase of a forest comprises the largest potential to adapt to new environmental conditions and altered forest functioning. (this thesis)

 Without effective forest management, European forests will lose vital ecosystem services. (this thesis)

3. In scientific progress, societal relevance outweighs scientific trends.

4. As in hunting, in science you have to aim above your target to hit it at long range.

 ${\sf 5}.$ Rising data availability fosters scientific progress but also risks impairing advancements.

6. Challenges, like those of today, are not a new phenomenon.

7. Work-life balance should be called life-work balance.

Propositions belonging to the thesis, entitled Modelling Forest Regeneration in Europe

Louis Andreas König Wageningen, 27 October 2023

Modelling Forest Regeneration in Europe

Louis A. König

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Modelling Forest Regeneration in Europe

Louis A. König

Thesis

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Chapter 1

General Introduction

1. European forests and climate change impacts

Covering more than one third of the European land surface (UN & FAO, 2021), forests provide a vast amount of ecosystem services that are vital for the well-being of humans (Thom & Seidl, 2016). Historically they have been intensively managed for timber production. Today, even though these forests comprise only four percent of the global forest cover, they supply about 20 percent of the global roundwood production (FOREST EUROPE, 2015). One third of those forests fulfil crucial protective functions to, for example, prevent soil erosion and avalanches in mountain regions or preserve water resources (FOREST EUROPE, 2020). Additionally, European forests are increasingly used for recreational purposes and play a key role in biodiversity conservation and climate protection (European Comission, 2020; Grassi et al., 2019). The latter two have been picked up by international climate policies that promote decarbonisation strategies to mitigate climate change (IPCC, 2022a, UNFCCC, 2018; UN & FAO, 2021). Even though carbon sequestration dynamics of forests are not fully understood under climate change, forests have obtained a fixed place in the EU's climate policy in order to reach net zero carbon emissions by mid-century and to stay within the 1.5 degrees warming scenario (European Comission, 2019).

On top of various societal demands, climate change is severely impacting European forests and disrupting the continuous supply of ecosystem services. Subsequent changes in growing conditions and tree species performances (Lindner et al., 2010) together with the increased occurrence and severity of natural disturbances (Patacca et al., 2023) strongly alters forest dynamics (Reyer et al., 2017; Seidl et al., 2020; Seidl et al., 2017). Those disturbances, like extreme heat waves, drought, storms, wild fires and insect outbreaks have boosted mortality rates in European forests (Gazol & Camarero, 2022; George et al., 2022), even in areas where impacts were not expected (Hartmann et al., 2022) and therefore challenge forest management evermore.

2. Adaptive forest management

Recognizing observed and projected climate change impacts, adaptive forest management in Europe is increasingly focused on fostering the adaptive capacity of forests (Lindner et al., 2008). Here, forest management aims to increase forest resilience to buffer the impacts of climate change and facilitate shifts towards forest ecosystems that are better adapted to withstand future impacts. Such forests are more likely to provide a continuous and sustainable supply of ecosystem services under changing site conditions (Bolte et al., 2009; Spathelf et al., 2018). Adaptive forest management strategies can be reactive (e.g. following disturbances) or proactive (trying to prevent disturbances) and can be applied at different spatial (e.g. stand, landscape) and temporal scales (e.g. short-term, long-term, UN & FAO, 2021). Those strategies must consider various climate impacts and assess whether these threaten or improve the provision of forest ecosystem services (Lindner et al., 2014). This applies to both observed and expected climate impacts, and similarly to those that are considered certain as well as those that are still uncertain. Further, per definition, adaptive

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forest management should not only prevent harm to ecosystems but additionally consider new opportunities (IPCC, 2022b). This may include, for example, management that facilitates productive species to increase tree growth and mitigate climate change. Even though forest scientists have suggested such opportunities (e.g. bioenergy, cf. Nabuurs et al., 2017; Wieruszewski & Mydlarz, 2022) it remains uncertain whether their effects substantiate with progressing climate change (Söderberg & Eckerberg, 2013; Giuntoli et al., 2022) and how to integrate them in practical and site-specific forest management (UN & FAO, 2021). With the emerging need for adaptation, forest management has become even more complex considering the wide range of interacting and often conflicting ecosystem services but also the long time horizons required for effective adaptation.

At the site level, adaptation is largely constrained by the current structure and species composition of a forest stand. As a result of timber-demand driven forest management, three quarters of European forests are even-aged and one third are composed of monocultures (FOREST EUROPE, 2020). Such stands are especially vulnerable to natural disturbances and often require adjustments of the current species composition to maintain desired ecosystem services (Knoke et al., 2008; Forzieri et al., 2021). A good example are the widespread Norway spruce monocultures across the central European lowlands that were cultivated outside the species' natural habitat due to its fast growth and high societal demand for construction wood (Jansen et al., 2017). However, as a species of precipitationrich montane forest ecosystems, Norway spruce is not well equipped to deal with current climate change impacts outside its natural distribution range. As a consequence, Norway spruce stands planted outside the natural distribution range are rapidly collapsing on large scales due to increasing occurrence and severity of natural disturbances such as drought, windstorm and bark beetles (Hlásny et al., 2021) and require conversion to mixed forests to increase their resilience (Hlásny et al., 2017; Huth et al., 2017). As an inherent property of trees, their longevity constrains rapid adjustments of forest stands towards the desired structure and species composition. Especially in advanced development stages of even-aged stands, stem densities and species richness are low and prohibit desired adjustments of the species compositions. In such stands, forest owners could, for instance, perform light thinnings to increase individual tree performances and subsequent stand resilience (reactive adaptation, mainly structural adjustment), or partly give up on the current rotation cycle and initiate regeneration of the stand (proactive adaptation, aimed at compositional adjustment).

3. The role of forest regeneration

The regeneration phase of a forest provides large opportunities for forest management to direct and shape its development and subsequent functioning over long time spans. Even though forest regeneration can occur at any development stage (cf. spontaneous regeneration) it is the early stage of forest succession that typically provides the highest stem numbers and allows a more flexible adjustment of the forest structure and the species

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composition compared to mature stands (Weiskittel et al., 2011). Thus, the complexity of future climate change impacts and prospective societal needs for ecosystem services need to be taken into account especially during the regeneration phase (Kolström et al., 2011; Torssonen et al., 2015).

Two third of European forests are regenerated naturally, which means that those trees either originated from seeds or from resprouting (FOREST EUROPE, 2020). Natural tree regeneration is characterized by several complex ecological processes of which many are driven by environmental factors. Some of those factors can be influenced by forest management. For example, thinning to adjust tree densities subsequently influences microclimate and the availability of resources crucial to forest regeneration such as light, nutrients and water, which may increase regeneration success (Käber et al., 2021). Other factors, however, are strongly determined by climate and weather conditions. Most species require specific chilling and forcing events to occur before their seeds germinate (Finch-Savage & Leubner-Metzger, 2006). Once germinated, those seedlings compete for resources like light, water and nutrients (Casper & Jackson, 1997). At this stage, the young plants are especially vulnerable to competition, browsing and drought because of their small resource storage and their shallow root system (Thrippleton et al., 2018). Limiting climate effects on tree regeneration have already been observed at the edges of species distributions (e.g. Silva et al., 2012; Jensen et al., 2023) and in dry forests (Petrie et al., 2017; Enriquez-de-Salamanca, 2022; Pozner et al., 2022; Shriver et al., 2022). There, forest retreat has been linked to failing tree recruitment even though adult trees are still able to grow and provide seeds. As a natural response to changing environmental conditions, when seeds are available, species may colonise new habitats through seed dispersal. Such species shifts have been observed in European forests (Lindner et al., 2014; Penuelas et al., 2007) but not all species may be able keep up with the pace of climate change (Delzon et al., 2013; Kremer et al., 2012).

Natural regeneration does not always match the demands of forest managers with regard to the trees needed for future functioning. Maladapted regeneration occurs, for instance, when dispersal limitations or browsing constrain the desired species mixtures or tree densities (Honnay et al., 2002; Ramirez et al., 2019). Another example is the natural regeneration of a spruce monoculture that was killed by a combination of drought and bark beetle infestation. Due to seed availability, the regenerating tree population is likely to be dominated by spruce again. A conversion into a more resilient mixed forest through natural succession in such a system may require several die-backs causing undesired interruptions of ecosystem services for longer time spans. In such cases forest managers may decide to adjust the species mixture through tending or, in case the desired species does not regenerate sufficiently, by planting. This may include assisted migration of better adapted species or provenances (cf. Dumroese et al., 2015; Fanta, 1997). The ongoing discussion about assisted migration is yet inconclusive. Advocates of close-to-nature management argue that natural species compositions have a good chance to adapt to climate change through selective population

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dynamics and genetic adaptations at the tree level (Gömöry et al., 2020). Supporters of assisted migration argue that introducing species which are adapted to future climate conditions ensures forest functioning under climate change, protects species from extinction and therefore outweighs potential risks (Mauri et al., 2023; Pötzelsberger et al., 2020).

The central questions, however, which forest managers ask themselves remain (Dumroese et al., 2015; Park & Talbot, 2018; Sousa-Silva et al., 2018): Does the expected tree regeneration provide sufficient flexibility to fulfil future needs and how can this be assessed considering the complex interactions between ecological processes, forest management, climate change impacts and shifts in societal demands?

4. Forest dynamics modelling

Given the enormous entanglement of factors influencing forest dynamics, simulation models offer a suitable option to evaluate potential trajectories and guide informed decision making in forest management and forest policy (Schou et al., 2015). Challenges, as described above, are not new. The overexploitation of timber resources at the beginning of the 16th century led to unstable timber supply and facilitated the formulation of sustainability principles (Weiskittel et al., 2011). This marked the beginning of planned forest management and was followed by the development of growth and yield tables (cf. Schwappach, 1890; Wiedemann, 1949). Growth and yield tables formed the first type of forest growth models with the purpose to estimate the increment and timber harvesting volume of even aged and single species stands as a function of time, site conditions and species with the aim to plan and maximise timber harvest sustainably (Pretzsch, 2009). Growth and yield tables allow a useful and quick assessment of forest stands and required management actions until today but fail to answer more complex questions, especially under changing environmental conditions.

With increasing support of computer technology in the 1980's, more complex models of forest dynamics were developed. The beginning was marked by JABOWA, the first computerised model that was able to simulate natural forest succession in mixed stands (Botkin et al., 1972). Ever since, hundreds of forest models have been developed and suited to a diversity of forest systems and objectives (cf. Bugmann & Seidl, 2022; Vanclay, 1994). Following the model principles of JABOWA, gap models simulate long-term forests dynamics (Shugart & Smith, 1996). Shortcomings of gap models (Bugmann, 2001), like the lack of processes acting on larger spatial scales (e.g. seed dispersal, natural disturbances), were taken into account in landscape models (cf. Lischke et al., 2006; Mladenoff, 2004). Efforts were made to increase our understanding of global biogeochemical cycles, which led to the development of dynamic global vegetation models (Prentice et al., 2007). But also growth and yield models have become more abundant (Hasenauer, 2006). As the name already suggests, those models focus on tree growth and timber yield in managed forest systems. Natural tree regeneration and natural mortality are neglected and stand establishment and tree removal are user-defined to represent planting and harvesting of stands with specific

rotation times (cf. Landsberg & Waring, 1997; Mohren, 1987; Schelhaas et al., 2018b). Over time, all models have been made increasingly sensitive to climate in order to understand underlying ecological processes but also to project climate change impacts on ecosystem dynamics themselves.

5. European forest resource projections, forest regeneration modelling and the rationale of this thesis

With the purpose to explore and improve management strategies, sophisticated forest growth and yield models have been developed for many forest types and countries (Barreiro, 2017). Those models are tailored to simulate specific forest systems and therefore vary greatly regarding model formulations (e.g. different growth functions). Thus, the underlying assumptions prohibit a direct comparison of the simulation results across different modelling frameworks. For European resource projections, universally valid model formulations ensure sufficient consistency to compare the simulation results. Such large-scale growth and yield modelling frameworks form a crucial tool to inform national and international policies and industries about the availability and development of forest resources (cf. Dixon, 2002; Nabuurs et al., 2019; Pilli, 2018). On a European scale, however, forest resource simulators are yet rare (cf. Kindermann et al., 2006; Nabuurs et al., 2002; Vauhkonen et al., 2019).

In view of recent climate change impacts on European forests and the required adaptation of those forests, the implemented mechanisms of forest regeneration become crucial to simulate ongoing species changes. The available simulators are characterised by rather simple approaches that lack an adequate representation of forest regeneration and the associated compositional changes under adaptive forest management and climate change (cf. Schelhaas et al., 2017). All European-scale forest simulators rely hereby on user-defined assumptions regarding species changes. Species shifts are either driven by expected effects on net primary productivity through active forest management or aim to mimic natural dynamics under climate change based on climate envelope modelling.

The reality, however, lies somewhere in between as forest regeneration is affected by forest management *and* climate change. Consequently, current simulators fail to adequately represent the combined effects and hence, transient compositional changes of forest regeneration and ultimately forest development. In order to define and explore suitable management strategies on a European scale, a dynamic representation of tree regeneration is required in models of forest dynamics. A dynamic approach should be more data driven to bridge the gap between static regeneration models and climate envelope models.

6. Research aims and thesis outline

This thesis aims to provide a quantitative description of forest regeneration in relation to local site conditions and forest management to, ultimately, enable realistic forest resource projections across Europe that include species change, and that can be used to identify suitable forest management strategies under climate change (cf. Figure 1).

In order to find the right level of detail regarding the quantitative description of forest regeneration, I review regeneration approaches in 29 existing models of forest dynamics (Chapter 2). Based on the conclusions of Chapter 2, I develop and parameterize a forest regeneration model (Chapter 3) which is then implemented into the pan-European forest resource model EFISCEN-SPACE. Chapter 4 comprises scenario analyses across 17 European countries to test the new tree recruitment model within EFISCEN-SPACE. Concluding remarks about the model development, its functioning and relevance for European forest resource projections are presented in the general synthesis (Chapter 5).



Figure 1 Conceptual diagram showing the general structure of the thesis.

Chapter 2 addresses the question how tree regeneration is represented in models of forest dynamics (MFDs) and how sensitive the available approaches are in respect to changing climatic conditions. Therefore, I reviewed 29 MFDs spanning a wide variety of tree regeneration modelling approaches. After describing the underlying ecological processes, the implementation of corresponding processes is discussed with regard to their ability to capture environmental changes based on the purpose, structure and scale of the models.

Chapter 3 presents the development of a probabilistic tree recruitment model based on repeated national forest inventory data. It investigates how biotic and abiotic factors affect the number of recruitment trees and the corresponding species on a European scale taking into account the differences in survey methods. It is expected that the number of ingrowth trees decreases with increasing stand density and decreasing water and nutrient availability due to negative effects on germination rates, seedling establishment and sapling growth. Further, I hypothesise that the composition of the recruitment is largely determined by the availability of seed sources and environmental constraints linked to water and nutrient availability.

Chapter 4 investigates potential forest dynamics across Europe with climate change scenario analyses after the integration of the dynamic tree recruitment model developed in chapter 3 within EFISCEN-SPACE. The recruitment species compositions of 17 European countries are compared to the present overstory compositions for the climate change scenario RCP 6.0. Recruitment densities are expected to decline with ongoing climate change with more severe impacts in the European south. Compositional shifts between the overstory and the recruitment compositions are expected to occur all over Europe. Their disparity is expected to increase with progressing climate change.

The general synthesis integrates the main findings of the previous chapters with respect to global change induced altered tree regeneration patterns across Europe. It provides an appraisal for potential consequences on forest ecosystem functioning and further model development. Ultimately, this combined assessment is utilised for recommendations regarding future research perspectives and forest management implications.

Chapter 1



Chapter 2

Tree regeneration in models of forest dynamics – Suitability to assess climate change impacts on European forests

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Abstract

Climate change impacts on Europe's forests are becoming visible much sooner than previously anticipated. The increase in natural disturbances leads to tree mortality and raises concerns about the forest's adaptive potential to sustain vital ecosystem services. In this context, the regeneration phase is crucial and comprises the largest potential to adapt to new environmental conditions with long lasting implications. Yet, forest regeneration is particularly susceptible to climatic changes due to the many directly climate-dependent processes, such as seed production and germination but also seedling and sapling development. Models of forest dynamics (MFDs) are essential to describe, understand and predict the effects of changing environmental and management factors on forest dynamics and subsequently on associated ecosystem services. We review a large variety of MFDs with regard to their representation and climate sensitivity of regeneration processes. Starting with a description of the underlying biological processes, we evaluate the various approaches taking into account specific model purposes, and provide recommendations for future developments. We distinguish between models based on ecological principles and models based on empirical relationships. We found an ample mix of regeneration modelling approaches tailored to different model purposes. We conclude that current approaches should be refined to adequately capture altered regeneration trends. Specifically, refinement is needed for MFDs that rely on ecological principals, as they suffer from knowledge gaps and underrepresented processes, thereby limiting their ability to accurately simulate forest regeneration under climate change. Global vegetation models are strongly constrained by their weak representation of vegetation structure and composition, and need to include more detail regarding structural complexity and functional diversity. Models focused on timber yield often rely on strong assumptions regarding the abundance and composition of the next tree generation, which may no longer hold true with changes in climate and forest management. With the increased utilization of natural regeneration as a source of forest renewal, more dynamic representations of tree regeneration are needed. Our review highlights the necessity to increase the data basis to close knowledge gaps and to enable the adequate incorporation and parameterization of the involved processes. This would allow to capture altered regeneration patterns and subsequent effects on forest structure, composition and, ultimately, forest functioning under climate change.

1. Introduction

The impacts of climate change on forest ecosystems are becoming more and more visible. Especially the augmented occurrence and severity of natural disturbances such as wildfires, windstorms, insect calamities, droughts and periods of extreme heat have increased tree mortality and raise concerns about the future provisioning of ecosystem services under progressing climate change (Allen et al., 2010; McDowell et al., 2020; Seidl et al., 2020). Under this premise, the regeneration phase comprises the largest potential for the long-term adaptation of forests to new environmental conditions, by adjusting the species composition and the structure of the next tree generation (Kolström et al., 2011; Qiu et al., 2021).

Models of forest dynamics (MFDs) are an important tool to describe, understand and predict the effects of biotic (e.g. competition, browsing), abiotic (e.g. climate, weather, and soil) and management factors on forest dynamics and resource availability. Initially developed to assist forest management and to understand forest successional processes, MFDs are often used to assess potential effects of global change on forest ecosystems and their mitigation potential, and also to assess biogeochemical cycles to improve understanding of global change itself. Over the past 50 years, a large variety of MFDs has been developed, tailored to various objectives across different spatio-temporal scales. The available models feature major differences in the formulation of the basic processes of regeneration, growth and mortality (Shifley et al., 2017).

A general distinction within MFDs can be made between models that rely mainly on empirical relationships (empirical models) and models that rely on a more detailed representation of ecological processes (mechanistic models, (Shugart & West, 1980), with a fundamental difference in applicability. On the one hand, empirical models generally rely on regression techniques that require extensive long-term records to predict the basic processes (e.g. tree growth via diameter increment) from one (cf. age in yield tables) or more independent variables. The resulting equations are usually bound to specific site and stand conditions, and their uncertainties are to some extent known within the range of data used for calibration (cf. Hasenauer, 2006; Ledermann, 2002; Wykoff et al., 1982). Empirical forest growth models are used to simulate resource development with an emphasis on timber production. On the other hand, mechanistic models seek generality by modelling the underlying mechanisms that drive forest processes and succession, and hence aim to understand and explain phenomena at higher levels of integration on the basis of underlying ecological processes (cf. Bugmann, 1996; Reyer et al., 2014; Seidl et al., 2012a; Sitch et al., 2003). Mechanistic models often combine features of both (i.e., empirical and ecologically founded) approaches, e.g. when processes at lower integration levels are described in an empirical way, but the integration at higher levels is done in a conceptual way, based on the physical and physiological understanding of the system involved. Ultimately, there is no purely mechanistic model, and any ecological model is at least partly based on empirical relationships.

Whereas tree and stand growth have been subject of extensive research and are reasonably well understood (cf. Burkhart & Tomé, 2012; Pretzsch, 2009; Weiskittel et al., 2011), population dynamics processes such as individual tree mortality have only received more attention in recent years (cf. Bigler & Bugmann, 2003; Bugmann et al., 2019; Hülsmann et al., 2017). This holds even more for forest regeneration, which is a highly complex process that depends on a large variety of influencing environmental factors (Clark et al., 1999); (Sharma et al., 2022) and on forest management, introducing a high level of spatial and temporal variation (Miina et al., 2006) and thus high uncertainty with respect to long-term forest development. New trees can establish naturally from seeding and sprouting, or artificially through direct seeding or planting. Tree regeneration starts with the production of seeds on the mother tree as a result of flowering and pollination. Following the dispersal of seeds, germination, seedling establishment and sapling development are largely determined by site and weather conditions (cf. Price et al., 2001).

In MFDs, tree regeneration is often simulated with sub-models that keep track of individuals or groups of young trees throughout the different development stages until a certain size threshold is reached and the young trees are recruited into the main model (cf. Lexer & Hönninger, 2001; Lischke et al., 2006). Alternative approaches ignore the early stages of tree development, and new trees enter the population through a probabilistic process of passing the size threshold of the main model after a certain time lag (cf. Pretzsch et al., 2002; Zell, 2016), or – in the case of purely management focused models – allow regeneration only by artificial means through planting (cf. Gracia et al., 1999); Sallnäs, 1990). Limited by computational power and the limited availability of long-term observations combined with the uncertainties regarding the parametrization of the processes involved, a wide variety of regeneration modelling approaches has been developed that deal with the challenges mentioned above in different ways (cf. Krinner et al., 2005; Seidl et al., 2012; Zell et al., 2019).

Tree regeneration modelling approaches have, to our knowledge, only been reviewed for small selection of MFD's, in particular, for forest gap models (Price et al., 2001), selected forest growth models (Hasenauer, 2006; Larocque, 2016) and recently for earth system models (Hanbury-Brown et al., 2022). However, a general review of tree regeneration approaches across the various model families that deal with forest development is lacking. Thus, our study aims to provide an overview of the tree regeneration approaches in commonly used MFDs across different spatial and temporal scales. We describe and evaluate various approaches with regard to different model purposes, and distinguish between models based on ecological principals and models based on empirical relationships. We assess their capability to capture climate change effects and discuss shortcomings and

opportunities for improvement. We put an emphasis on applicability at large (e.g., European) scales.

2. Review process

2.1 Overview of reviewed models

We reviewed 29 MFDs of which we selected 14 to discuss in greater detail. The selection was based on their approach with regard to spatial and temporal structure (Table 1) as well as their tree regeneration approach and the main model purpose (Figure 1). The models contain typical approaches or new developments, including both empirical and ecological principles based models that are being applied today spanning stand, landscape and dynamic global vegetation models (cf. He, 2008; Prentice et al., 2007; Weiskittel et al., 2011). A comprehensive list and annotated description of all reviewed models and their tree regeneration approaches can be found in Supplement 1. The majority of models were developed for application in boreal, temperate and Mediterranean forest ecosystems in Europe. Our primary sources of information were the published model descriptions, supplemented by additional information obtained through personal communication with the model developers, and from examining source code (Table 1). We did perform neither model simulations nor statistical analyses on the information obtained.

	Regeneration approach	Involved processes	Ecological principles	Empirical relationships	
Tree development	Regeneration model	flowering PICUS Regeneration pollination FORSPACE model seed production TreeMig seed dispersal i-Land germination LandClim 4C			
	Recruitment model	recruits passing size threshold	SILVA v2.2 FORCLIM v3.0 LPJ LPJ-GUESS	EFISCEN SwissStandSim Prognaus	

Figure 1 Tree regeneration modelling approaches and processes considered (after Vanclay, 1994). Reviewed forest models are arranged according to their tree regeneration approach and underlying model concept (ecological principles vs empirical relationships). Regeneration models typically include the processes found in recruitment models.

2.2 Conceptualizations of tree regeneration

The sheer magnitude and complexity of the ecological factors influencing forest regeneration presents a major challenge to forest dynamics modelling. The term "regeneration" is hereby associated with both the underlying ecological processes and the resulting generation of new trees (Hasenauer, 2006). We follow the classification by Vanclay (1994), who split tree regeneration modelling approaches into regeneration models and recruitment (or ingrowth) models (Figure 1). On the one hand, regeneration models can include basic processes such as flowering and pollination, seed production, seed dispersal. germination, seedling establishment and performance of seedlings and saplings (Figure 2) until a specific size threshold is reached where the saplings are transferred into the main model (e.g. Lischke et al., 2006). We distinguish between seedlings and saplings based on their age. Plants up to four years old are considered seedlings whereas older trees are called saplings. Seedling and sapling growth is determined by competition for resources such as light, water and nutrients. On the other hand, recruitment models predict the number of seedlings or saplings and their biometric properties (e.g., species and dbh) at a predefined minimum tree dimension threshold, without explicitly taking into account earlier development stages (e.g. Pretzsch et al., 2002).

Table 1 Overview of reviewed models and the corresponding source of information together with their general characteristics and tree regeneration approach (p.c. = personal communication).

	Model	Reference	Model type	Spatial	Temporal	Tree	
				structure	structure	regeneration	
Process based	PICUS	Lexer & Hönninger, 2001	stand	individual	month	Regeneration model	
	FORMIND	Fischer et al., 2016	stand	individual	Year		
	4C	Lasch-Born et al., 2020, p.c.	stand	cohort	day		
	iLand	Seidl et al., 2012a	landscape	individual	month		
	FORSPACE	Kramer et al., 2001, p.c.	landscape	cohort	month		
	TreeMig	Lischke et al., 2006	landscape	cohort	year		
	LandClim	Schumacher et al., 2006, p.c.	landscape	cohort	year		
	FORCLIM	Bugmann et al., 1996; Didion et al., 2009	stand	cohort	year		
	LPJ	Sitch et al., 2003	DGVM	area	year		
	LPJ-GUESS	Smith et al., 2001	DGVM	individual	year		
Empirical	SILVA	Pretzsch et al., 2002, p.c.	stand	individual	5 year	Recruitment	
	PROGNAUS	Ledermann, 2002	stand	individual	5 year	model	
	SwissStandSim	Zell et al., 2019, p.c.	empirical	individual	5 year		
	EFISCEN	Sallnäs, 1990, Nabuurs et al., 2010	stand	stand	5 year		

3. Review of regeneration models

Regeneration models are solely found in MFDs that focus on ecological processes (cf. Table 1). Simulations studies usually span several centuries to investigate compositional changes in forest stands and related ecosystem functions (Bugmann, 2001). Regeneration models include processes that determine the availability of seeds for germination and subsequent development of seedlings and saplings (Vanclay, 1994). These models are characterized by the incorporation of the complex interactions between tree physiology and environmental factors (Price et al., 2001). Most models start with the simulation of available seeds for dispersal, which is typically derived from the size of the mother tree, whereas the follow-up processes, such as dispersal, germination and the development of seedlings and saplings in competition with forest floor vegetation and with each other, have a greater diversity between the different modelling approaches (Figure 2). The regeneration models hereby vary in range and intensity of incorporated factors like stand properties and climate which are limited by knowledge and data gaps, leading to a wide variety of modelling approaches geared towards different applications. In the following section we first describe the underlying ecological processes involved in tree regeneration and link them to specific model applications before providing qualitative appraisals for their improvement.

3.1 Flowering and pollination

A prerequisite of sexual reproduction is the maturity of the parent tree. It has been argued that sexual maturity depends on tree size rather than age, but for successful seed production also the social position of the tree is important, indicating that a more accurate measure for the capacity of sexual reproduction material could be the available carbohydrate pool, although these two are intrinsically linked (Greene et al., 1999). The timing of budburst has been linked to species-specific chilling (winter temperature) and forcing (spring temperature) requirements (Chuine et al., 1998; Harrington & Gould, 2015). Pollination success is driven by the availability of pollen, the mode of pollination, the distance to the nearest individual of the same species, and the timing of flowering (Bogdziewicz et al., 2020a). Attempts to include the process of flowering and pollination have been made for some MFDs (Leak, 1968), but generally regeneration models start with the empirical estimation of available seeds for dispersal as an aggregated process comprising flowering, pollination and seed production, and some level of stochasticity (Lexer & Hönninger, 2001; Lischke et al., 2006). Preceding processes such as flowering and pollination are commonly neglected based on the rationale that the understanding of these processes is incomplete and the amount of available long-term observations insufficient for parameterization. However, a more detailed representation of flowering and pollination is, at least from an ecological point of view, desirable. For example, the blossoming of trees responds to winter chilling and spring temperatures, whereas missing chilling requirements may lead to delays (Guo et al., 2015), and higher spring temperature leads to earlier blossoming (Nordli et al., 2008). This has two possible effects on regeneration success. Firstly, if late frost retreats more slowly than blossom advances in spring, late frost risk increases (Bigler & Bugmann, 2018; Darbyshire et al., 2013) and pollination success may decline for insect-pollinated species because the symbiotic insects are not active at the time of flowering (Ramirez & Kallarackal, 2018), thus creating a negative feedback loop (Scaven & Rafferty, 2013). Secondly, if chilling requirements are no longer met, seed production can be severely reduced due to irregular late flowering (Luedeling et al., 2009). Unfortunately, climate change effects on flowering and pollination have mostly been studied in the context of commercial fruit trees rather than forest trees . Bogdziewiczet al. (2020a) investigated drivers of seed production for three European wind pollinated tree species and identified pollen abundance as the best predictor. They also linked pollen abundance to warm preceding summers and short pollen season to warm spring temperatures (Bogdziewicz et al., 2020b). Future impacts on flowering and pollination can be expected but it remains unclear to which extent and in which direction, as some species may regenerate prolifically while others retreat (cf. Sharma et al., 2022).

3.2 Seed production

The more common approach in regeneration models is to start with seed production as an aggregated process. Seed production is determined by factors like tree size, age, vigour, canopy position, genetic characteristics, and mast year cycles (Greene et al., 1999; Koenig & Knops, 2000). The stand model PICUS v1.2, for example, starts with the simulation of seed production and dispersal (Lexer & Hönninger, 2001). Seed production of mother trees depends on their size, light absorption, chilling requirement, and species-specific seed production characteristics, which are derived from open-grown trees with a crown length equal to tree height and a tree height of 2/3 of the maximum tree height for that species. Mast years are simulated stochastically based on empirical data. Seed production is supressed if a species' chilling requirement is not met. The availability of species is limited to the species of mature trees present in the simulated stand. In contrast, 4C as a largely process-based MFD (Lasch-Born et al., 2020) does not explicitly simulate mast vears but derives the amount of available seeds stochastically from a species-specific annual potential seed (Rogers & Johnson, 1998). Because seed dispersal is not simulated, the available species for seed production are user defined and can also contain species that are not present in the stand. The model FORMIND (Fischer et al., 2016; Köhler & Huth, 1998) provides two alternatives to calculate the seed pool. The first approach simulates tree typeand site-specific seed production of mother trees. Depending on the project, tree types represent either species or plant functional types. Maturity of trees and the number of seeds produced are user defined and tree type specific. Available species are, similar to PICUS, restricted to species present in the stand. The second approach uses a globally constant seed influx, assuming an intact surrounding forest ecosystem. The amount of arrived seeds is species-specific and can, by default, only germinate during the next time step.

The three approaches described above differ substantially. The regeneration model in PICUS incorporates detailed process representations and environmental feedbacks, which renders this approach most demanding with regard to parameterization effort, and limited to well-

studied tree species. The partly stochastic and user-defined approach, as implemented in 4C, reduces such efforts but also removes direct effects of climate change and forest structure on the species specific amount of available seeds for germination. Hence, an adequate simulation of regeneration under climate change may be compromised. The FORMIND approach requires good knowledge of the studied system to determine whether the assumption of constant seed rain is valid, and is likely to constitute a strong assumption under climate change conditions. Similarly, the alternative approach in FORMIND should only be used if the particular system is well understood. If this is not the case, this approach can be misleading when investigating forest ecosystem dynamics.

Nevertheless, seed production itself may further be affected by changes in photosynthesis, which determines the carbon resources available for reproduction (Müller-Haubold et al., 2015) and altered mast year cycles (Figure 3a). Mast years cycles have been studied thoroughly, and plant resources as well as weather have been linked to mast year initiation (Kelly & Sork, 2002). However, it remains unclear whether environmental factors serve as a cue for synchronizing seed production, or if they have a direct physiological effect on the production of flowers, pollen, and seeds. It seems likely that a combination of both hypotheses provides the best explanation and that mast years will occur more frequent but less pronounced under climate change (Koenig et al., 2015). This could imply a decrease of tree regeneration as pre-dispersal seed predation is expected to increase with more regular seed production processes, the before mentioned mechanisms need to be further investigated, including a larger set of tree species, and knowledge gaps need to be closed to enable further model development.

3.3 Dispersal

Seed dispersal is another crucial process that determines the ability of species to colonize new sites and persist *in situ*. Seed dispersal is determined by the species' dispersal mode and seed availability. Seeds can be dispersed by wind or animals, but also by water transport in streams and rivers (Howe & Smallwood, 1982). The dispersal distance by wind is largely determined by the shape and weight of the seed as well as wind speed, whereas the dispersal distance of animal dispersed seeds depends on the radius of movement of the dispersing animal (Clark et al., 1999). Especially when climatic conditions change, a species' movement in space enhances its chance of survival by colonizing new sites that match its environmental requirements (Kremer et al., 2012). Seed dispersal in stand models is constrained by the spatial setup. Without the spatial context of neighbouring stands, seed influx in MFDs is limited to the adult trees within the stand, or relies on the user's assumptions regarding available seed sources. This issue has been tackled with the development of landscape models (cf. Lischke et al., 2006; Schumacher et al., 2006; Seidl et al., 2012a), which pay particular attention to differentiated species movement through time and space.

In stand models like **FORMIND**, seeds are dispersed into neighbouring patches whereas the distance and direction of the dispersed seed are drawn stochastically. Landscape models incorporate more detailed dispersal mechanisms. A sophisticated approach can be found in the landscape model **iLand** (Seidl et al., 2012a). Dispersal processes are closely linked to formulations of well-established landscape models TreeMig (Lischke et al., 2006) and Landis II (Scheller et al., 2007). A cone-shaped density function around the centre of a seed producing individual is used to simulate seed dispersal and seed rain. The dispersal kernel is defined as a linear combination of two negative exponentials to capture both short- and long-distance dispersal. The sum of all density functions covering a particular patch determines the amount of available seed per species, which is further modified by stochastic and species-specific fecundity to represent mast years, following the approach developed in **PICUS** (Lexer & Hönninger, 2001).

As the main determinant of available species for germination, seed dispersal has received a lot of attention in regeneration modelling and detailed approaches have been made for MFDs (cf TreeMig, LANDIS II). However, some potentially influencing assumptions regarding dispersal distances require further attention. Animal dispersal, for instance, remains challenging because animal behaviour may have extreme properties and may render parameterizing the dispersal distance using an animal's home range (average dispersal distance) pointless if the distance is irregularly exceeded (Zwolak & Sih, 2020). Yet, a simulation study by Le Corre et al. (1997) suggested that such long distance dispersal events are likely the most important factor for the recolonization of oak species in Europe since the last glacial period. A major issue is the fact that such events are extremely rare and, hence, challenging to observe and to parameterize. Many stand models and also dynamic global vegetation models therefore assume unlimited seed availability and ignore dispersal altogether (e.g. Warnant et al., 1994). This approach may seem invalid at first sight, but may actually have merit due to higher parsimony, an issue that is present in all complex ecological processes.



Figure 2 Depiction of tree regeneration processes and its influencing biotic and abiotic factors. Some of the processes are incorporated in regeneration models in quite some details, while recruitment models generally aggregate those processes. Climate change affects next to the site conditions also forest management practices.

3.4 Seed bank dynamics

Seed bank dynamics are strongly connected to a species' regeneration strategy. A general distinction can be made between species which rely on seed banks, seed rain, or seedling banks (lida & Masaki, 2002). Shade-tolerant species dominantly invest in seedling banks by maintaining a viable population of seedlings and saplings on the forest floor at all time, and seeds which do not germinate in the same year are usually lost. If the conditions are insufficient to maintain respiration cost, the seedlings will die off and be replaced by newly germinating seeds until more favourable conditions occur that support seedling growth (Shugart, 1984). Pioneer species often build up seed banks e.g. in cones (conifers) or in the soil. These seeds germinate only when environmental conditions become favourable, for example after disturbance. Such seeds can persist in the seed bank for several years although they are subject to grazing and senescence (Tiebel et al., 2018). Serotinous species, for example, release their seeds only after an environmental trigger such as a fire. The advantage lies in exploiting biotic and abiotic conditions favourable for establishment where competition from ground vegetation is low while nutrient availability is high (Hernández-Serrano et al., 2013).

The majority of the MFDs reviewed here rely on the assumptions that either enough seeds for germination are available or that seed bank dynamics can be neglected as most seeds are not viable for longer time spans. The process-based landscape model **LandClim** (Schumacher et al., 2006), for instance, does not keep track of seeds between the decadal simulation steps but reduces the amount of seeds available for germination by 90 percent in case of fire

unless a species is fire-adapted. **FORSPACE**, another process-based landscape model that focuses on vegetation dynamics and landscape formation processes (Kramer et al., 2001) simulates seed bank dynamics by reducing the number of seeds by an annual constant to account for losses due to senescence and predation. If fire occurs, the amount of seeds is set to zero. A more detailed approach was developed for the **TreeMig** model (Lischke et al., 2006), which focuses on the representation of multi-species population dynamics for spatial scales ranging from the single stand to the subcontinent. Species-specific losses are explicitly taken into account and separated for senescence, predation and germination.

Seed bank dynamics in MFDs which focus on ecological principals are still rare and often treated indirectly as an aggregated process within the previous process of dispersal, or subsequently during germination (cf. Seidl et al., 2012a; Schumacher et al., 2006). Seed bank dynamics have a strong influence on the composition of the seeds available for germination (Small & McCarthy, 2010). Especially after disturbance, seed sources from the seed bank can play an important role in the reforestation process (Van Calster et al., 2008). We therefore emphasise the utility of an explicit representation of this process and its dynamics in further model development.

3.5 Germination

Whether a seed germinates or not depends largely on the species-specific environmental and microsite requirements as determined by weather, litter layer properties and soil type, and the surrounding vegetation. These factors shape light, water and nutrient availability driving germination (Finch-Savage & Leubner-Metzger, 2006). Many species additionally require winter chilling for germination and can also be delayed by insufficient spring temperatures (Black & Bliss, 1980). Rarely it is assumed that all available seeds germinate. **PICUS v1.2**, for example, applies a species-specific germination rate to determine the number of successfully germinated seeds. In **FORMIND**, seeds germinate if species-specific light requirements on the forest floor are met. Common approaches also include temperature and heat sums (cf. Lischke et al., 2006), winter chilling and soil water availability (cf. Lasch-Born et al., 2020; Seidl et al., 2012a). **FORSPACE** restricts germination to the first month of the growing season, and germination is only possible when the species is not already present in the herb layer, enough space and light is available, and the litter layer is not too deep. If these requirements are met, a soil type-dependent fraction of the available seeds will germinate.

Similar to flowering and pollination, germination has also been linked to winter chilling, spring temperatures and soil moisture. With progressing climate change, the latter may become increasingly important. Moisture-dependent germination mechanisms are not common in MFDs, and germination is rather modelled to depend on species-specific temperature and light requirements, which may not adequately represent climate change impacts on germination success. Future model development should therefore include soil moisture when determining germination success.

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3.6 Seedling and sapling development

Like adult trees, seedlings and saplings compete for light, water and nutrients. Shallow root systems and low carbon storage can induce high mortality rates in the first years of development due to competition with grasses and herbs but also increased drought effects in the upper soil layers (Casper & Jackson, 1997). The classical approach in MFDs is to simulate seedling and sapling development in response to light availability on the forest floor. **iLand**, for instance, keeps track of seedlings and saplings at 2 x 2 m resolution after establishing seedlings with a height of 5 cm. Height growth is derived from a mean tree approach (Rammig et al., 2006) determined by physiological and environmental constraints. Trees exceeding a height threshold of 4 m are recruited into the main model.

However, the shallow root system of young trees makes them especially vulnerable to decreases of water availability under climate change, as the small plants have limited opportunities to adjust to e.g. water shortage. This implies that competition with herbaceous ground vegetation may become more pronounced, as has been shown in a study with the **LandClim** model (Thrippleton et al., 2016). The model projects strong long-term effects of competition between forest regeneration and the herbaceous understory, reducing regeneration biomass by more than fifty percent. We strongly recommend the inclusion of competition with the herbaceous understory for forest dynamics under changing climatic conditions, as implemented in **LandClim** and **FORSPACE**.

Additionally, seedlings and saplings are subject to browsing (Figure 3f). A simulation study on the effects of varying browsing intensities showed that using constant browsing rates had more severe impacts on the species composition than applying oscillating functions to represent temporal browsing fluctuation (Didion et al., 2009). In both cases, browsing strongly affected the number and composition of most tree species. Such a dynamic approach is implemented in the FORSPACE model (Kramer et al., 2001). Rather than applying grazing constants or stochastic functions, herbivore population dynamics and their required food intake are explicitly simulated with feedbacks to vegetation structure and composition. Other herbivores such as rodents and insects affect predominantly artificial regeneration on large open areas. Such areas often provide suitable habitats for their development such as grass cover for mice (Heroldová et al., 2012) or remaining trunks for insects (Schwenke, 1974). Herbivory impacts are widely neglected in MFDs but have strong effects on the early life cycle stages of trees through seed predation, uprooting, and browsing of leaves and buds during the seedling and sapling phase, and ultimately on forest management (Figure 3e; Reimoser & Gossow, 1996). In temperate forests particularly, population sizes of wild ungulate species have experienced a steady increase throughout the past century (Ramirez et al., 2019). Partly caused by current management practices, habitat qualities improved while food competition with domesticated animals declined. The lack of predators in large parts of managed forests worldwide and increasing winter temperatures facilitate herbivore survival and increase browsing pressure, which often hampers artificial but also natural regeneration (Reimoser et al., 2003; Rooney, 2001). The effects of ungulate species on the structure and composition of forests have been studied thoroughly, showing particularly that via selective browsing, ungulates can actively shape canopy composition and ecosystem functioning (Ramirez et al., 2019). They therefore require a better representation in regeneration models.

Further development of successfully germinated seeds is often modelled in a similar way as adult tree growth, i.e. as a function of resource competition. This has shown biologically sound results with increasing survival probabilities the larger the tree size. However, due to lower carbon storage and their shallow root systems, seedlings and saplings are more vulnerable to droughts as evidenced in various empirical studies (cf. Canham & Murphy, 2016; Engelbrecht et al., 2005; Gómez-Aparicio, 2008; Petrie et al., 2017). Hence, separate growth and mortality functions for regenerating trees vs. adults should be considered for an adequate representation of potential drought effects under future climate, which severely affect species distribution ranges (Delzon et al., 2013) and thus forest composition (Dyderski et al., 2018; Penuelas et al., 2007). Especially on the rear edge of species distributions, forests are less resilient to natural disturbances (Reyer et al., 2014) and can be replaced by other vegetation types (de Dios et al., 2007).

3.7 Vegetative reproduction

New trees may originate from seeding or from sprouting. Model developments have mostly focused on generative regeneration from seeds, but vegetative regeneration through sprouting can be an important mechanism for regeneration in natural forests, and in the case of coppice also for managed forests (Figure 3c; Dietze & Clark, 2008). Among the reviewed models, few incorporate mechanisms of vegetative reproduction. **4C**, for example, allows short rotation coppice for Aspen (*Populus* spp.) and Black locust (*Robinia* spp.) using specific biomass allocation rules for sprouts.

In temperate and boreal forest ecosystems of the Northern hemisphere, approximately one third of the deciduous tree species are capable of sprouting (Price et al., 2001). Bond & Midgley (2001) suggest that gaps created by fallen trees or disturbances may be occupied much faster by shoots of fallen trees rather than by seedlings from the surrounding trees or from the seedbank. Such sprouts have the advantage of utilizing available energy sources stored in the trunk or roots combined with an already established root system that can offset harsh environmental conditions, especially water shortages, which are more likely to occur in such gaps. Thus, sprouting may affect forest regeneration in terms of the species composition but also because sprouts may grow much faster than trees that originate from seed, and hence vegetative reproduction can provide a competitive advantage to the species. While it may be valid to ignore vegetative reproduction in managed forest (except for coppice, and also because resprouting trees are usually removed owing to their low timber quality), vegetative reproduction may have substantial effects on the dynamics in natural forests and deserves more attention in future modelling efforts, particularly because disturbances are expected to become more frequent and more severe (Senf & Seidl, 2018).



Figure 3 Examples of forest regeneration: a) 2-year-old oak saplings after full mast b) silver fir regenerating on old trunk in a natural forest reserve c) rare case of resprouting beech in mountain coppice d) assisted migration of walnut in between natural poplar regeneration e) beech enrichment planting after disturbance in spruce monoculture f) herbivory impacts on natural regeneration of silver fir (top: inside enclosure, below outside exclosure)

4. Recruitment models

Recruitment models lump the detailed processes that are resolved explicitly in regeneration models by a single aggregated 'process' that simulates the appearance of young trees. Under the premise that earlier processes such as flowering, pollination, seed production, dispersal, germination, are difficult to parameterize and validate for a wide range of species based on the limited amount of long-term data, recruitment models often apply species-specific environmental 'filters' to account for these effects in an aggregated way. The applied filters are often based on ecological reasoning, supported by scientific literature, rather than empirical relationships (cf. Bugmann et al., 1996; Shugart, 1984; Sitch et al., 2003), whereas other approaches apply solely a combination of probabilistic functions to derive the amount and composition of recruits (cf. Ledermann, 2002; Zell et al., 2019) or allow only user-defined recruitment (cf. Landsberg & Waring, 1997; Van Oijen & Cameron, 2017; Harkönen

et al., 2019). Recruitment models predict the number of new trees by species that are exceeding a predefined minimum tree dimension (size threshold) and their biometric properties (e.g. dbh and height). They are often calibrated to either match the expected stand structure and canopy species composition, or using empirical regeneration data.

4.1 Recruitment in MFDs that focus on ecological principals

Recruitment modules in MFDS that rely on ecological principals typically treat the establishment of seedlings or saplings as a stochastic process rather than a deterministic one. **FORCLIM** (Bugmann, 1996), for instance, disables sapling establishment if minimum winter temperature, the annual sum of degree-days, light availability at the forest floor, browsing pressure or soil moisture fall below (or above) a species-specific threshold. The probability of sapling establishment is the product of these binary environmental flags and a general probability whether seedling establishment is successful in a given year. This probability lies between 0 and 1 (with a default of 0.1) to simulate random diminishing micro-habitat effects. If it is smaller than a random number from a uniform distribution between 0 and 1, the actual number of saplings to be established in a given year is drawn from uniformly distributed number between 1 and a species-specific maximum. The latter is estimated from site-specific maximum tree density and an indicator of species' shade tolerance, to account for differences in regeneration strategies.

An alternative to applying environmental filters was developed for the single tree-based stand simulator SILVA v2.2 (Pretzsch et al., 2002), which relates seedling establishment to biotic factors with an emphasis on competition among trees (Biber & Herling, 2002). The maximum amount of seedlings that can establish is derived from the relationship between average diameter of the trees in the stand and maximum stem density, as described by (Reineke, 1933). Because the maximum number of establishing saplings is in reality only reached during mast years and average numbers are lower, they can be adjusted by the user, where a value of 10% has yielded reasonable results in simulations (Biber, 2002). In SILVA, competition among trees is taken into account by calculating the occupied space of trees inside and outside the regeneration square. The actual number of establishing seedlings in the lowest horizontal layer is derived from the unoccupied space within the regeneration square, where it is assumed that trees have reached a height of 25 cm. Height growth is simulated with an average species- and site-specific growth rate. Tree mortality occurs in a density-related manner and under unfavourable growing conditions, while the number of trees is reduced starting at the bottom layer. Depending on the height of a regenerating tree, its new position and allometric relationships are calculated. A tree that exceeds a height of 7 m is added to the main stand once its diameter, crown dimensions and coordinates are estimated.

The recruitment approaches implemented in FORCLIM and SILVA contrast the regeneration models of other MFDs that rely on biological principles at high resolution. Simulating recruitment instead of detailed regeneration processes has the advantage of higher

parameter parsimony and relies therefore on fewer assumptions which may potentially yield more accurate results, provided the underlying datasets are sufficiently large and robust for the simulation conditions of interest.

4.2 Recruitment modules in biophysical models

Scaling up vegetation dynamics to continental scales necessitates a simpler depiction of vegetation structure and composition compared to stand-scale models. Not doing so would result in an excessive parameter demand that may prevent model application, and it would introduce unwanted uncertainties including the problem of uncontrolled error propagation (Woodward & Cramer, 1996). Process-based global vegetation models calculate primary production of vegetation as a function of light interception and other environmental factors. To avoid separate parameterisation of the large number of species, groups of species, so-called Plant Functional Types (PFTs) are defined that occupy fractions of different vegetation layers in each grid cell. PFTs are characterized by similar traits and eco-physiological responses (Smith et al., 1993).

This PFT approach is implemented in LPJ, a widely applied process-based dynamic global vegetation model that was developed to simulate terrestrial vegetation dynamics and landatmosphere carbon and water exchanges. Vegetation dynamics are simulated based on average individuals of PFTs (Sitch et al., 2003). Establishment of new individuals in the original LPJ model is simulated at an annual time step and depends on a fixed maximum establishment rate of saplings. This approach is going back to the concept developed for the FORSKA model (Prentice et al., 1993) and questionably neglects existing differences between tree species. New individuals can establish within their bioclimatic limits in the proportion of a grid cell that is currently not occupied by woody PFTs. Sapling establishment is inhibited below an annual precipitation of 100 mm. The establishment rate is reduced by shading, which is determined via foliage projective cover. Growth of successfully established saplings is not explicitly modelled but added to the annual NPP in a grid cell. The sapling biomass is distributed over the different tissues of the PFT's average individual according to allometric functions. This is a shortcoming of LPJ as it merges sapling properties with the properties of the existing average individual. As a consequence, dynamics of life cycle stages are neglected which could otherwise significantly influence vegetation dynamics. LPJ has also been adopted for other modelling frameworks such as IMAGE (Stehfest et al., 2014) and **ORCHIDEE** (Krinner et al., 2005).

LPJ-GUESS combines the gap model approach of FORSKA (Prentice et al., 1993) with the original LPJ to represent vegetation dynamics based on the consideration of individual trees (Smith et al., 2001). Seed production and dispersal are not simulated. The model draws the number of new saplings of a PFT in each patch at random from a Poisson distribution. The expected value is influenced by the "propagules pool", which is linked to the allocation to reproduction of a species population, and the PFT-specific maximum establishment rate. The maximum establishment rate differs between shade-tolerant and shade-intolerant PFTs by a

factor of four (Hickler et al., 2004). The actual establishment rate is further reduced by canopy cover, which affects hypothetical NPP. The hypothetical NPP in turn is derived from photosynthetically active radiation (PAR) at the forest floor. Below a certain PAR-threshold, no saplings can establish. Thresholds differ between shade-tolerant and light-demanding species. Saplings are initialized with a dbh of 1 cm plus a uniformly distributed random fraction of the potential dbh increment that a sapling could achieve in that year.

In conclusion, recruitment models can be found in biophysical models across multiple spatial scales, ranging from single tree-based stand models to dynamic global vegetation models. The majority of approaches combines a deterministic part, representing limiting environmental factors, with a probabilistic component to account for random variation of successful regeneration, but also to compensate for missing parameters due to model abstraction of the actual forest conditions, such as the spatial context of mother trees in the global vegetation models. Whereas allocation rules in LPJ are sensitive to successfully recruited PFTs, this issue has been resolved in ORCHIDEE by using dynamic diameter class boundaries. As a result, the redistribution of biomass among the diameter classes of successful recruitment affects stand structure and thus vegetation dynamics directly. Sapling growth is similar to the growth of adult trees, but the allocation rules are size dependent. The integration of a gap model approach into a dynamic global vegetation model (LPJ-GUESS) further enhanced the representation of structural complexity as an essential aspect for tree regeneration. However, there are also models that allow only user-defined recruitment parameters, such as 3-PG (Landsberg & Waring, 1997) or GOTILWA+ (Gracia et al., 1999).

4.3 Recruitment models in growth and yield models

Static recruitment approaches that assume a constant amount of recruits in a given time period are common in growth and vield models (hereafter G&Y; cf. model based on empirical relationships in figure 1, Weiskittel et al., 2011). With a focus on the effects of management on forest resources G&Ys are primarily geared towards quantifying and maximising the amount of merchantable timber across short time periods (usually one rotation period; Vanclay, 2014). Historically, a forest stand would be clear-cut at the end of a rotation period, and a new generation of trees would be seeded or planted. Thus, no natural regeneration processes would need to be considered in such a model. A typical approach is implemented in the European Forest Scenario model EFISCEN, an empirical, area-based matrix model that projects forest development on a regional and European scale using age and volume classes (Sallnäs, 1990). Forest stands are removed through clearcuttings that are simulated by moving the clearcut area into a separate non-stocked class. Recruitment of non-stocked areas occurs with varying time delays depending on forest and management type by moving the non-stocked area into the lowest volume and age class when the next simulation step starts. Recruitment of tree species not present can be determined by rules dictating the transition and is limited to clearcuts. Hence it does not occur under thinning and partial mortality (Verkerk et al., 2017).
In a traditional management perspective, forest stands are assumed to originate from plantings or sowing, and therefore it is the user who sets the appropriate regeneration method (e.g., clearcut, shelterwood) or planting parameters in a G&Y to achieve the desired species composition and tree density. However, a good understanding of the particular forest system is required to achieve biologically realistic simulation results when tree species are selected or when environmental conditions are changing. Additionally, the use of static approaches necessitates the acceptance of an unknown bias resulting from possible additional recruitment throughout the simulation period. Yet, static recruitment approaches require considerably less development efforts and have in the past provided sufficient flexibility for the simulation of managed forest systems under otherwise constant growing conditions.

Refined approaches in growth and vield models derive recruitment from empirical relationships in from of probabilistic functions whose parameters are linked to stand variables, site conditions, climate and management. Recruitment is treated in two independent steps (i.e., a hurdle model) where the first part is a binary process that determines whether recruitment occurs in a plot or not, and the second step provides the number of recruiting trees (Vanclay, 1992). For example, this approach is used in the distance-independent single-tree forest growth model **PROGNAUS**. The model specifically simulates forest management interventions and provides additional information on wood assortments (Ledermann, 2002). Based on data from the Austrian National Forest Inventory (NFI), the probability of recruitment is modelled in form of a logistic function that takes into account the mean quadratic diameter of the trees on the plot, basal area, a crown competition factor, development stage, elevation, slope, vegetation type, soil type, growth district and forest type. The number of recruiting trees is estimated with a log-linear model that was parameterized from those plots where at least one recruitment tree was observed. The tree species of the recruits is determined by 13 logistic functions that contain as additional predictors the plot's aspect and the dominant canopy species. Two further probabilistic functions are applied to assign DBH and height to the recruits.

A similar approach is used in the Swiss counterpart of PROGNAUS, **SwissStandSim** (Zell, 2016). The probability of recruitment and the number of recruiting trees are modelled in a single aggregated process rather than separating these two. The difference is that zeros can originate from both, the binary but also the count process. Such models may be more parsimonious, especially when the data is over-dispersed, which is often the case for recruitment data (Zell et al., 2019).

There are only few large-scale G&Ys with a stochastic recruitment model (cf. Ledermann, 2002; Zell et al., 2019). Many ingrowth models were developed for specific site conditions or species (cf. Adame et al., 2010; Bravo et al., 2008; Eerikäinen et al., 2014; Klopcic et al., 2012; Li et al., 2011; Moon et al., 2019; Mugasha et al., 2017; Yang & Huang, 2015; Zhang et al., 2012). It is important to note that recruitment definitions depend on the smallest

measured size class of the specific forest survey and that there is considerable variation among surveys. Austria's NFI, for instance, starts measuring trees with a DBH of 5 cm whereas Switzerland measures trees only if they pass a threshold of 12 cm. While the smallest trees in Austria's NFI are still in the thicket phase and experience strong competition for light, those in the Swiss NFI are already in the pole phase with much lower stem densities, underlying different ecological mechanisms.

5. Discussion

Given the nature of any model, the quantification and conceptual abstraction of any process is always a simplified representation of the real world. The abstraction of the major processes underlying forest dynamics, such as growth, mortality and regeneration, varies greatly across the different model types, and the behaviour of simpler models is naturally easier to assess than that of more complex models that feature a vast number of parameters and process interactions. The perfect model does not exist, and among the many concepts to choose from it is up to the user to decide which one is best suited for the particular system of interest and the purpose of the modelling effort, taking into account the various constraints and assumptions but also possibilities of the different approaches.

5.1 Shortcomings related to model purpose and structure

Regeneration approaches in MFDs are in most cases constrained by the structure of the main growth model and its application purpose. For example, when studying the effects of environmental changes on forest dynamics in more detail, the application of MFDs based on ecological principals is, at least in theory, desirable to detect and investigate the key tree regeneration processes. However, this integration of higher process resolution comes at the cost of increased parameterisation efforts, particularly in multi-species systems. Species specific parameters are often obtained from existing case studies. A potential issue of such parameters is their lack of generality as they are obtained from different geographical regions but also time spans (cf. Lischke et al., 2006; Seidl et al., 2012a). Only few are obtained from purposely conducted field experiments. If species specific parameters cannot be obtained, typically the parameters of a closely related species serve as substitutes. The scarcity of data for direct observation based parameterizations increases the risk of making erroneous predictions (Nabel, 2012). Hence, the question remains whether tree regeneration should be modelled in such detail even though the represented processes may not be adequately parameterized or if it may be more beneficial to make robust predictions by applying recruitment models as generally done in growth and yield models.

Growth and yield models aim to project forest resources, eventually under different management scenarios, and often rely on empirical growth functions which naturally provide robust results for short-term projections in well-known systems. Given the purpose and the underlying data base of the main model, a recruitment model would be the obvious choice to simulate tree regeneration in G&Ys. Following this example, it may be that

underlying assumptions become invalid due to environmental or societal changes, which may affect forest management itself. Forest management in Central Europe has shifted from even-aged systems towards uneven-aged mixed systems, favouring natural regeneration over planting (Hengeveld et al., 2012). Static recruitment approaches, as often implemented in G&Ys, make the implicit assumption that in highly managed forest systems sufficient regeneration is always available and will establish continuously. Delayed ingrowth of spontaneous regeneration is neglected in static recruitment approaches and does not affect forest dynamics (Weiskittel et al., 2011). In many cases, this renders static recruitment approaches obsolete, and more dynamic recruitment methods are needed for accurate (large-scale) resource projections under changing forest management paradigms (Li et al., 2011).

Other structural constraints for more detailed regeneration modelling are related to the abstraction of space or even the trees themselves. For example, seed dispersal in stand models is constrained by the spatial setup. Without the spatial context of neighbouring stands, seed influx is limited to arise from adult trees within the stand; seed influx from neighbouring stands relies entirely on the user's assumptions. This has been resolved with the development of landscape models, which pay particular attention to species movement through time and space by simulating a mosaic of forest stands that can serve as potential seed sources (cf. iLand, LandClim). A further increase of spatial scale leads to a simplified representation of vegetation composition and structure, as can be seen in models that are applied across continents or on a global level, spanning multiple biomes. As pointed out by Hanbury-Brown et al. (2022), dispersal between grid cells is, on the one hand, largely lacking in global vegetation models, compromising their ability to represent post-disturbance recovery. The often applied unlimited dispersal within a grid cell, on the other hand, overestimates tree regeneration potential (Hooper et al., 2005). The loss of species-specific environmental responses through the collation of species communities into PFTs has been widely accepted, as parameterization efforts would otherwise exceed the available means. However, it is doubtful whether the definition of PFTs provides sufficient flexibility for an adequate representation of the ecological processes and the differences between species (Purves & Pacala, 2008). Recent developments have complemented PFTs with individual traits and this approach provides more flexibility by taking into account the functional diversity of tree species (Sakschewski et al., 2015). There are successful attempts to incorporate a representation of the structural complexity and functional diversity of forests based on trait schemes (cf. LPJ-GUESS, LPJ-FIT, ORCHIDEE), which merits more attention especially with regard to the recruitment processes that largely determine potential species range shifts under climate change and subsequent future ecosystem functioning.

5.2 Constraints due to ecological knowledge gaps and underrepresented processes

Among the regeneration approaches reviewed here, we noted several known and influential factors to be underrepresented. It is, for example, unclear how climatic change will affect seed availability as a result of poorly understood flowering and pollination mechanisms. Also

the role of mast year cycles may change in unanticipated ways (Bogdziewicz et al., 2021), as they are affected by climate change through altered weather and potentially reduced plant resources (drought stress), but are generally not well understood (Koenig et al., 2015).

We furthermore encourage a larger focus on vegetative reproduction, competition with ground vegetation and herbivory impacts in future model developments, as they may play an important role for the composition and structure of forest regeneration and prospective ecosystem functioning, particularly under climate change with an enhanced occurrence of extreme events (e.g., droughts) and large-scale disturbances such as windthrow or insect attacks (cf. Cailleret et al., 2014; Dietze & Clark, 2008). Especially models that focus on ecosystem dynamics over long time spans should incorporate more sophisticated approaches to implement mechanisms of vegetative reproduction because it has a stronger influence in natural compared to most managed forest ecosystems. Browsing and competition with ground vegetation severely affect tree regeneration in both natural and managed forests, and may lead to arrested succession and a reduction of tree species richness (Thrippleton et al., 2018). Valuable attempts for further development of herbivory impacts are available (cf. FORCLIM, FORSPACE), have shown to improve model simulations (De Jager et al., 2017) and can serve as a template for models without or with a very simple representation of browsing effects. Continuous long-term monitoring could facilitate a more complete understanding of the processes involved and would allow for a more accurate parameterization of regeneration modelling approaches.

5.3 Theoretical desires meet practical limitations

Many climate scenarios for Europe predict precipitation shifts from summer to winter, together with an increase of mean annual temperature, thus promoting drier growing conditions (Lindner et al., 2014) with an increased likelihood of extreme heat waves (IPCC, 2014), boosting tree mortality in forests. Globally, increased tree mortality due to climatic change has been recorded in many forest types, and new species may appear (Neumann et al., 2017); (Yu et al., 2019), a trend that is expected to continue with progressing climate change (Allen et al., 2010). This emphasizes the relevance and need for a much improved and robust representation of forest regeneration as a key component of the resilience and adaptive capacity of European forests under climate change.

MFDs that include population dynamics over periods exceeding a tree's life span and stand development often incorporate complex regeneration models. As in recruitment models, those MFDs aim to provide an appropriate correct number of regenerating trees as input for the main model, rather than investigating trends in tree regeneration and the underlying driving forces. Some MFDs such as Silva or FORCLIM ignore preceding processes such as flowering and pollination, seed production, dispersal and germination based on the rationale that the understanding of those processes is incomplete and the amount of available long-term observations insufficient for appropriate parameterization. Yet, the ultimate goal of regeneration modelling must be to identify meaningful processes and fill existing knowledge

gaps to allow the development of summary approaches that ensure sufficiently accurate predictions under unknown future conditions. We therefore emphasise that future research efforts should specifically focus on the functional verification in relation to prediction accuracy of forest regeneration modelling.

A initial question to be tackled could be if and how the inclusion of more processes can improve the simulated climate change impacts on forest regeneration, and how this relates to the accuracy and uncertainty of predictions (cf. Fisher & Koven, 2020; Koyen et al., 2020). Initially, this can be done for the suite of species currently occurring in a region. With progressing climate change, it may become relevant to investigate new species. Natural species movements have already been observed in European forests (Peñuelas et al., 2007) but more influential may be management shifts towards increasing the forests' adaptive capacity by introducing new, hitherto unobserved species (Figure 3d). Such non-native species often lack a sufficient data base for parametrization, especially in regional or national modelling frameworks. Assisted migration therefore presents a new challenge to tree regeneration models and raises the general question how to handle situations with a paucity of data. Modellers are left with few choices. Parameters may be calibrated until the results match expectations or the can be based on best reasonable guesses, e.g. by applying parameters of closely related species, ignoring competition between these species.

In general, pattern-oriented modelling may provide a way forward to maintain sufficient objectivity regarding model formulations and parameter calibration. It describes an approach to design, select and calibrate models of complex systems (Grimm & Railsback, 2012) such as tree regeneration models, following a systematic protocol (scientific method) that allows tracking of how model formulations and parameters were obtained and how they affect the outcomes. Additionally, model developments should be accompanied by parameter sensitivity analyses to quantify uncertainties (cf. Koyen et al., 2020; Nabel, 2012). In the long run, data scarcity must be tackled to overcome the present knowledge gaps and to allow sufficient parameterization. This will be facilitated by international research collaboration to collect and share observational data and perhaps design and conduct common experiments.

6. Conclusion

The list of potential and acknowledged ecological and climatic effects on regeneration success is long, and substantial efforts have been made in forest dynamic modelling to incorporate evident ecological mechanisms. However, several ecosystem processes that are crucial for forest regeneration are still neither fully understood nor sufficiently quantified, thus limiting the ability to accurately predict forest dynamics under climate change. This leaves considerable freedom for the modellers in the choice of specific approaches and formulations. It is noteworthy that this freedom comes with heavy responsibility to select adequate and robust formulations given the objectives of the modelling study. It is the objective in combination with inherent parameterization limitations that determine the

choice between a regeneration or a recruitment model and the associated level of detail. Especially models that aim to represent long-term forest dynamics should target a refinement of regeneration processes, which must be accompanied by increased effort to collect long-term regeneration data, when climate change impacts on forest composition are to be represented. We identified very simple regeneration approaches in common forest resource models that, depending on the particular management system, may well be acceptable. However, as natural regeneration is becoming more frequently used in managed forests, models aiming to support forest management strategies need to include this option. Altogether, the combination of changes in forest management and climatic conditions results in altered regeneration patters across Europe, ultimately necessitating an improvement of current regeneration modelling approaches.

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Supplement 1

Detailed model descriptions

FVS

The Forest Vegetation Simulator (FVS) is an individual tree forest growth model developed to support forest management decisions (Dixon, 2002). It is calibrated for several regions in the US.

FVS has two regeneration models available. The "full" establishment model is calibrated and available for only a few regions in the US and simulates natural regeneration and stump sprouting and ingrowth automatically when trees have been removed. Predictions are made for small plots of about 13.5 m². The stocking probability, density and species composition is derived from stand characteristics and the forest structure such as slope, habitat type. topographic position, and site preparation, basal area and species composition to enable within-stand variation. The regeneration model runs for 20 years after a disturbance and produces a list of regenerating trees. Because a lot more trees can regenerate than will mature, the model defines "best" trees based on height and species which are expected to contribute the most to future yield. Four of those trees are passed on to the main model and five additional "acceptable" trees (not classified as best trees) after each simulation cycle (usually 5 years). FVS also simulates ingrowth in the absence of disturbance to account for continuing regeneration in sparsely stocked stands. Ingrowth occurs for 20 years after a regeneration period and if no other regeneration activity is planned. In case FVS is initialised with forest inventory data, the regeneration model adjust its pre-calibrated stocking probability. In case the model is applied outside the calibrated range, the "partial" regeneration model is used which requires optimally data of 50 regeneration plots for calibration. Plantings are possible in both models multiple times throughout the year. Planting parameters are defined by the user.

Samsara2

Samsara2 is a spatially explicit individual-based forest dynamics model (Courbaud et al., 2015). A forest stand (typically 1 ha) is described as a list of trees with x, y and z coordinates and the individual diameter at breast height. Forest stands are divided into 25 m^2 cells. Tree height, crown base height and crown radius are derived from allometric functions. Growth is dependent on the energy interception of the canopy. Mortality is driven by a tree's dbh and its growth. The model has been calibrated for *Abies alba* and *Picea abies* in the French Alps.

The recruitment module of Samsara2 simulates adult fecundity and seed production dependent on tree basal area. Seeds are randomly dispersed within a fixed radius around the mother tree. It is assumed that all seeds germinate. A binomial trial is used to simulate

seedling survival dependent on irradiance on the forest floor. Survival probability and irradiance stand in bell shaped relationship to describe trade-off effects. Irradiance has a positive effect on seedling survival under low irradiance levels due to increased photosynthesis rates. Relying on the assumption that under further increasing irradiance levels competition and browsing increases, seedling survival declines. Height growth of seedlings is simulated as a function of irradiance. Saplings are recruited as adult trees when they reach a user-defined height threshold.

SILVA v.2.2

SILVA is an individual-based and spatially explicit forest growth model with emphasis on competition among trees (Pretzsch et al., 2002). It was developed to assess effects of forest management on stand development. The simulated area rarely exceeds 1 hectare. The beginning of a 5-year simulation step is marked by the calculation of a competition index determined by the crown areas of neighbouring trees. In the following step the natural mortality and possible user defined thinning removes trees from the stand before diameter and height growth are simulated based on the competition and site index. The model provides typical information on stand structural development but also indicators for diversity and monetary yield.

The regeneration model of SILVA2.2 simulates annual establishment, height growth and mortality of regenerating trees (Biber & Herling, 2002). Former processes such as seed production, dispersal and germination are neglected as they remain difficult to parameterize with the amount of available long-term regeneration data. The regeneration is modelled in spatially explicit squares with a side length of 2.5 metres and 14 horizontal layers with a height of 0.5 metres. The maximum amount seedlings that can establish is derived from the relationship between average diameter and the maximum stem density as described by Reineke (1933). Since the regeneration model is only simulating height growth, the formula was modified using the allometric relationship between height and diameter (Biber, 2002). Competition among trees is taken into account by calculating the occupied space of trees inand outside the regeneration square. The space that is occupied by each tree is derived from an allometric relationship with tree height. Competition from mature trees outside the regeneration square is calculated as the intersection between the tree crown and a conic section on top of the regeneration square. The actual number of establishing seedlings in the smallest horizontal layer is derived from the unoccupied space within the regeneration square where it is assumed that trees have already reached a height of 25 cm. Height growth is simulated with an average species specific and site dependent growth rate which is added to a random normal distributed number to simulate height differences among the regenerating individuals. Tree mortality occurs density related and under unfavourable growing conditions whereas the number of trees is reduced starting at the bottom layer. Depending on the new height of a regenerating tree, it's new position and allometric relationships are calculated. A tree that exceeds the height of 7 metres is added to the main stand after its diameter, crown dimensions and coordinates are estimated.

PROGNAUS

PROGNAUS is an distance independent single tree forest growth model parameterised on Austrian forest inventory data (Ledermann, 2002). Processes of forest dynamics such as growth, mortality and ingrowth are derived from empirical relationships between tree dimensions, competition factors, stand density, and several site dependent factors. PROGNAUS was designed to specifically simulate forest management interventions and can additionally provide information on available wood assortments.

The ingrowth model of PROGNAUS follows a multistep approach where first the probability of ingrowth is estimated and then the number of ingrowing trees and their biotic properties such as species, DBH and height. The probability of ingrowth is based on observations from the Austrian NFI for plots of a radius of 2.6 meters. Trees are defined as ingrowth when they pass a DBH threshold of 5cm. The probability of ingrowth is modelled as a logistic function that takes into account the plots' mean guadratic diameter, basal area, crown competition factor, development stage, elevation, slope, vegetation type, soil type, growth district and forest type. The number of ingrowing trees is estimated with a log-linear model that was parameterized with plot observations where at least one ingrowth tree was observed. In contrast to the ingrowth probability model, vegetation and soil type were insignificant for the estimation of the number of ingrowing trees and removed from the log-linear model. To estimate the probability that an ingrowing tree belongs to a certain species, 13 logistic functions were parameterized that additionally to the model for ingrowth probability contain the plots aspect and a dummy variable that shows whether the tree species for which the probability is estimated is already present in the overstory. The DBH of an ingrowing tree is derived from a Weibull equation that takes into account the number of ingrowing trees as calculated in the previous step and the plot basal area. The height of an ingrowing trees is modelled for 5 different species groups using a natural logarithm as base. Independent variables include the ingrowing tree's DBH and species as well as the plot's n guadratic diameter, basal area, crown competition factor, elevation and relief.

FORMIND

FORMIND is a process and individual based model that simulates forest dynamics in temperate, subtropical and tropical forests using the gap model approach (Fischer et al., 2016). The main processes recruitment, growth and mortality are dependent on site-specific environmental conditions and the three tree types: pioneer, mid-successional, climax.

Recruitments is divided into three processes: dispersal, germination, space limitation. FORMIND provides two alternatives to calculate the seed pool. The first approach uses a global constant of seed influxes, assuming an intact surrounding forest ecosystem. By default the arrived seeds can only germinate during the next time step. The second approach explicitly simulates type specific seed production of mother trees and their dispersal into neighbouring patches whereas the distance and direction of the dispersed seed are drawn stochastically. Seeds leave the seed pool through germination and user-defined seed pool mortality. Germination success depends on the light availability on the forest floor. If the type specific light requirements are met, the potential seedling size is calculated. Seedlings are established if the space at the specific seedling height is not yet occupied.

FORCLIM v3.0

FORCLIM is a process-based gap model parameterized for the main tree species in temperate forests (Bugmann, 1996). Successional processes such as establishment, growth, competition and mortality are modelled separately in patches of a size of 1/12 ha. The patches are filled with tree cohorts rather than individual trees. The model aims to simulate competition and climate effects on plant population dynamics. General succession patterns are derived from the simulation results of many patches. FORCLIM consists of four submodels: plant, weather, water, management.

Regeneration is part of the plant model and linked to the other three submodels. Seed production, dispersal, germination, seedling establishment and growth are neglected. Saplings are established in cohorts with a DBH of 1.27 cm after they pass species specific environmental filters. Additionally a general establishment probability is applied to simulate diminishing micro-habitat effects. Sapling establishment is impossible if the minimum winter temperature, annual sum of degree days, light availability at the forest floor, browsing pressure, and soil moisture, fall below a species-specific threshold (Didion et al., 2009). The number of establishing saplings is drawn as a uniformly distributed number between 1 and the maximum sapling establishment rate which is dependent on a species' shade tolerance.

4C

4C is process-based forest model that aims to assess forest dynamics under changing environmental conditions (Lasch-Born et al., 2018). The model is parameterized to the main European tree species and simulates establishment, growth and mortality of tree cohorts. The model results describe pools and fluxes of water, carbon and nitrogen of forest stands including the soil.

The regeneration model of 4C simulates the amount of available seeds, growth and mortality of successfully germinated seeds. Successfully germinated seeds are recruitment as seedling cohorts to the main model where they follow the same processes as mature trees. The amount of available seeds per tree species is similar to the approach developed in SIMSEED. (Rogers & Johnson, 1998) and is drawn stochastically from the annual potential seed rate and an equal distributed random number between 0 and 1. The available species for seed production are user defined and can also contain species that are not in a stand. Light availability, temperature and moisture conditions in the litter layer determine the success rates of seed germination. Germination fails if a patch already covered with seedlings. Seeds that cannot germinate are lost. The number of germinated seeds is reduced to the uncovered fraction of a patch. Successfully germinated seeds are organized in seedling cohorts. Biometric parameters of the seedlings are calculated using empirical relationships between shoot, root and foliage mass of a seedling. Seedling height is derived from species specific allometric relationships. Growth and mortality of seedlings is simulated similar to adult trees whereas growth rates depend on radiation, temperature, CO2 concentrations, water and nutrient availability and mortality includes an intrinsic age and stress dependent mortality rate. Seedling cohorts are transformed to tree cohorts when they pass a defined height threshold. 4C additionally allows for planting of saplings. Height distribution of planted cohorts are set as default while the number of planted saplings can be modified. Biomass allocation, growth and mortality are similar to seedlings. Planting is enabled under clear cut, shelter wood and not specified management systems. Short rotation coppice is possible for Aspen and Black locust using special biomass allocation rules for sprouts.

FORSPACE & ForGEM

FORSPACE is a spatially explicit process based forest growth model that simulates vegetation dynamics and landscape formation processes with an emphasis on herbivory and fire impacts using the concept of gap dynamics (Kramer et al., 2001).

The production of seeds is a stochastic process where 2 random numbers are drawn to determine the maximum seed production class and the corresponding number of seeds. Four seed production class are distinguished with different percentages of the maximum seed production to simulate mast year variation. The maximum seed production is scaled to relative crown volume. Seed dispersal depends on the amount of seeds and the dispersal range. Dispersal to neighbouring plots is modelled in form of a Gaussian distribution. Seed loss is simulated by a constant throughout the year which are set to 0 after fire. Larger seeds are additionally subject to grazing. Germination is restricted to the first month of the growing season and only possible when the species is not already present in the herb layer, enough space and light is available, and the litter layer is not too deep. If these requirements are met, a soil type dependent fraction of the available seeds will germinate. Seedlings and

saplings follow the same growth and mortality functions of adult trees and can additionally be killed through grazing and wildfire.

ForGEM stands for FORest Genetics, Ecology and Management and combines ecophysiological and genetic modelling approaches in an individual-based tree model to assess the adaptive potential of forests (Kramer et al., 2008). It's regeneration approach is adopted from the FORESPACE model.

GOTILWA+

GOTILWA+ (acronym for: Growth Of Trees Is Limited by WAter) is a process based forest growth model that simulates carbon and water balances (Gracia et al., 1999). Stands are composed of tree cohorts which are represented by an average tree. It has been developed to assess management practices in Mediterranean forest region but it is general enough to be applied also in other forest regions.

GOTILWA+ does not explicitly simulate tree establishment. The user can either define the number of planted seedlings after each thinning, or, in uneven-aged management, determine the number of new saplings growing after each thinning by assuming an investment from the remaining trees as a percent of their mobile carbon.

3D-CMCC-FEM

The three Dimensional Forest Ecosystem Model of the euro-Mediterranean Centre for Climate Change (3D-CMCC-FEM) was developed to simulate eco-physiological, structural and compositional processes at resolution of one hectare (Collalti et al. 2016; Marconi et al., 2017). The model combines a light use efficiency model with a three dimensional forest structure model to reduce the amount of initialization parameters, as required in conventional process based models, to project forest development in mixed multi-layer forests in the Mediterranean.

The regeneration module of 3D-CMCC calculates the number of available seeds for germination from the available fruit biomass which is allocated from the net primary production. Germination rates are independent from abiotic variables and rely mainly on available literature. Establishment of seedlings is not explicitly modelled and seedling growth is similar to adult trees which is sensitive to tree age. The regeneration module has not yet been validated and is only used internally to ensure carbon balance closure in the forest ecosystem.

3PG

3PG is a process-based forest growth model developed to simulate carbon fixation in forest stands (Landsberg & Waring, 1997). The model calculates the absorbed photosynthetically active radiation absorbed by the forest canopy. The photosynthesis model takes into account the effects of soil drought, atmospheric vapour pressure deficits and stand age.

3PG was developed for even aged monospecific evergreen stands and does not simulate natural regeneration. Planting of seedlings is possible at the beginning of a simulation or after a clear cut by defining the seedling mass and species.

BASFOR

BASFOR (BASic FORest) is a process-based forest growth model simulating biochemistry and growth of deciduous and coniferous stands without simulating horizontal heterogeneity (Van Oijen & Cameron, 2017). It particularly simulates carbon, nitrogen and water cycles.

The model was developed for managed forests and does not take into account natural regeneration. Forest stands are regenerated in form of plantings after final cuttings according to user-defined parameters.

EFISCEN

The European Forest Scenario model (EFISCEN) is an empirical area based matrix model that projects forest development on a regional and European scale using age and volume classes (Sallnäs, 1990; Nabuurs, et al. 2010; Verkerk et al., 2017). Regeneration is not explicitly modelled but simulated after clearcutting by moving the clear-cut area into a separate non-stocked class which is initialized in the lowest age class when the next simulation step starts. Species shifts are determined by the user.

FORMIT-M

FORMIT-M is a climate-sensitive hybrid model that was developed to simulate silvicultural treatments at the stand level (Härkönen et al., 2019). GPP is calculated with the semiempirical canopy model PRELES (Mäkelä et al., 2008; Peltoniemi et al., 2015). NPP:GPP ratios are derived empirically using NFI-data from 10 European countries.

Regeneration is depending on user-defined settings such as the number and the species of regenerating trees. A dynamic regeneration module is not available.

CBM-CFS3

CBM-CFS3 is a landscape model developed to assess carbon stocks in forest ecosystems (Kull et al., 2019). Its structure is simple, forests are considered even aged, single species stands which grow from one age-class to another. Growth is derived from yield-tables depending on the species and growth-region. Regeneration takes place after a disturbance event. Hereby, the model distinguishes between stand replacing and partial mortality caused by either harvesting or natural disturbances such as storm or fire. If no instructions are given by the user, a stand replacing disturbance sets the stand age back to the age 0 after which it starts growing normally according to the yield tables. Those instructions include transition rules which can changes the species composition and delay or speed up (planting) the regeneration. If partial mortality occurs, the corresponding increment and stand age remain unchanged unless defined differently through the transition rules, and no regeneration occurs.

iLand

iLand is a process based forest growth model that simulates the fundamental demographic processes such as growth, mortality and regeneration at a landscape scale and a monthly time step (Seidl et al., 2012a).

The regeneration approach follows the landscape model LANDIS-II and TreeMig (Seidl et al., 2012b). iLand differs by not keeping track of the seeds from individual trees but applying a dispersal kernel around cells that contain mature trees. Additionally, iLand takes into account species-specific fecundity which is sensitive to mast years. After calculating the amount of available seeds and their dispersal, the establishment probability is derived from a stochastic process. Establishment is sensitive to the availability of seeds, light, water availability and temperature limitations.

LANDIS-II v7.0

Landis-II is process based landscape model simulating fundamental ecological processes such as growth, competition, regeneration and disturbances (Gustafson et al., 2000). The landscape is represented as an array of grid cells of equal and user-defined size that contain a mosaic of tree cohorts of different species and ages. The Landis-II operates at an 10-year time step while available extensions (e.g. disturbance, regeneration) may have smaller time steps.

A tree cohort dies if the longevity of the species is exceeded after updating the cohort age and no disturbance occurred before. Reproduction is simulated in every successional time step and additionally immediately after disturbances. New tree cohorts can establish in the Chapter 2

following order through planting, resprouting, serotiny and seeding. Planting typically follows harvesting. The establishment probability of the planted cohort must be greater than 0. If a planted species is successfully established a new tree cohort is created for that species, no other species can arrive on the site through resprouting or dispersal during that time step. The newly established tree cohort has the age 1. Resprouting can occur for certain species after a tree cohort dies naturally or following fire. In order to resprout, a tree cohort must be of a certain age and the species' light requirements must be met. Under those conditions, the species' probability of resprouting must exceed a random number between 0 and 1. If resprouting is successful, no other species can reproduce through seeding during that time step. Establishment through seeding follows several steps. First the initial conditions for germination and establishment are checked before the model searches for possible seed sources. Neighbouring sites can serve as seed sources for a specific species if one of the cohorts of the same species reached maturity and the dispersal distance is not exceeded. Hereafter, the probability of seed arrival is calculated based on the effective and maximum dispersal distance. The effective and maximum seeding distance must be defined for each species. Parameterization can be based on empirical data or derived from ecosystem process models (He et al., 1999). The model provides two non-spatial seeding options: no dispersal of neighbouring sites, universal dispersal (no distance limitation). Serotiny can only happen after fire and follows the rules of seeding.

LandClim

LandClim is a stochastic process-based forest growth model. It was designed to simulate forest dynamics spatially explicit at the landscape level. LandClim is the successor model of LANDIS, a raster based forest growth model. It incorporates an improved tree growth and succession model. Tree growth is based on the forest gap model FORCLIM. Regeneration is modelled after the LANDIS approach (He et al., 1999) which is less detailed as the processes in LANDIS-II.

Seed dispersal is simulated from available seed source locations. Only mature trees can provide seeds for dispersal. The probability to arrive at a given site is affected by a species specific effective and maximum dispersal distance. Hereafter the light and site conditions determine the germination ability (Mladenoff & Baker, 1999). Seeds that did not germinate in a given year are lost. The potential of tree establishment depends on light availability, temperature, soil moisture, browsing and other user defined factors (Bugmann, 1994). Establishment conditions are checked annually while the actual establishment of a new tree cohort can only occur every 10 years. In case of a fire, the number of trees that could establish is reduced by 90% unless it is a fire-adapted species due to the effects on the seedbank.

LandscapeDNDC

LandscapeDNDC is a process based landscape model which simulates GHG fluxes across the landscape between 6 different ecosystems (Haas et al., 2013). Next to the biosphere-atmosphere-hydrosphere fluxes of forests, grasslands and agricultural land, it also takes into account land-use changes between those ecosystems.

Forest growth is simulated by the PnET module, a process based and climate sensitive leafarea specific photosynthesis model which allocates the resulting NPP to fine roots, wood and foliage (Aber & Federer, 1992). The module is linked to a complex soil model to capture N and C fluxes. PnET does not take into account successional changes of biomass accumulation and hence disregards regeneration and mortality dynamics of forest stands. The implemented alternative to PnET takes canopy structure and mixture into account but suffers the same shortcomings regarding successional processes (Grote, 2007).

The third option, MoBiLE-PSIM, takes into account the tree dimensions and models DBH growth. Consequently trees are aging and can die. The mortality function is empirical. Thinning and harvesting can be applied as well but regenerative processes are still neglected (Grote et al., 2011).

Picus v1.2

Picus is a model family based on a patch model approach operating at different physiological scales. Three model variants are available up-to-date. Picus v1.2 (Lexer & Hönninger, 2001) is a spatially explicit 3-dimensional individual-based forest growth model with patch sizes of 10 X 10 X 5 m. Interactions between cells are taken into account in the light regime and seed dispersal simulations. The model is linked to a soil module to represent carbon and nutrient cycling in the forest stand. Picus v1.3 (Seidl et al., 2005) represents a hybrid approach between the patch model Picus v1.2 and the process-based forest production model 3PG to derive net primary production. The latest version, Picus v2.0, represents a refined version of Picus v1.2. The resolution of canopy cells has been reduced to 1m to capture linked physiological processes more accurately. Further, the soil module was exchanged for a multi-layer soil module, allowing a more detailed representation of available soil water.

The regeneration module of the Picus model family is based on the version of Picus v1.2 and calculates the probability of regeneration establishment of trees above 1.3 m height. The model starts with the simulation of seed production and dispersal. Seed production of adult trees depends on their size, light consumption, chilling requirement, and species specific seed production characteristics. Unsatisfied chilling requirements of a species result in the suppression of the seed production in that year. Seed production characteristics are derived from open grown trees with a crown length equal to tree height and a tree height of 2/3 of the maximum tree height for that species. Mast years are simulated stochastically based on

empirical data. Seed production is supressed if a species' chilling requirement is not met. A cone-shaped density function around the centre of seed producing patches is used to simulates seed dispersal. The shape of the cone is hereby defined by the seed producing tree height and the species specific dispersal distance under the assumption of within-stand wind-velocity of 2.5 m/s. The sum of all density functions covering a particular patch determines the amount of available seed per species. Animal dispersal is considered for a selection of tree species with an even distribution of a fixed percentage of produced seeds around the mother tree. The amount of available seeds is further reduced by a species-specific germination rate. Seedlings which don't germinate in a particular year are lost. The number of possible recruitments is a function of available recruitment places, reduced by the area un-available for regeneration, and the species' average environmental response. The environmental response of a species is derived from a light dependent growth response and the response to winter temperature.

The resulting possible recruitments are ranked by proportion to selected the tree species of the recruit using a uniform random number. Recruits are initialised with a height of 1.3 m and a diameter at breast height of approximately 1 cm. Due to the initial size of the trees, their density is limited to 1 individual m⁻². The regeneration model of Picus 1.3 was refined and also models height growth of germinated saplings (Woltjer et al., 2008). Reaching the threshold of 1.3 meters height takes between 5-15 years depending on the species, light conditions and site properties.

TreeMig

TreeMig is a spatially explicit forest landscape model (Lischke et al., 2006). Tree dynamics are based on the distribution-based, height-structured tree population model DisCForM (Lischke et al., 1998; Löffler & Lischke, 2001). Parameters and process functions are derived from the forest gap model ForClim. The model simulates forest dynamics on spatial grid of 0.0625 - 1 km². It captures the basic environment dependent processes of annual reproduction, growth, competition, and mortality, including spatial interaction between the cells.

TreeMig explicitly simulates the regeneration processes such as seed production, seed dispersal, seed bank, recruitment, and development of seedlings and saplings. The seed production depends on the tree species, the tree height and the mast seeding period. The seed inflow builds up the seed bank in a cell. It is calculated through the number of produced seeds in all cells, multiplied by the dispersal probability function which describes the probability of a seed to arrive from a source cell into a target cell. The probability function takes into account the species' mean dispersal distance and the distance between the two cells. Taking into account the different dispersal methods, TreeMig combines two negative exponential functions, a short distance transport (e.g. seed rain with and without

wind, small animal transport) and long-distance transport (e.g. strong wind, birds, large animals). Seed dispersal can be simulated deterministically and stochastically. New seedlings originate from the seed bank. The number of new seedlings depends on the germinability and the establishment rate. Germination is constructed from the winter temperature, degree-day sum and browsing. Germination is not light dependent. The model takes into account species-specific antagonists and alternatively intra-specific competition which reduces the number of seedlings. The seedlings that germinate are added to the saplings which grow similar to the adult trees but are additionally light dependent.

CARAIB

CARAIB (Carbon Assimilation in the Biosphere) is a large-scale process-based dynamic vegetation model initially developed to assess the role of vegetation in the global carbon cycle (Warnant et al., 1994). It simulates photosynthesis at the leaf-level, taking into account the hydrological budget and stomatal regulation. CARAIB contains a soil and a fire module.

Successional processes are implemented through competition between biological affinity groups (BAGs; Dury et al., 2011). BAGs are collections of taxa with similar plant morphology, phenology and climate affinity. BAGs can establish on a grid cell if free space is available and if the climatic requirements for germination are met. Germination success is limited by the minimum monthly soil water content, the yearly sum of daily temperatures above 5°C and the coldest mean monthly temperature. CARAIB initialises equal cover fractions of successfully germinated BAGs on a grid cell. Biomass of herb and shrub BAGs are initialised with 5 g C m⁻², trees with 10 g C m⁻². Gaps in the vegetation cover are formed by mortality through aging, thermal and water stress and fire disturbance. Within the climatic boundaries, dispersal limitations of BAGs are not taken into account. Seeds from BAGs that were already present on a grid cell are initialised according to the NPP proportion of the previous year, newly arriving BAGs are initialised with 5 g C m⁻² for trees.

ED

The Ecosystem Dynamics model (ED) is an individual based, terrestrial biosphere model that predicts carbon and water fluxes between the atmosphere and the ecosystem (Moorcroft et al., 2001). Vegetation dynamics are represented by simulating individual based successional processes such as growth, mortality and reproduction for PFTs in 15x15 m cells. Gap dynamics are up-scaled and coupled to biogeochemical cycles at spatial resolution of $1^{\circ} \times 1^{\circ}$.

NPP is allocated first to leaf and fine root tissue and what's left over goes into growth and reproduction. Hence, only trees with a positive carbon balance are able to reproduce. The

reproductions fractions is derived from seed trap data and constant for all species. Dispersal is random between gaps within the same grid cell and all recruits are initialized with the same size and survivorship to establishment. An alternative formulation of explicit dispersal within and between gaps is presented by Hurtt et al. (2008).

The successor model ED2 refines biophysical components linked to fluxes of CO2, moisture, and energy for an improved representation of short-term and long-term processes that interact in a non-linear way (Longo et al., 2019a; Longo et al., 2019b; Medvigy et al., 2009). The potential density of new recruits is derived from the allocated carbon for reproduction divided by the standard-sized recruit (as derived from the allometric function for the different PFT's; default height: 1.5 m). Seedling survival is not explicitly modelled but the amount of carbon required for flower and pollen production as well as demographic losses from seed to recruitment stage (e.g.: seed bank mortality, grazing) are subtracted from the reproduction carbon pool.

LPJ

LPJ is a process based dynamic global vegetation model, which was developed to simulate terrestrial vegetation dynamics and land-atmosphere carbon and water exchanges (Sitch et al., 2003). The original version was developed by the eponymous collaboration between partners of research centres in Lund, Potsdam, and Jena and has its roots in the BIOME family. Since then, several new version evolved (LPJ-GUESS, LPJmL3, LPJmL4, LPJmL5). LPJ describes the vegetation as fractional coverage of populations of different plant functional types (PFTs). PFTs describe the structural and functional variety among plants. Each PFT is simulated as the average individual and is later up-scaled to the population in a 0.5x0.5° grid-cell. LPJ-GUESS is characterized by a more detailed species and stand-based simulation tool which is based on a gap approach (Smith et al., 2001). LPJmL3 contains an agricultural module. LPJmL4 brings together multiple new model extensions like a plant phenology and a fire module (Schaphoff et al., 2018). LPJmL5 implemented a module which additionally simulates the global nitrogen cycle (von Bloh et al., 2018). LPJ is also adopted in other modelling frameworks such as IMAGE and ORCHIDEE.

Establishment of new individuals in the original LPJ model is simulated annually and depends on the maximum establishment rate of 0.24 saplings m2 a⁻¹ (Prentice et al., 1993). New individuals can establish within their bioclimatic limits in the proportion of a grid cell which is currently not occupied by woody PFTs. Sapling establishment below an annual precipitation of 100 mm is inhibited. The establishment rate is reduced by shading which is determined through the foliage projective cover. LPJ assumes a LAI of 1.5 for established saplings. Growth of successfully established saplings is not explicitly modelled but added to the annual NPP in a grid cell. The sapling biomass is distributed over the different tissues of the PFTs average individual according to the implemented biomass distribution functions. This is

a short-coming of LPJ because it merges sapling properties with the existing average individual properties. As a consequence, dynamics of life cycle stages are skipped which could significantly influence vegetation dynamics.

The difference between the original establishment model and the one in the LPJmL versions is the maximum establishment rate for woody PFTs which has been reduced to 0.12 m2a -1 according to Luyssaert et al. (2007).

LPJ-GUESS is a also a dynamic vegetation model that simulates biogeochemical cycles and additionally vegetation dynamics of forest ecosystems from regional to global scale. It combines the gap model approach of the FORSKA model (Prentice et al., 1993), to represent vegetation dynamics, with the original LPJ model which simulates mechanistic processes of plant growth and resource competition. Tree growth is sensitive to temperature, atmospheric CO2, radiation, soil hydrology and nitrogen availability. The annual NPP is allocated to fine roots, leaves and sapwood. Disturbances such as fire and wind are implemented as a stochastic process based on actual observations, drawn at random.

Seed production and dispersal are not simulated by LPJ-GUESS. The model draws at random the number of new saplings of a PFT in each patch. The maximum expectation is influenced by the "propagules pool", which is linked to the allocation to reproduction of a species population, and the maximum establishment rate. The maximum establishment rate ranges between 0.068 m2 a⁻¹ for shade-tolerant and 0.272 m2 a⁻¹ for shade-intolerant PFTs (Hickler et al., 2004). The actual establishment rate is further reduced by the canopy cover which affects the hypothetical NPP. The hypothetical NPP is derived from photosynthetic active radiation levels (PAR) on the forest floor. Below a certain PAR-threshold no saplings can establish. Thresholds differ between shade-tolerant and light-demanding species. Saplings are initialized with a dbh of 1 cm and an additional uniformly distributed random fraction of the potential dbh increase that a sapling could achieve that year.

ORCHIDEE

ORCHIDEE is dynamic global vegetation model based on three submodels (Krinner et al., 2005). SVAT SECHIBA (Ducoudre et al., 1993) simulates atmosphere-biosphere exchanges of water and energy and explicitly the soil water budget. The global vegetation model LPJ (Sitch et al., 2003) served as a template for the description of successional processes and disturbances. A third submodel, called STOMATE, was developed to combine the first two submodels in order to simulate phenology and carbon dynamics of the terrestrial biosphere. Similar to LPJ, ORCHIDEE describes the composition of vegetation in plant functional types (PFTs, 10 natural and 2 agricultural).

Under the assumption that enough seeds for germination are available, germination and recruitment of saplings depends on the amount of light on the forest floor. Other abiotic or

biotic limitations are not accounted for. Saplings are initialized with species specific heights. Different from the approach in LPJ, ORCHIDEE uses dynamic diameter class boundaries. As a result, redistribution of biomass among the diameter classes of successful regeneration affects the stand structure and consequently vegetation dynamics directly. Alternatively regeneration can be disabled or user-defined. Sapling growth is similar to the growth of adult trees but allocations rules are size dependent.

EFDM

The European Forestry Dynamics Model (EFDM) is an area-based Markov chain model which assesses the development of forest resources, taking into account various intercontinental conditions (Packalen et al., 2014). Regeneration is not explicitly modelled. Instead, the age of a harvested or disturbed area is set back to 0 (similar to CBM).

IMAGE 3.0

IMAGE is a modelling framework that combines large-scale and long-term interactions between human and natural systems to investigate processes of global environmental change (Stehfest et al., 2014). Vegetation dynamics within IMIAGE 3.0 are simulated with the global vegetation model LPJmL.

Recruitment is similar to LPJmL with additional afforestation.

G4M

G4M was developed by the International Institute for Applied System Analyses (IIASA) to assess the effects of land-use changes and forestry activities on biomass and carbon stocks within 0.5x0.5° grid cells (Kindermann et al., 2006). Land-use change takes place when the net present value of a land-use form falls below the net present value of another land-use form. For the calculation of the net present value, G4M takes wood demand and timber prices as well as the product of carbon prices and carbon emissions into account which are derived from the global partial equilibrium model GLOBIOM (Havlík et al., 2018). The growing stock in European countries is initialised from the biomass map of Gallaun et al. (2010). Countries outside Europe are derived from the biomass map of Kindermann et al. (2008). The model handles age classes with a width of 1 year but it is unclear where the initial age class distribution is coming from . Afforestation and disturbances can alter the age class structure. G4M aims for an evenly distributed age class structure in the forest after each rotation period which is directed through alterations of final cuttings. Forest management can be simulated through thinning and rotation length. NPP is translated to net

annual increment which can be adjusted to the age structure and the stocking degree. Potential net primary productivity is adopted from Cramer et al. (1999). A dynamic increment function, sensitive to temperature, precipitation and CO2 concentration, can be implemented. Species composition changes can be incorporated manually through NPP adjustments. A dynamic regeneration model is not present. Regeneration is assumed to follow removals with a user-defined delay. The regenerating species group can be selected by the estimated yield under future site conditions, whereas a business as usual scenario would not simulate a species shift.

Chapter 2



Chapter 3

Combining national forest inventories reveals distinct role of climate on tree recruitment in European forests

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Abstract

Tree recruitment forms an essential process in forest growth models as it determines the amount and composition of the next generation of trees and, hence, the provision of forest ecosystem services over long time spans. With global change and the hereby associated changes in environmental conditions and forest management adaptations, the common static tree recruitment modelling approaches have become largely obsolete and necessitated the development of more dynamic models. Limited by the availability of data for the parameterisation of tree recruitment processes, such models have only been developed for single species or national frameworks and largely failed to detect climatic influences. In this study, we developed a dynamic tree recruitment model for Europe, utilising National Forest Inventory data from 8 countries with more than 95,000 repeated plot observations and nearly 138,000 individual tree recruitment events. We investigated the effect of forest management, forest structure, soil characteristics, nutrient deposition and five groups of weather and climate variables on the quantity and the species of recruiting trees. The climatic groups spanned annual averages, intra annual averages, annual variability, intra annual extremes and a combination of the aforementioned groups. The model with the combination of climate and weather variables outperformed all other groups. We found distinct climatic effects on tree recruitment quantities linked to water limitations and temperature extremes. The results as such showed that tree recruitment quantities benefit from stable climatic conditions, high precipitation and suffer from high maximum temperatures. These factors also drive the ratio between recruiting broadleaves and conifers. The recruitment species was largely determined by the lead species in a plot. Furthermore, the results confirm the important role of forest structure in tree recruitment and enable forest managers to steer the next generation of trees. Especially multi-species stands show a clear advantage over single-species stands regarding tree recruitment quantities and diverse species compositions. Our research enables dynamic and state-of-theart recruitment simulations across forests in Europe. It presents a reproducible method that can be applied to forest simulation modelling frameworks.

1. Introduction

Models of forest dynamics are essential tools to describe, understand and predict forest dynamics under climate change and alternative management strategies (Weiskittel et al., 2011; Vanclay, 2014; Bugmann & Seidl, 2022). In modelling forest dynamics, key population processes are recruitment (also referred to as ingrowth), growth and mortality of trees (Beers, 1962). Of these processes, growth is best understood and has been studied across a large variety of species and ecosystems (e.g. Hasenauer, 2006; Pretzsch, 2009; Burkhart & Tome, 2012). Mortality has received increased attention in recent years (e.g. Hülsmann et al., 2017; Bugmann et al., 2019), after apprehensive increases of natural tree mortality were observed in many forest ecosystems around the globe (Allen et al., 2010; Neumann et al., 2017). As a result, increased tree mortality has led to increased efforts to more accurately represent tree mortality and tree recruitment in forest growth models (e.g. (Ledermann, 2002; Zell, Rohner et al., 2019), as both are crucial factors for long-term projections of forest dynamics under changing environmental conditions (König et al., 2022).

Sample-based models of forest dynamics are often initialised with tree diameter distributions originating from forest inventories. Hereby, tree recruitment is defined as trees that pass the inventory-specific size threshold (system property of the sampled tree population) over a defined period of time (model property, Tomppo, 2010). Historically, tree recruitment was simulated by applying a constant amount of recruitment trees (Weiskittel et al., 2011), assuming, e.g. sufficient homogenous natural regeneration after strip-cutting or planting preceding clearcuts. Such static approaches were sufficiently accurate when applied to e.g. stand table projections or matrix models in equilibrium (Vanclay, 1992). However, socioeconomic, political and environmental changes have promoted forest management shifts towards uneven aged, multi-species forestry systems in large parts of Europe (FOREST EUROPE, 2020). In those systems, rotation cycles do not exist anymore and heterogenous natural regeneration has become a more common source of forest regeneration (Mason et al., 2022). As a result transition rather than equilibrium conditions are the rule.

Static recruitment models have therefore become less appropriate and necessitate the development of dynamic approaches that take into account variability in stand characteristics, forest management and changing site conditions, usually using regression techniques (Vanclay, 1992). These dynamic models have proven to be more accurate but, like the static models, would always predict recruitment numbers greater than zero which does not align with forest survey observations (Shifley et al., 1993). Furthermore, these models were not able to account for the large variation that is often observed in tree recruitment data. Tree recruitment remains a rare event, seemingly random, and does often not occur in a given period of time. Standard regression models, however, assume a rather small overdispersion. To tackle this issue, advancements have been made that simulate tree recruitment in two stochastic steps where, first, the probability of observing recruitment is modelled, and second, the amount of recruitment (cf. Adame et al., 2010; Ledermann,

2002). This approach was later refined into zero-inflated models which essentially combine the two probability functions of the two-step approach to achieve higher model fits and parameter parsimony (Fortin & DeBlois, 2007).

Dynamic tree recruitment models have been developed for a selection of single species (cf. Bravo, et al., 2008; Eerikäinen et al., 2014; Klopcic et al., 2012; Li et al., 2011; Moon et al., 2019; Mugasha et al., 2017; Yang & Huang, 2015; Zhang et al., 2012) and a few national modelling frameworks that include multiple species (cf. Ledermann, 2002; Zell et al., 2019). These national frameworks have in common that they are applied to forest ecosystems which are specific to *one* forest inventory sampling procedure. The application of such a model to a system with a different sampling procedure may be impossible (if the size threshold of predicted recruitment trees is lower than the size threshold of the sampled trees) or introduce undesired biases, compromising model predictions (if the threshold is higher). A dynamic tree recruitment model, sensitive to the sampling procedure and size threshold of recruitment trees, has once been developed on a stand level using multiple regression techniques (Shifley et al., 1993). A large-scale dynamic tree recruitment model, sensitive to sampling procedures, does not exist.

In this study, data from over 95,000 permanent sample plots collected across 8 European countries were utilized, encompassing various sampling procedures, environmental conditions, and nearly 138,000 individual tree recruitment events. A survey-sensitive, dynamic recruitment model was parameterized to simulate the number and species of recruiting trees, with a specific focus on previously weakly detectable or undetectable climatic effects (Käber et al., 2021; Zell et al., 2019). The influence of forest management, forest structure, soil characteristics, nutrient deposition, and five groups of weather and climate variables, including annual averages, intra-annual averages, annual variability, intra-annual extremes, and combinations thereof, were tested on both the quantity and species composition of recruiting trees.

The study aimed to accomplish the following objectives: (I) evaluate the predictive accuracy of recruitment in relation to different sampling procedures and (II) identify environmental and management factors that influence recruitment. By achieving these goals, the research contributes to the development of advanced and dynamic simulations of tree recruitment in European forest surveys. It is tailored towards the implementation into the European Forest Information Scenario Model EFISCEN-Space (Lerink et al., 2023; Schelhaas et al., 2022, Schelhaas et al., 2018a) and presents a reproducible method that can also be applied to other empirical forest growth modelling frameworks. This would decrease their specificity to the sampling method and, hence, increase their applicability and sensitivity to climate impacts.

2. Materials and methods

2.1 Data

All the data for this study was obtained from repeated forest inventories, mostly National Forest Inventories (NFI, Table 1). For the Czech Republic, we used the CzechTerra Landscape Inventory (Cienciala et al., 2016). From Finland a repeated forest inventory dataset (1985-86 and 1995) from the forest health monitoring network was used, for details see Mäkipää & Heikkinen (2003). The inventory design in Poland and the Netherlands allows plot sizes to vary between censuses, depending on the forest age or the number of trees. The tree observations of those plots were reduced to the minimum observed plot radius across the censuses and checked for spatial biases by visual inspection and consultation of the corresponding country experts. All data was put into a standard format for further processing (Esquivel-Muelbert, in prep.). 182 tree species were recorded in the data set (Supplement 2). Because most species were observed rarely, we grouped them into species groups after the approach described in (Schelhaas et al., 2018a). Grouping the tree species allows sufficient amounts of observations in each group for adequate parameter estimation. A group was formed if a species showed more than 5% observation coverage or formed an important commercial or regional species. Additionally, three rest groups were made for short-lived broadleaves, long-lived broadleaves and other conifers, resulting in 19 groups in total (Figure 2, Supplement 2).

The dataset spans a total of 95,037 repeated plot observations with the records of 3.5M trees and 137,984 recruitment trees (Table 1). For some countries more than two observations per plot were available. In this case we selected the observations that had the largest overlap in time with the remaining dataset. All forest inventories in our dataset consist of two or more concentric plots with different radii, except Poland and the Netherlands with a single circular plot. The size threshold for trees to be included in the sample varies between 4 to 12 cm diameter at breast height (DBH) among the inventory datasets. In the case of several concentric plots, recruitment refers to the trees which pass the DBH threshold of the smallest plot. Trees passing the DBH threshold of the larger plots are referred to as ongrowth and are not part of this study (Beers, 1962). Country-specific differences between the size of the smallest plot, the DBH threshold and the average time interval between two observations are recorded in Table 2.

Country	Census period	Plot overlap	No. of trees	No. of recruits
Belgium, Flanders	1997-1999		14,816	
	2009-2018	689	17,337	4,009
Belgium, Wallonia	1994-2004		13,155	
	2008-2011	1,221	16,927	535
Czech Republic	2008-2009		10,066	
	2014-2015	344	10,234	86
Finland	1985		48,732	
	1995	2,490	64,596	4,719
The Netherlands	2001-2005		24,417	
	2012-2013	1,307	35,496	7,327
Poland	2005-2009		518,328	
	2010-2014	24,365	592,140	62,991
Spain	1986-1996		642,208	
	1997-2007	46,415	873,015	43,872
Sweden	2003-2008		270,759	
	2008-2013	13,762	309,963	8,570
Switzerland	1993-1996		58,955	
	2004-2007	4,444	63,522	5,875
Total		95,037	3,584,666	137,984

Table 1 Forest inventory overview per country. Plot overlap refers to the number of repeatedly measured plots between two subsequent censuses. Tree and recruitment observations refer to overlapping plots.

The dependent variables, quantity of recruitment trees per plot (*n.in*) and the species of recruitment trees (*in.sp*) were, together with the forest structural variables, directly derived from the NFI data. Forest structure was represented by six variables calculated at the first census: basal area of living trees per hectare (*ba.alive*), basal area of trees removed between the censuses per hectare (*ba.dead*, does not correspond to dead wood), number of living trees per hectare (*n.ha*), distribution of observed basal area per hectare (*ba.skew*), lead species in a plot (*lead_sp*), and forest type, a categorical variable with two levels (*forest.type*, single-species stand or multi-species stand depending on the number of species observed at plot level). For the calculation of unbiased numerical forest structural variables only trees with a DBH >= 12cm were used (equal to the largest DBH threshold in the dataset, see Table 2).

Soil characteristics were derived from the SoilGrids dataset which consists of nine variables at seven different soil depths with a resolution of 1 km (Hengl et al., 2014). From the available variables we included only cation exchange capacity (Forzieri et al., 2021) and the percentage of silt content at a soil depth of 15 cm (*SLTTPT*) because of high collinearity between the variables and between the soil depths. Nutrient deposition was represented by reduced nitrogen (*RedN*) from the EMEP data set at a grid of 50 km² (EMEP, 2021) for which we calculated the average from 1990 to 2010 (Table 2).

Daily weather data was obtained from the Agri4Cast system (JRC, 2021) with a resolution of 25 km for the period 1985 to 2019. We extracted monthly values of mean temperature, total precipitation, total potential evapotranspiration and total radiation to calculate the mean, minimum, maximum and standard deviation at different temporal aggregation levels (monthly, warmest quarter, coldest quarter, driest quarter, wettest quarter and annual) and additionally six weather indices (Supplement 1). All variables were calculated for the specific period between two observations at the plot level. A detailed description is provided in (Schelhaas et al., 2018a). The weather variables were complemented with climatic variables obtained from WorldClim (Hijmans et al., 2005), GEnS (Metzger et al., 2013), based on WorldClim) and CGIAR-CSI (Trabucco et al., 2008; Zorner et al., 2008) averaged over the period 1950 - 2000 at a resolution of 1 km (Table 3). A total of 103 biotic and abiotic covariates consisting of forest structural variables and gridded soil, nutrient deposition, weather and climate variables were compiled to explain patterns in the quantity and the species of recruitment trees (full list of considered variables in Supplement 1).

Table 2 Sampling procedures and country-specific recruitment characteristics: DBH threshold, mean plot area and mean time interval between observations of the smallest circular plot and corresponding mean observed plot tree recruitment and the percentage of plots without tree recruitment. Numbers in brackets show the standard deviations.

Country	DBH threshold [mm]	Mean plot area [m2]	Mean time interval [years]	Mean plot ingrowth [trees/plot]	Plots without ingrowth [%]
Belgium (Flanders)	70	254 (0)	14.5 (2.6)	5.82	15.5
Belgium (Wallonia)	64	64 (0)	10.7 (3.6)	0.44	79.8
Czech Republic	70	28 (0)	5.9 (0.3)	0.25	85.5
Finland	46	100 (0)	9.8 (0.4)	1.9	45.3
Netherlands	50	329 (245)	9.6 (1.6)	5.61	28.3
Poland	70	274 (96)	5 (2)	2.59	50.6
Spain	75	79 (0)	11.2 (0.9)	0.95	63
Sweden	40	38 (0)	5 (0.2)	0.63	72.8
Switzerland	120	200 (0)	10.9 (1.1)	1.33	54.9



Figure 1 Average observed (triangles) and standardised (dots) plot recruitment per country over country-specific diameter thresholds. Plot recruitment was standardised over a plot area of 500 m² and a time interval of 5 years. The standardised average plot recruitment shows a logarithmic relationship with the DBH threshold (logistic regression line and confidence intervals: black lines).

2.2 Statistical analyses

A data-analytical model selection approach based on Maximum Likelihood estimates was chosen. This so-called Information-Theoretic Model Selection (I-T) encourages the examination of multiple alternative models, contrasting the classical null hypothesis significance testing (Newland, 2019). This approach enabled the testing of a comprehensive set of collinear explanatory variables in separate models, facilitating the exploration of alternative hypotheses. For instance, the investigation focused on determining whether tree recruitment is primarily driven by averaged climate variables, climatic variability or if it is influenced to a greater extent by climatic extremes (maximum and minimum values).

First, base variables were selected that contained only the forest structural, deposition and soil variables (Table 3). An interaction effect was included between the basal area of living trees and stem density to account for different development stages of the forest. From the full set of available variables (Supplement 1) a stepwise removal of variables with a variance inflation factor (VIF, Zuur et al., 2010) larger than 4 was performed, removing the variable with the largest VIF, first. The Pearson and Spearman correlation coefficients was additionally checked between variables to detect potentially remaining collinearity issues.

Collinearity was highest between the weather and climate variables because most variables differ only in their spatial and temporal resolution. For example, the mean annual temperature of the weather dataset was strongly correlated with the mean annual temperature of the climate dataset (Pearson correlation coefficient r = 0.96). In case a

variable was present in both datasets, we included the weather variable due to the higher temporal resolution and the expected direct effect on tree development. But collinearity was also present within the weather and the climate datasets. A typical example in the weather dataset is the mean annual temperature which correlates strongly with the mean temperature of the warmest quarter of the year (r = 0.95), the standard deviation of monthly mean temperature (r = -0.72) and the maximum temperature of the warmest month (r = 0.94). Therefore, we grouped the weather and climate variables into four groups: annual averages, intra annual averages, annual variability and intra annual extremes (Supplement 1). The number of variables in those groups was, in combination with the base variables, further reduced based on VIF. A fifth group was formed based on the combined selection of the previous four groups. Final selection of retained variables in this group was, similar to the previous groups, based on a step-wise selection based on the VIFs (Table 3).

Table 3 Description of response and explanatory variables. In subsequent analyses the base variables were combined separately with the variables from group 1-5. Group 5 forms a combination of uncorrelated variables from group 1-4. The mean and standard deviation are shown before transformation and standardisation. The variables listed under NFI method were only used to model the quantity of recruitment trees.

	Category	Variable	Abbreviation	Unit	Mean (± std)
	Response	Number of recruitment trees per plot	n.in	n	1.45 (±3.72)
		between two observations			
		Species group of recruitment trees	in.sp	class	
		Time in decimal years since last	interval	years	8.62 (±3.29)
	Inventory	Plot area of the smallest circular plot	nlot area	m2	133 55 (+109 69)
	method	(modelled as offset)	piotiarea		100100 (1100100)
		DBH threshold (dbh) transformed to dbh'	dbh'	mm	69.45 (±16.74)
		= log(dbh)	n ha'	n/ha	402 E8 (±220 E7)
		(n.ha) transformed to n.ha' = log(n.ha+1)	11.11d	11/11d	405.56 (±550.57)
		Basal area of living trees per hectare	ba.alive'	m2/ha	18.3 (±14.27)
		(ba.alive) transformed to ba.alive' =			
Base variables		sqrt(ba.alive) Basal area of removed trees per bectare	ha dead'	m2/ha	2 51 (+5 73)
	Frank	(ba.dead) transformed to ba.dead' =	bulucuu	1112/110	2.51 (15.75)
	structure	log(ba.dead+1)			
		Basal area distribution of living trees	ba.skew	index	0.77 (±0.84)
		skewness			
		Forest type with two levels (single-species	forest.type	class	n.mixed=55522,
		stand, multi-species stand)			n.mono=39515
		Lead species group in a plot based on basal area (n=19)	lead_sp	class	
	Soil	Cation exchange capacity	CEC	cmol·kg-1	16.04 (±3.84)
		Silt content mass fraction	SLTPPT	%	29.7 (±5.32)
	Donosition	Deposition of reduced nitrogen	RedN	mg(N)·m−2	516 (±342)
	Deposition	Moon annual temperature	W Mat	۰، ، ۰	10.29 (+4.05)
	Weather	Total annual precipitation	w_IMa1 w TaP	mm	555 (±198)
Group 1 Annual averages		Thorntwaite 1948 humidity index	w_ThHUi	index	126.94 (±57.18)
	Climate	Annual actual evapotranspiration	c_TaAET	mm	505.24 (±99.99)
		Mean wettest quarter temperature	w_MweqT	°C	12.49 (±3.09)
Group 2 Intra	Weather	Mean warmest quarter temperature	w_MwaqT	°C	19.12 (±3.29)
annual averages		Mean driest quarter precipitation	w_MarqP	mm	19./1 (±11.63)
	Climate	Total precipitation for months with mean	c_Tmm0P	mm	606 (±216)
		Mean diurnal temperature range	w MaDR	°C	9.5 (±2)
Group 3 Annual variability	Weather	Standard deviation of monthly mean	w_SDmT	°C	6.98 (±1.25)
		temperature			
		Standard deviation of monthly	w_SDmP	mm	32.63 (±10.08)
		Standard deviation of monthly radiation	w_SDmR	GJ·m−2	217.96 (±13.96)
	Climate	Precipitation seasonality	c_seaP	mm	31.53 (±11.08)
		PET seasonality	c_seaPET	index	4624 (±637)
Group 4 Intra annual extremes		Maximum monthly temperature	w_MAXmT	°C	20.47 (±3.2)
	Weather	Maximum monthly precipitation	w_MAXmP	mm	116.49 (±36.46)
		Minimum monthly precipitation	w_IVIINMP	mm	9.14 (±7.19)
	Climate	Min Dec Jan Feb precipitation	c_MINdjbP	mm	46.05 (±25.2)
Group 5 Combined selection	Model 1	w_ThHUi, c_TaAET			
	Model 2	w_MweqT, c_Tmm0P			
	Model 3	w_MaDR, w_SDmT, w_SDmR, c_seaP,			
	Model 4	c_seaPET w_MAXmT, w_MAXmP, w_MINmP			

2.2.1 Modelling the quantity of recruitment trees

Tree recruitment is a rare event, hence, recruitment data is often zero-inflated (Table 2, Supplement 3). Discrete probability (count) distributions like the Poisson distribution (P) and the Negative Binomial distribution (NB) are generally able to reproduce data with large zero counts but the fit can be poor if not all assumptions are met (e.g. missing covariates, collinearity between covariates). Despite that, the Negative binomial is more flexible because the probability mass function contains two parameters in contrast to the Poisson distribution with one parameter. We combined the base variables separately with the five weather and climate groups (Table 3) and fitted a Poisson and a Negative binomial model, resulting in 10 different combinations. In case of presence of overdispersion (e.g. high number of zeros) we expanded to zero-inflated Poisson and zero-inflated Negative binomial models (Zuur & leno, 2012). We additionally fitted models to the base variables to compare those fits to models including climate and weather variables. Thereafter, we performed a backward selection of the full models based on the Akaike Information Criteria (AIC; Burnham & Anderson, 2002) to remove uninformative covariates. We fitted the models with the "glmmTMB" package (Brooks et al., 2017) in R (Core Team, 2022).

The probability of observing recruitment in a plot increases with plot size, time between the measurements and decreasing DBH threshold (cf. Table 3, Figure 1). To account for differences between NFI methods of countries, the diameter threshold was included as a covariate while plot area and time interval between observations were treated as offsets. An offset assumes a coefficient of 1 to ensure a proportional effect or to maintain a rate. All forest structural variables were normalised using transformations (cf. Table 3). The diameter threshold was additionally log-transformed due to the logarithmic relationship between the DBH threshold and the number of recruitment trees (Figure 1). To prevent computational problems while fitting the models, all covariates were rescaled to a mean of 0 and a standard deviation of 1.

The regression equation is represented as

$$y = \alpha + \beta_1(x_1) + \beta_2(x_2) + \dots + \beta_n(x_n) + offset(\log(plot.area)) + offset(\log(interval))$$

where *y* represents the recruitment abundance, which follows either a Poisson distribution or a negative binomial distribution with a log-link function and x the covariates. The offsets accounts for differences in time intervals and plot area. Furthermore, in the context of zero-inflated models, *y* also represents the probability of observing recruitment as a function of the described covariates.

2.2.2 Modelling the species of recruitment trees

We fitted multinomial logistic regression models (MLRM) to predict the probabilities of each of the 19 recruitment species groups (cf. Zell et all. 2019). MLRMs solve a set of probability

equations for each group simultaneously. The probability to observe species group i is gives as:

$$p_{i} = exp(\beta_{0} + \beta_{1}x_{1} + \beta_{2}x_{2} + ... + \beta_{k}x_{k}) / (1 + \sum [exp(\beta_{0} + \beta_{1}x_{1} + \beta_{2}x_{2} + ... + \beta_{k}x_{k})])$$

where p_i represents the probability of the outcome being in category i, β the regression coefficients, and x the covariates. This equation calculates the probability of each species group relative to the sum of probabilities across all species groups. The exponentiated linear combination of the regression coefficients and predictor variables in the numerator represents the odds of the specific outcome occurring, and the denominator ensures the probabilities sum up to 1 across all outcome categories.

Even though model assumptions regarding collinearity are more relaxed in MLRs, we fitted a separate model for each of the five weather and climate groups (cf. Table 3). In contrast to the discrete probability distributions used for the quantity of tree recruits, variables linked to the sampling design were removed due to perfect separation between the species groups which would lead to a violation of MLRM model assumptions. Uninformative covariates were removed based on the AIC (Burnham & Anderson, 2002). The models were fitted using the function "multinom" from the "nnet" package (Venables & Ripley, 2002).



Figure 2 Species group composition of tree recruits across countries. A table with percentages per species group and country is presented in Supplement 3.
3. Results

3.1 Recruitment count model

The Poisson models were unable to account for the observed zero-inflation of recruitment counts in the dataset (Table 4). The zero-inflated Poisson models reproduced the amount of zeros best but were outperformed by the Negative binomial models in all 5 model categories. Because the Negative Binomial models were able to handle the dispersion of the data, those models were not extended to zero-inflated models. In general, differences between the performances of the 5 model groups was small (Table 4). Based on the AIC, the best performing model was group 5 with a Negative Binomial distribution (Table 4). The model did not fit to all countries equally well (cf. Supplement 4). Further results are shown for group 5, the results of group 1-4 are recorded in Supplement 5.

Table 4 Performance overview of the recruitment count models: the number of factors retained in the model (for the zero-inflated models the number of variables are split up into the conditional model and the zero-inflation model in brackets); the Akaike Information Criteria (based on the maximum likelihood); the AIC differences to the lowest AIC; and the ration between the average number of zeros in 1,000 simulated datasets and the observed number of zeros (56,893).

	Distribution	Factors	AIC	deltaAIC	Zeros
Daca madal	Poisson	9	407439	143806	0.66
Forest structure	Zero inflated Poisson	9 (8)	337653	74021	1.00
i oreșt ști acture	Negative binomial	9	268793	5160	1.00
Model 1	Poisson	15	397312	133679	0.67
Annual averages	Zero inflated Poisson	14 (12)	331822	68189	1.00
, and a verages	Negative binomial	13	264707	1074	1.01
Model 2	Poisson	15	391963	128330	0.69
Intra annual	Zero inflated Poisson	13 (12)	327544	63911	1.00
averages	Negative binomial	14	264072	439	1.00
Model 2	Poisson	16	395114	131481	0.68
Annual variability	Zero inflated Poisson	16 (14)	329159	65526	1.00
, and a variability	Negative binomial	15	264529	896	1.01
Model 4	Poisson	15	396833	133200	0.68
Intra annual	Zero inflated Poisson	15 (11)	330509	66876	1.00
extremes	Negative binomial	14	264671	1038	1.01
Model F	Poisson	18	390112	126479	0.69
Combined selection	Zero inflated Poisson	19 (16)	326021	62388	1.00
	Negative binomial	17	263633	0	1.00

Except for the lead species group and skewness of basal area, all forest structural variables (*forest.type*, *n.ha*', *ba.alive*', *ba.dead*') as well as soil and depositions variables (*CEC*, *SLTPPT*, *RedN*) were significant (Table 5). From eleven climate and weather variables, seven were retained. Those variables originated from all four weather and climate categories (cf. Table 3). Total annual actual evapotranspiration (c_TaAET), total precipitation for months with a mean temperature above 0°C (c_TmmOP) and the standard deviation of monthly

temperature (*w_SDmT*) and monthly radiation (*w_SDmR*) did not improve model performance and were removed from the final model.

The small differences between the performances of the five models (Table 4) in combination with the effect size of the parameters (Table 5) shows that the number of recruitment trees is largely determined by forest structure. The strongest effect was found for the basal area of living trees and the stem density. Both function as a proxy for stand density, controlling the amount of resources available for the regeneration, such as light, water and nutrients.

Category	Variable	Coefficient	95% CI	Pr (> z)
	forest.type (multi-species stand,			
	Intercept)	-6.703	[-6.722 <i>,</i> -6.684]	< .001
- ·	ba.alive'	-1.203	[-1.225, -1.181]	< .001
Forest	ba_dead'	-0.322	[-0.335, -0.309]	< .001
structure	forest.type (single-species stand)	-0.779	[-0.807, -0.751]	< .001
	n.ha'	1.181	[1.15, 1.212]	< .001
	ba.alive' X n.ha'	0.343	[0.329, 0.357]	< .001
Inventory method	dbh'	-0.125	[-0.146, -0.104]	< .001
Cailand	RedN	0.052	[0.035, 0.069]	< .001
Soli and	CEC	-0.117	[-0.135, -0.099]	< .001
deposition	SLTPPT	0.063	[0.046, 0.08]	< .001
	w_ThHUi	-0.102	[-0.12, -0.083]	< .001
	w_MaDR	-0.092	[-0.116, -0.069]	< .001
Masthonord	w_MweqT	0.224	[0.205, 0.244]	< .001
climate	w_MAXmT	-0.244	[-0.267, -0.221]	< .001
ciinate	w_MAXmP	0.22	[0.201, 0.238]	< .001
	c_seaP	-0.204	[-0.224, -0.184]	< .001
	c_seaPET	0.052	[0.033, 0.07]	< .001

Table 5 Coefficients of the tree recruitment count model 5 (combined variables, using a Negative binomial distribution). Confidence intervals and p-values were computed using a Wald-test.

The largest effects of weather and climate variables were found for variability and extremes of temperature and precipitation (cf. Table 5, Figure 3K-P). The results illustrate the sensitivity of tree recruitment to temperature and precipitation. While higher temperatures in the wettest quarter in the year facilitate recruitment, higher maximum monthly temperatures (observed during summer) limit recruitment. Further, higher numbers of tree recruits are expected with increasing maximum monthly precipitation. High precipitation seasonality, however, reduces the amount of expected recruitment.

3.2 Species model

Similar to the recruitment count model, the performance of the five multinomial logistic regression models differed strongly between Model 5 and the remaining models (Table 6). Model 5, which included a combination of variables from Model 1-4, performed best and

was further investigated (Table 6). None of the models with distinct climate and weather groups outperformed another regarding accuracy. The full set of parameters is reported in Supplement 6. The most important set of variables to predict the species probabilities was forest structure, followed the weather and climate variables (Supplement 6).



Figure 3 Simulation results of the final Negative binomial recruitment count model. A) Observed (black) and simulated plot recruitment (green = negative binomial, orange = zero-inflated Poisson) with standard errors. Plot recruitment was derived from the average of 1,000 simulated datasets. B-P) Expected recruitment count (mean of the negative binomial distribution) on 500 m² and a 5 year period. B) Expected recruitment count over diameter threshold for mixed forests (solid line) and monocultures (dotted line). C) Visualisation of interaction effect between basal area and stem density on the expected recruitment counts. Dots show observed plot values. D-P) Expected recruitment count over the 1-99% percentiles of retained variables. Predictions are shown for the two levels of forest type and two diameter thresholds (40mm = black, 100mm = yellow).

Table 6 Model performances of the different species models. The null model contains only an intercept. Given are the effective degrees of freedom (EDF) together with the Akaike Information Criterion (AIC) and the model accuracy. Model accuracy was assessed with 10-fold cross-validation.

	EDF	AIC	deltaAIC	Accuracy
Model 1 Annual averages	558	310646	6444	64.76
Model 2 Intra annual averages	558	311477	7275	64.60
Model 3 Annual variability	594	311952	7750	64.81
Model 4 Intra annual extremes	558	312831	8629	64.65
Model 5 Combination	684	304202	0	65.37

The largest contribution of a single variable to predict the recruitment species probabilities in a plot was the leading species group. The recruitment probability was highest for the leading species group in that plot (see also Supplement 6), showing that seed limitations play the most important role for species recruitment. This is also reflected in the effect of the categorical variable *forest.type*. The share of broad-leaved species and the diversity of recruiting species in general was higher in multi-species stands compared to single-species stands, independent from weather and forest structural variables (Figure 4).

An example of the model's sensitivity to climate is given in Figure 4 A.1. The recruitment probability of Norway spruce, for instance, declines from over 75% at a maximum monthly temperature of 10°C to below 20% at 25°C in spruce-dominated forests, a trend that was present across all shown leading species groups. Thermophilic tree species profited from higher temperatures such as black locust and fir species. The share of broad-leaved tree species groups increased consistently with increasing temperatures across all leading species groups.



Figure 4 Sensitivity analyses of the predicted species group probabilities for three variables of species model 5 (A.1, B.1, C.1) for both forest types (mixed forest, monoculture). The effects of continuous variables on the predicted probabilities are shown for four levels of the categorical variable lead species (main timber species in Europe: beech, common and sessile oak, Norway spruce, Scots pine) while setting all other continuous variables to their mean. A.2 presents the distribution of maximum monthly temperature observations and C.2 for the observed basal area per hectare, respectively.

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4. Discussion

4.1 Climatic constraints of tree recruitment

Even though strong evidence of climatic effects on tree regeneration processes is present, few studies have investigated such effects in the context of tree recruitment (Price et al., 2001; König et al., 2022). Zell et al. (2019) and Käber et al. (2021) provide rare examples of tree recruitment modelling in combination with climate. Nevertheless, both studies found weak climatic effects. Käber et al. (2021) provide three possible explanations which we shortly introduce here to further the discussion on tree recruitment responses to climate and potential shifts under climate change: (1) geographic ranges of the study areas are usually small which may result in insufficient variation among climate variables and, hence, the lack of significant effects; (2) ontogenetic shifts at young tree ages, meaning that trees may regenerate sensitive to climate but die off before they reach the required size threshold to be recorded as recruits; (3) micro-climate is more important than the climate outside the forest stand.

The strong and consistent climate effects, found in this study, supports the hypothesis of insufficient geographical coverage in past studies for the detection of significant climatic influence. The range of the 2.5th and 97.5th percentile of mean annual temperature in this study, for instance, is almost twice as large as the range covered by Zell et al. (2019). Our information-theoretic approach revealed that none of the distinct climate variable groups outperformed another and that the best model performance was achieved by the combined group. Collinearity between the groups in combination with the spatial resolution was assumed to be too high to detect large differences. Alternatively, all groups may contain equally influential variables that describe driving recruitment processes. The chosen combination of variables from different groups preserves the potential to capture the latter explanation.

The results indicate that variables linked to drought and water limitations have a substantial effect on recruitment densities and species compositions. Higher recruitment densities are found in areas with high and stable rainfall conditions. Further, while high temperatures in the wettest quarter of the year promote tree recruitment, high maximum temperatures form a limiting factor. Those patterns could be explained by processes linked to altered growth performances and mortality rates. Higher winter temperatures have been linked to higher growth rates of adult trees (cf. Graumlich, 1991; Harvey et al., 2020; St George et al., 2010) which could have a positive effect on seed production (Koenig & Knops, 2000; Müller-Haubold et al., 2015). Simultaneously, young trees likely also benefit from better growth conditions due to increased resistance to natural disturbances while reaching the required size threshold in shorter time spans. The effects of maximum temperature and precipitation indicate that elevated mortality rates occur under dry conditions and strongly drive tree recruitment densities (Ibanez et al., 2007).

4.2 Ecological or demographic process? The confounding effects of forest structure on tree recruitment

There is widespread agreement on the effects of forest structure on tree recruitment. The strongest influence is commonly found for the basal area of living trees (cf. Klopcic et al., 2012; Mugasha et al., 2017; Yang & Huang, 2015) which serves as a proxy for stand density and, hence, resource competition (Casper & Jackson, 1997; Feldmann et al., 2018), High values of basal area are usually associated with the presence of large trees and dense canopies. Such structures limit the availability of essential resources for successful tree regeneration like the amount of light reaching the forest ground (Binkley et al., 2013; Kara & Topacoglu, 2018; Willson et al., 2020) and soil moisture (Dalsgaard, 2007; Marryanna et al., 2019: Metzger et al., 2017). However, the interpretation of forest structural variables demands caution. Not all forest structural variables follow ecological expectations but represent demographic processes. As pointed out by Käber et al. (2021) and Zell et al. (2019), the effect of basal area must be considered in combination with stem density. The combination of the two provides a good estimate for the development stage of a forest stand (Feldmann et al., 2018). While high basal area values and low stem numbers sketch the structure of mature and dense forest stands, low basal area and low stem number represent young stands with high abundance of resources for tree regeneration.

Whereas forest ecologists would expect a negative effect of increasing stem density on the number of recruitment trees due to higher resource competition, the effect is positive (cf. Figure 3 C&E, Käber et al., 2021; Zell et al., 2019). Due to the lack of an ecological explanation, it is more obvious that the predicted increase of recruitment trees is linked to its demography. Recruitment trees have already successfully passed the vulnerable stages of tree seedlings and saplings (tree regeneration). Only years later, some of the regenerated trees may pass the size threshold to be recorded as recruitment, causing high stem densities at the plot level. However, more trees may yet just be below the threshold and pass the size threshold only in the subsequent observation which results in high recruitment under high stem densities. Stem density therefore forms a demographic process rather than an ecological one and does not represent the environmental conditions of the presence but shows that the environmental conditions in the past must have been favourable for the establishment of tree regeneration. This explanation is supported by the fact that the stem density effect weakens with increasing basal area, hence, is only present in young forests (Figure 3 C). Even so, stem density forms a valuable variable in the context of recruitment modelling, not only because of its predictive power, but also because it ensures an ecologically correct interpretation of the basal area effect. Lastly, using stem density as driver of tree recruitment in a forest growth model requires the presence of a wellfunctioning mortality submodule that limits stem densities in relation to stand density (Pretzsch & Biber, 2005) to prevent the development of unrealistic forest structures in simulation studies.

A similar but less pronounced effect is found for the basal area of dead trees. While the ecological expectation of reduced stand density indicated by a high presence of dead trees would cause higher recruitment rates, the opposite was found. The most likely explanation is that the time delay between favourable conditions (lower basal area) and the presence of tree recruitment is too large to be captured between two consecutive plot observations. Recruitment trees regenerate years before they are measured. Hence, high basal areas of dead trees are more likely observed in dense stands with poor recruitment conditions and may cause a recruitment increase only later. Zell et al. (2019), who investigated the proportion of harvested basal area, directly accounted for the relationship between removed and living basal area and found only a weak positive effect. Within a few years. more than two consecutive plot observations will be available from National Forest Inventories which enables the investigation of effects of harvesting and mortality events further in the past. For now, an alternative explanation for the weak effect of basal area reduction could be linked to species-specific regeneration strategies. Shade-tolerant species tend to maintain seedling banks, meaning that a viable population of seedlings is available at all times. In case of unfavourable growing conditions, those seedlings die off and are replaced with a new population of seedlings in the subsequent year (lida & Masaki, 2002; Shugart, 1984). Low levels of basal area removal may already be sufficient to provide the resources needed for successful regeneration of shade-tolerant species. If stand density decreases fast, light-demanding pioneer species, dominantly relying on seed banks in the forest soil or cones, are outperforming shade-tolerant species and able to quickly colonise the new site (Tiebel et al., 2018). Given that tree regeneration may occur under both low and high levels of basal area reduction may explain the minor effect we found, as recruitment is possible under a wide range of stand density changes. While the regeneration density under light conditions is expected to be higher than that under shade, the recruitment density seems to equalise throughout stand development (Feldmann et al., 2018; Glatthorn et al., 2018; Pretzsch, 2009), so that no major recruitment density differences can be observed between the two situations. Käber et al. (2021) incorporated the level of light availability on the forest floor in their recruitment model and found distinct effects depending on the species' shade-tolerance which decreased with increasing tree size and coincides with our results that show species-specific recruitment success depending on the stand density (cf. Figure 4 C.1).

4.3 Moderate influence of soil and nutrients on tree recruitment

The effects of soil variables on tree recruitment have rarely been studied in the context of tree recruitment modelling (cf. Käber et al., 2021; Zell et al., 2019). Base research on tree regeneration processes, however, revealed strong effects of soil moisture and nutrient availability on seedling regeneration and forest dynamics (Catovsky et al., 2002). Increased nitrogen availability, for instance, improves the growth performance of trees and leads to higher seed production rates (Rohner et al., 2018). Nevertheless, the increased abundance of seeds is not converted into higher tree recruitment because of higher seed predation

(Bogdziewicz et al., 2017) and seedling mortality, even though sapling growth shows positive effects (Catovsky & Bazzaz, 2002). The only weak positive effects found in this study are in line with the findings of Zell et al. (2019) and could be caused by a combination of missing species interactions (Proll et al., 2011) and the use of gridded soil and nutrient deposition data. Gridded data was required to achieve full coverage over the whole study area but might only roughly indicate the actual situation in a plot. Small-scale differences of soil factors might have a stronger influence on micro-habitats and, hence, the chance to observe tree recruitment.

The slightly positive effect of silt content, found in the present study, likely serves as an indicator of plant available water in the soil. The water holding capacity increases with silt content (Jabro et al., 2009) which may reduce drought stress of young trees and result in higher recruitment rates. Cation exchange capacity, however, revealed a counterintuitive effect. A negative effect on the density of tree recruits was found with increasing CEC. While CEC is a measure of nutrient availability for plant uptake and should subsequently promote tree performance and recruitment, a similar effect was found in a study on tree regeneration in Vietnam (Pham et al., 2022). The authors hypothesise that the positive relationship could be caused by a methodological artefact related to the soil depth at which CEC was measured which may not represent the real conditions of CEC. However, under the premise that a similar directional effect was found in our study, we propose an alternative explanation for the negative relationship. Increasing CEC may lead to increased competition with the herbaceous layer which also benefits from higher CEC (van der Waal et al., 2009) which in return causes positive feedback on ungulate densities and hence browsing pressure (Bowyer et al., 2014). A simulation study by Thrippleton et al. (2018) suggests that the effects of competition with the herbaceous layer in combination with browsing in European forests may lead to arrested forest succession. Overall, soil and nutrient related factors should receive more attention in further research with a focus on species-specific effects.

In order to investigate environmental effects on tree recruitment across a large geographical range, we decided to fit *one* general model, taking the non-proportional effect of the diameter threshold (cf. Figure 1) into account as a covariate. Our approach allowed the parameterisation of previously undetected weather and climate effects and was able to reproduce the distribution of observed recruitment counts from the complete dataset (Figure 3A). However, adverse fits were found for Flanders and the Netherlands that resulted in undesired residual patterns (Supplement 4). This is caused by country-specific sampling strategies. While the expected effect of the diameter threshold was well captured (cf. Figure 1, Figure 3B), the remaining two factors of the sampling methods (plot area and time interval), set as offsets, were unable to capture the combined effect. The unique combination of large plot sizes (>200m²) and long time intervals (>10 years) led to strong below-average percentages of plots without recruitment (cf. Table 3, all countries 59.9%) in Flanders (15.5%) and the Netherlands (28.3%), even though standardised plot recruitment fell within the expectations (cf. Figure 1). Poland, for instance, with its similarly large plot

sizes but short time interval did not deviate too strongly from the average percentage of plots without zeros (50.6%). Attempts to correct for the country-specific sampling strategies by either introducing a random effect at the country level or defining plot area and interval as fixed factors including an interaction effect between them did not reduce the residual patterns nor improve the model fit. In fact, the latter resulted in an overfitted model to the specific forest surveys and therefore compromised the estimates of remaining environmental covariates. Additionally, model convergence issues appeared due to a high level of collinearity between the sampling design parameters. The failure of those attempts showed that the discrepancies between the recruitment count distributions are too large to be captured by discrete probability distributions. With the main objective to investigate environmental drivers on the process of tree recruitment and the high confidence of their effects (cf. Table 5, Supplement 4), we accepted those inconsistencies caused by the heterogeneity of sampling strategies.

5. Conclusions

Combining forest surveys to cover larger geographic ranges allows the detection and parameterisation of important climatic factors on tree recruitment. Our study revealed strong effects of climate on recruitment densities and species compositions. Recruitment success may experience a general decline under progressing climate change, with climatic variability, water limitations and temperature extremes as the main driver. Nevertheless, the results confirmed the major role of forest structure on forest regeneration that allows forest management to actively adapt to climate change. Nurturing mixed forests and measures that reduce drought impacts would promote higher tree recruitment densities and facilitate long-term benefits of resilient forest ecosystems. Lastly, effects of sampling strategies could not be eradicated entirely and alternative modelling approaches should be explored with the aim to further reduce potential biases.

6. Acknowledgements

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Full list of considered variables. Weather and climate variables are ordered according to the described grouping: annual average, intra annual averages, annual variability, intra annual extremes.

		Variable	Abbreviation	Unit	Source/temporal resolution/spatial resolution
	nse	Number of recruitment trees per plot between two	n.in	n	NFI/census/plot
	Respo	Species group of recruitment trees	in.sp	class	NFI/census/plot
-	~ -	Time in decimal years since last observation	interval	years	NFI/census/plot
	hoc	Plot area of the smallest circular plot	plot.area	m2	NFI/census/plot
	Inve	DBH threshold (dbh) transformed to dbh' = log(dbh)	dbh'	mm	NFI/census/plot
-		Stem number of living trees per hectare (n.ha) transformed to n.ha' = log(n.ha+1)	n.ha	n	NFI/first measurement/plot
	ıre	Basal area of living trees per hectare (ba.alive) transformed to ba.alive' = sqrt(ba.alive)	ba.alive	mm2	NFI/first measurement/plot
	structu	Basal area of dead trees per hectare (ba.dead) transformed to ba.dead' = log(ba.dead+1)	ba.dead	mm2	NFI/between two measurement/plot
del	orest	Basal area distribution of living trees calculated as Peason's coefficient of skewness	ba.skew	mm2	NFI/first measurement/plot
se mo	LL.	Forest type with two levels (single-species stand, multi-species stand)	forest.type	class	NFI/first measurement/plot
Ba		Leading species group in a plot based on basal area	lead_sp	class	NFI/first measurement/plot
		Depth to bedrock (R horizon) up to maximum 240 cm	BDRICM	cm	SoilGrids /1 km2
		Bulk density of the fine earth fraction	BLD	kg·m−3	SoilGrids /1 km2
		Cation exchange capacity	CEC	cmol·kg-1	SoilGrids /1 km2
		Clay content mass fraction	CLYPPT	%	SoilGrids /1 km2
	Sc	Coarse fragments (> 2 mm fraction) volumetric	CRFVOL	%	SoilGrids /1 km2
		Soil organic carbon	ORCDRC	%	SoilGrids /1 km2
		pH in H2O × 10	PHIHOX	рН	SoilGrids /1 km2
		Silt content mass fraction	SLTPPT	%	SoilGrids /1 km2
-		Sand content mass fraction	SNDPPT	%	SoilGrids /1 km2
	on	Deposition of reduced nitrogen	avgDepRedN	mg(N)·m−2	EMEP/ average 1990–2010 /50 km
	siti	Deposition of oxidised nitrogen	avgDepOxN	mg(S)·m−2	EMEP/ average 1990–2010 /50 km
	Depo	Deposition of oxidised sulphur	avgDepOxS	mg(N)·m−2	EMEP/ average 1990-2010 /50 km
		Mean annual temperature	w_MaT	°C	Agri4Cast / study period / 25 km2
		Isothermality	w_ISO	index	Agri4Cast / study period / 25 km2
		Degree days above 0 degrees Celsius	w_DD0	°C	Agri4Cast / study period / 25 km2
		Degree days above 5 degrees Celsius	w_DD5	°C	Agri4Cast / study period / 25 km2
	her	Degree days above 10 degrees Celsius	w_DD10	°C	Agri4Cast / study period / 25 km2
	eat	Total annual precipitation	w_TaP	mm	Agri4Cast / study period / 25 km2
	Š	Total annual potential evapotranspiration (PET)	w_TaPET	mm	Agri4Cast / study period / 25 km2
		Total annual radiation	w_TaR	GJ·m−2	Agri4Cast / study period / 25 km2
ges		Aridity index	w_ARi	index	Agri4Cast / study period / 25 km2
era		Thorntwaite 1948 humidity index	w_ThHUi	index	Agri4Cast / study period / 25 km2
ave		Thorntwaite 1948 aridity index	w_ThARi	index	Agri4Cast / study period / 25 km2
ual		Annual mean temperature	c_MaT	K	worldclim/1950-2000/1km2
nn		Degree days above 0 degrees Celsius	c_DD0	°C	worldclim/1950-2000/1km2
1/		Degree days above 5 degrees Celsius	c_DD5	°C	worldclim/1950-2000/1km2
del		Number of days with mean temperature > 10	c_NM10	index	worldclim/1950-2000/1km2
β		Inermicity index	C_11	index	worldclim/1950-2000/1km2
	te	lotal annual precipitation	c_TaP	mm	worldclim/1950-2000/1km2
	ma		C_ISU	K mm	worldclim/1950-2000/1km2
	U	Annual actual evapotranspiration Annual notential evapotranspiration (PET)	C_TARET	mm	worldclim/1950-2000/1km2
		Coefficient of annual moisture availability	c coefmoist	index	worldclim/1950-2000/1km2
		Aridity index	c Ari	index	worldclim/1950-2000/1km2
		Thorntwaite 1948 humidity index	c_ThHUi	index	worldclim/1950-2000/1km2
		Thorntwaite 1948 aridity index	c ThARi	index	worldclim/1950-2000/1km2
		Embergers pluviothermic quotient	c_EmPQ	index	worldclim/1950-2000/1km2
		•	_		

		Total annual radiation	c TaR	index	worldclim/1950-2000/1km2
		Mean warmest guarter temperature	w MwaqT	°C	Agri4Cast / study period / 25 km2
		Mean coldest guarter temperature	w McogT	°C	Agri4Cast / study period / 25 km2
		Mean wettest quarter temperature	w MwegT	°C	Agri4Cast / study period / 25 km2
		Mean driest quarter temperature	w MdraT	°C	Agri4Cast / study period / 25 km2
		Mean warmest quarter precipitation	w MwagP	mm	Agri4Cast / study period / 25 km2
		Mean coldest quarter precipitation	w McoaP	mm	Agri4Cast / study period / 25 km2
		Mean wettest quarter precipitation	w MweaP	mm	Agri4Cast / study period / 25 km2
	her	Mean driest quarter precipitation	w MdraP	mm	Agri4Cast / study period / 25 km2
	eat	Mean warmest quarter radiation	w MwagR	Gl·m-2	Agri4Cast / study period / 25 km2
	≥	Mean coldest quarter radiation	w McoaR	Gl·m-2	Agri4Cast / study period / 25 km2
ន		Mean wettest quarter radiation	w MweaR	Gl·m-2	Agri4Cast / study period / 25 km2
986 986		Mean driest quarter radiation	w MdraR	Gl·m-2	Agri4Cast / study period / 25 km2
IVEL		Mean warmest guarter PET	w MwagPET	mm	Agri4Cast / study period / 25 km2
ala		Mean coldest guarter PET	w McogPET	mm	Agri4Cast / study period / 25 km2
nu		Mean wettest guarter PET	w MwegPFT	mm	Agri4Cast / study period / 25 km2
a ar		Mean driest guarter PET	w MdraPET	mm	Agri4Cast / study period / 25 km2
- utre		Mean Temperature of Wettest Quarter	c MwegT	K	worldclim/1950-2000/1km2
21		Mean Temperature of Driest Quarter	c MdraT	К	worldclim/1950-2000/1km2
del		Mean temperature of warmest guarter	c MwagT	К	worldclim/1950-2000/1km2
β		Mean temperature of the coldest month	c McomT	К	worldclim/1950-2000/1km2
		Mean temperature of the warmest month	c_MwamT	К	worldclim/1950-2000/1km2
		Precipitation of the wettest month	c_MwemP	mm	worldclim/1950-2000/1km2
	ate	Precipitation of the driest month	c MdrmP	mm	worldclim/1950-2000/1km2
	<u>E</u>	Precipitation seasonality	c_seaP	mm	worldclim/1950-2000/1km2
	0	Precipitation of the wettest guarter	c TweaP	mm	worldclim/1950-2000/1km2
		Precipitation of the driest quarter	c TdraP	mm	worldclim/1950-2000/1km2
		Precipitation of the warmest quarter	c TwaqP	mm	worldclim/1950-2000/1km2
		Precipitation of the coldest guarter	c TcoaP	mm	worldclim/1950-2000/1km2
		Total precipitation for months with mean monthly	c Tmm0P	mm	worldclim/1950-2000/1km2
		temperature above 0	-		
		Standard deviation of monthly mean temperature	w_SDmT	°C	Agri4Cast / study period / 25 km2
ţ	L.	Mean diurnal range	w_MaDR	°C	Agri4Cast / study period / 25 km2
lide	the	Annual temperature range	w_aTR	°C	Agri4Cast / study period / 25 km2
aria	Vea	Standard deviation of monthly precipitation	w_SDmP	mm	Agri4Cast / study period / 25 km2
2	>	Standard deviation of monthly PET	w_SDmPET	mm	Agri4Cast / study period / 25 km2
nu _		Standard deviation of monthly radiation	w_SDmR	GJ∙m−2	Agri4Cast / study period / 25 km2
An		Temperature Annual Range (BIO5-BIO6)	c_aTR	К	worldclim/1950-2000/1km2
<u>9</u>	ate	Mean temperature of coldest quarter	c_McoqT	К	worldclim/1950-2000/1km2
lod	Ĕ.	Mean diurnal range	c_MaDR	mm	worldclim/1950-2000/1km2
Σ	Ū	PET seasonality	c_seaPET	index	worldclim/1950-2000/1km2
		Temperature seasonality	c_seaT	index	worldclim/1950-2000/1km2
		Maximum monthly temperature	w_MAXmT	°C	Agri4Cast / study period / 25 km2
		Minimum monthly temperature	w_MINmT	°C	Agri4Cast / study period / 25 km2
	Ŀ	Maximum monthly precipitation	w_MAXmP	mm	Agri4Cast / study period / 25 km2
nes	ath	Minimum monthly precipitation	w_MINmP	mm	Agri4Cast / study period / 25 km2
rer	Ne	Maximum monthly PET	w_MAXmPET	mm	Agri4Cast / study period / 25 km2
ext	-	Minimum monthly PET	w_MINmPET	mm	Agri4Cast / study period / 25 km2
ual		Maximum monthly radiation	w_MAXmR	GJ·m−2	Agri4Cast / study period / 25 km2
uu –		Minimum monthly radiation	w_MINmR	GJ∙m−2	Agri4Cast / study period / 25 km2
ra		Max Temperature of Warmest Month	c_MAXwamT	К	worldclim/1950-2000/1km2
Int		Min Temperature of Coldest Month	c_MINcomT	К	worldclim/1950-2000/1km2
el 4	e	Maximum temperature of the coldest month	c_MAXcomT	К	worldclim/1950-2000/1km2
po	nat	Minimum temperature of the warmest month	c_MINwamT	к	worldclim/1950-2000/1km2
Σ	Cli	Minimum June July August precipitation	c_MINjjaP	mm	worldclim/1950-2000/1km2
		Maximum June July August precipitation	c_MAXjjaP	mm	worldclim/1950-2000/1km2
		Min Dec Jan Feb precipitation	c_MINdjbP	mm	worldclim/1950-2000/1km2
		Max Dec Jan Feb precipitation	c MAXdjfP	mm	worldclim/1950-2000/1km2

Recorded species name in original dataset and the corresponding species groups. In total 182 different species names were recorded and reduced to 20 species groups.

	Recorded species name	Species Group		Recorded species name	Species Group
1	Abies alba	Abies spp.	92	Pinus radiata	Other indigenous Pinus
2	Abies concolor	Abies spp.	93	Pinus rigida	Other indigenous Pinus
3	Abies grandis	Abies spp.	94	Pinus strobus	Other indigenous Pinus
4	Abies pinsapo	Abies spp.	95	Pinus uncinata	Other indigenous Pinus
5	Betula	Betula spp.	96	Picea abies	Picea abies
6	Betula indet	Betula spp.	97	Picea sitchensis	Picea sitchensis
7	Betula pendula	Betula spp.	98	Pinus mugo	Pinus nigra+mugo
8	Betula pubescens	Betula spp.	99	Pinus nigra	Pinus nigra+mugo
9	Betula verrucosa	Betula spp.	100	Pinus nigra var. maritima	Pinus nigra+mugo
10	Castanea sativa	Castanea sativa	101	Pinus nigra var. nigra	Pinus nigra+mugo
11	Eucalyptus camaldulensis	Eucalyptus spp.	102	Pinus sylvestris	Pinus sylvestris
12	Eucalyptus globulus	Eucalyptus spp.	103	Populus	Populus plantations
13	Eucalyptus gomphocephalus	Eucalyptus spp.	104	Populus alba	Populus plantations
14	Eucalyptus nitens	Eucalyptus spp.	105	Populus alba, Populus canescens	Populus plantations
15	Eucalyptus viminalis	Eucalyptus spp.	106	Populus indet	Populus plantations
16	Fagus silvatica	Fagus sylvatica	107	Populus nigra	Populus plantations
17	Fagus sylvatica	Fagus sylvatica	108	Populus tremula	Populus plantations
18	Larix decidua	Larix spp.	109	Populus x canadensis	Populus plantations
19	Larix indet	Larix spp.	110	Pseudotsuga menziesii	Pseudotsuga menziesii
20	Larix kaempferi	Larix spp.	111	Quercus ilex	Quercus ilex
21	Acacia dealbata	long-lived broadleaves	112	Quercus indet	Quercus robur&petraea
22	Acacia indet	long-lived broadleaves	113	Quercus petraea	Quercus robur&petraea
23	Acacia melanoxylon	long-lived broadleaves	114	Quercus robur	Quercus robur&petraea
24	Acer	long-lived broadleaves	115	Quercus robur, Quercus petraea	Quercus robur&petraea
25	Acer campestre	long-lived broadleaves	116	Quercus suber	Quercus suber
26	Acer monspessulanum	long-lived broadleaves	117	Robinia pseudacacia	Robinia pseudoacacia
27	Acer negundo	long-lived broadleaves	118	Robinia pseudoacacia	Robinia pseudoacacia
28	Acer opalus	long-lived broadleaves	119	Ailanthus altissima	short-lived broadleaves
29	Acer platanoides	long-lived broadleaves	120	Alnus glutinosa	short-lived broadleaves
30	Acer pseudoplatanus	long-lived broadleaves	121	Alnus incana	short-lived broadleaves
31	Acer tataricum	long-lived broadleaves	122	Alnus indet	short-lived broadleaves
32	Aesculus hippocastanum	long-lived broadleaves	123	Alnus viridis	short-lived broadleaves
33	Buxus sempervirens	long-lived broadleaves	124	Amelanchier lamarckii	short-lived broadleaves
34	Carpinus betulus	long-lived broadleaves	125	Amelanchier ovalis	short-lived broadleaves
35	Ceratonia siliqua	long-lived broadleaves	126	Arbutus unedo	short-lived broadleaves
36	Fraxinus excelsior	long-lived broadleaves	127	Celtis australis	short-lived broadleaves
37	Fraxinus NA	long-lived broadleaves	128	Cornus alba	short-lived broadleaves
38	Fraxinus pennsylvanica	long-lived broadleaves	129	Cornus mas	short-lived broadleaves
39	Juglans regia	long-lived broadleaves	130	Cornus sanguinea	short-lived broadleaves
40	Laurus nobilis	long-lived broadleaves	131	Corylus avellana	short-lived broadleaves
41	Olea europaea	long-lived broadleaves	132	Crataegus indet	short-lived broadleaves
42	Ostrya carpinifolia	long-lived broadleaves	133	Crataegus laciniata	short-lived broadleaves
43	Other broadleaves	long-lived broadleaves	134	Crataegus monogyna	short-lived broadleaves

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44	Other exotic broadleaves	long-lived broadleaves	135	
45	Other indigenous broadleaves	long-lived broadleaves	136	
46	Phillyrea latifolia	long-lived broadleaves	137	
47	Platanus hispanica	long-lived broadleaves	138	
48	Prunus avium	long-lived broadleaves	139	
49	Quercus canariensis	long-lived broadleaves	140	
50	Quercus cerris	long-lived broadleaves	141	
51	Quercus faginea	long-lived broadleaves	142	
52	Quercus pubescens	long-lived broadleaves	143	
53	Quercus pyrenaica	long-lived broadleaves	144	
54	Quercus rubra	long-lived broadleaves	145	
55	Quercus species	long-lived broadleaves	146	
56	Tilia cordata	long-lived broadleaves	147	
57	Tilia indet	long-lived broadleaves	148	
59	Tilia platvobyllos	long-lived broadleaves	1/0	
50		long-lived broadleaves	145	
55		long-lived broadleaves	150	
61		long-lived broadleaves	151	
61	Ullinus glabia	long-lived broadleaves	152	
62	Ulmus miner	long-lived broadleaves	155	
63	Ulmus minor	long-lived broadleaves	154	
64	Ulmus scabra	long-lived broadleaves	155	
65	Ulmus species	long-lived broadleaves	156	
66	Viburnum opulus	long-lived broadleaves	157	
67	Abies indet	Other conifers	158	
68	Cedrus atlantica	Other conifers	159	
69	Cedrus deodara	Other conifers	160	
70	Cedrus libani	Other conifers	161	
71	Chamaecyparis lawsoniana	Other conifers	162	
72	Chamaecyparis thyoides	Other conifers	163	
73	Cupressus arizonica	Other conifers	164	
74	Cupressus indet	Other conifers	165	
75	Juniperus communis	Other conifers	166	
76	Juniperus indet	Other conifers	167	
77	Juniperus oxycedrus	Other conifers	168	
78	Juniperus phoenicea	Other conifers	169	
79	Juniperus thurifera	Other conifers	170	
80	Picea indet	Other conifers	171	
81	Picea omorika	Other conifers	172	
82	Pinus banksiana	Other conifers	173	
83	Pinus cembra	Other conifers	174	
84	Pinus contorta	Other conifers	175	
85	Taxus baccata	Other conifers	176	
86	Taxus baccata	Other conifers	177	
87	Thuja plicata	Other conifers	178	
88	Tsuga heterophylla	Other conifers	179	
89	Pinus halepensis	Other indigenous Pinus	180	
90	Pinus pinaster	Other indigenous Pinus	181	
91	Pinus pinea	Other indigenous Pinus	182	

Crataegus oxyacantha Cupressus Jusitanica Cupressus sempervirens Euonymus europaea Euonymus europaeus Euonymus verrucosa Ficus carica Frangula alnus Fraxinus americana Fraxinus angustifolia Fraxinus ornus Ilex aquifolium Laburnum anagyroides Ligustrum vulgare Malus silvestris Malus svlvestris Pistacia terebinthus Prunus cerasifera Prunus cerasus Prunus domestica Prunus indet Prunus insititia Prunus nadus Prunus serotina Prunus spinosa Pvrus communis Pyrus indet Rhamnus alaternus Rhamnus cathartica Rhamnus frangula Rhus typhina Salix Salix alba Salix atrocinerea Salix caprea Salix elaeagnos Salix fragilis Salix indet Salix spec Salix species Sambucus nigra Sambucus racemosa Sorbus aria Sorbus aucuparia Sorbus indet Sorbus intermedia Sorbus torminalis Tamarix indet

short-lived broadleaves short-lived broadleaves

~					••						
S	necies	group	composition	ot	recruitment	r trees i	ın	nercent	ner	country	/
-	peeres	5,000	00111000101011	۰.	i coi aitiiicii			percent	PCI	country	•

	Switzerland	Czech Republic	Finland	Flanders	Netherlands	Poland	Spain	Sweden	Wallonia	Total
Abies spp.	11.76				0.07	3.63	0.35			2.27
Betula spp.	1.53	3.49	33.86	16.81	12.65	8.62	0.79	27.11	14.77	8.31
Castanea sativa	1.72			1.92	0.45		1.62		0.75	0.67
Eucalyptus spp.							6.36			2.02
Fagus sylvatica	15.01	11.63		2.42	4.05	6.87	2.09	0.48	26.17	4.86
Larix spp.	3.64			1.22	2.39	1.05	0.01	0.04	2.06	0.81
long-lived broadleaves	14.81	25.58		16.81	10.17	15.46	15.49	0.56	29.35	13.81
Other conifers	0.89		0.28	0.05	1.06	0.04	2.05	1.84		0.89
Other indigenous Pinus	0.02			0.37	0.07	0.05	21.94			7.01
Picea abies	39.97	41.86	25.70	0.67	1.19	11.39	0.02	43.38	11.59	10.63
Pinus nigra+mugo	1.02			6.98	0.48	0.26	7.99			2.93
Pinus sylvestris	1.48	8.14	25.03	13.10	9.01	35.90	10.26	20.20	0.56	22.69
Populus plantations	0.14		1.74	1.00	0.94	0.90	0.47	0.88	0.75	0.76
Pseudotsuga menziesii	0.32			0.70	4.34	0.07	0.20		2.06	0.37
Quercus ilex							21.75			6.91
Quercus robur&petraea	0.80	5.81		12.15	10.30	1.13	2.40	0.61	5.61	2.28
Quercus suber							1.16			0.37
Robinia pseudoacacia	0.43			0.42	0.23	0.65	0.09		0.56	0.37
short-lived broadleaves	6.47	3.49	13.39	25.37	42.60	13.98	4.98	4.91	5.79	12.03

Observed and simulated plot recruitment per country. Simulated plot recruitment and standard deviation is derived from the average of 10,000 simulated datasets of Model 5 Negative binomial (Table 3).



Parameter estimates of the four climate model groups.

Model 1 Annual averages

Category	Variable	Coefficient	95% CI	Pr (> z)
Forest	forest.type (mixed forest, Intercept)	-6.676	[-6.695, -6.657]	< .001
structure	ba.alive'	-1.171	[-1.193, -1.149]	< .001
	ba_dead'	-0.327	[-0.34, -0.314]	< .001
	forest.type (monoculture)	-0.807	[-0.835, -0.778]	< .001
	n.ha'	1.168	[1.137 <i>,</i> 1.199]	< .001
	ba.alive' X n.ha'	0.350	[0.336, 0.364]	< .001
NFI method	dbh'	-0.196	[0.336, 0.364]	< .001
Soil	RedN	0.149	[0.134, 0.164]	< .001
and	CEC	-0.190	[-0.204, -0.176]	< .001
deposition	SLTPPT	removed		
Weather	w_MaT	-0.235	[-0.253, -0.216]	< .001
and	w_TaP	0.270	[0.251, 0.289]	< .001
climate	w_ThHUi	-0.203	[-0.221, -0.185]	< .001
	c_TaAET	0.092	[0.073, 0.111]	< .001

Model 2 Intra annual averages

Category	Variable	Coefficient	95% CI	Pr (> z)
Forest	forest.type (mixed forest, Intercept)	-6.699	[-6.718, -6.68]	< .001
structure	ba.alive'	-1.183	[-1.205, -1.161]	< .001
	ba_dead'	-0.326	[-0.339, -0.313]	< .001
	forest.type (monoculture)	-0.765	[-0.793, -0.737]	< .001
	n.ha'	1.165	[1.135, 1.196]	< .001
	ba.alive' X n.ha'	0.34	[0.127, 0.161]	< .001
NFI method	dbh'	-0.098	[0.127, 0.161]	< .001
Soil	RedN	0.078	[0.061, 0.095]	< .001
and	CEC	-0.126	[-0.143, -0.109]	< .001
deposition	SLTPPT	0.069	[0.052, 0.086]	< .001
Weather and				
climate	w_MweqT	0.298	[0.281, 0.314]	< .001
and	w_MwaqT	-0.3	[0.281, 0.314]	< .001
climate	w_MdrqP	0.083	[-0.324, -0.275]	< .001
	c_Tmm0P	0.144	[0.058, 0.108]	< .001

Category	Variable	Coefficient	95% CI	Pr (> z)
Forest	forest.type (mixed forest, Intercept)	-6.688	[-6.707, -6.669]	< .001
structure	ba.alive'	-1.172	[-1.194, -1.15]	< .001
	ba_dead'	-0.339	[-0.352, -0.326]	< .001
	forest.type (monoculture)	-0.785	[-0.813, -0.757]	< .001
	n.ha'	1.175	[1.144, 1.206]	< .001
	ba.alive' X n.ha'	0.350	[0.336, 0.364]	< .001
NFI method	dbh'	-0.087	[-0.105, -0.068]	< .001
Soil	RedN	0.129	[0.113, 0.145]	< .001
and	CEC	-0.143	[-0.161, -0.125]	< .001
deposition	SLTPPT	0.060	[0.043, 0.077]	< .001
Weather	w_MaDR	-0.244	[-0.264, -0.225]	< .001
and	w_SDmT	0.123	[0.107, 0.139]	< .001
climate	w_SDmP	0.184	[0.166, 0.202]	< .001
	w_SDmR	-0.031	[-0.048, -0.013]	< .001
	c_seaP	-0.167	[-0.186, -0.149]	< .001

Model 3 Annual variability

Model 4 Intra annual extremes

Catagony	Variable	Coofficient		Dr(> z)
Category	Variable	coencient	95% CI	PI (2 2)
Forest	forest.type (mixed forest, Intercept)	-6.679	[-6.698, -6.659]	< .001
structure	ba.alive'	-1.159	[-1.182, -1.137]	< .001
	ba_dead'	-0.33	[-0.343, -0.317]	< .001
	forest.type (monoculture)	-0.816	[-0.844, -0.788]	< .001
	n.ha'	1.173	[1.142, 1.204]	< .001
	ba.alive' X n.ha'	0.354	[0.34, 0.368]	< .001
NFI method	dbh'	-0.082	[-0.102, -0.062]	< .001
Soil	RedN	0.243	[0.227, 0.26]	< .001
and	CEC	-0.149	[-0.167, -0.132]	< .001
deposition	SLTPPT	0.068	[0.051, 0.085]	< .001
Weather	w MAXmT	-0.333	[-0.355, -0.311]	< .001
and	_ w_MAXmP	0.264	[0.247, 0.282]	< .001
climate	w MINmP	-0.131	[-0.152, -0.11]	< .001
	_ c_MINdjbP	-0.14	[-0.156, -0.123]	< .001

Multinomial logistic regression parameters of species model 5. The description of variables is reported in Table 2 and Supplement 2.

	Intercent									
species group	(mixed	ha alive	n ha	ha dead	ha skow	mono	lead sn10	lead sn11	lead sn12	lead sn13
species group	(mixed	bulanve	11.110	balacaa	00.5KC W	culture	icuu_spio	icuu_spii	icuu_spiz	icuu_spis
Potula con	2 170	1 502	0.429	0 722	0.465	0.040	2 2 2 2 2	7 225	2 000	0 202
Castanea sativa	-0.302	-1.553	0.438	-0.733	-0.403	0.349	2.333	1.233	-12 618	0.392
Eucalyntus snn	-6.823	-0.854	0.130	-0.441	-0.169	-0.020	5 884	9.089	-3 129	4 798
Fagus sylvatica	-2.919	-1.847	0.613	-0.862	-0.363	2.249	5.549	7.037	-2.377	1,136
Larix spp.	-6.813	-1.486	1.156	-0.617	-0.434	1.605	6.812	-0.722	-2.760	-19.821
Other conifers	-3.430	-1.512	0.968	-0.555	-0.377	3.130	0.340	6.354	6.240	-3.481
Other indigenous										
Pinus	-3.764	-0.786	-0.179	-0.563	-0.218	0.110	4.233	7.505	-1.811	1.802
Picea abies	-0.421	-1.241	0.278	-0.509	-0.193	-0.176	5.207	8.063	4.898	0.152
Pinus nigra+mugo	-7.128	0.057	-0.386	-0.184	-0.054	0.712	6.892	14.139	7.629	3.988
Pinus sylvestris	-12.458	-1.587	0.769	0.057	-0.439	1.811	-4.249	10.445	11.843	-12.277
Populus plantations Pseudotsuga	0.191	-0.022	-0.376	-0.186	-0.207	-0.007	2.130	4.222	-3.932	2.936
menziesii	-6.869	-0.616	0.032	-0.168	-0.155	-0.287	6.018	11.161	7.638	3.129
Quercus ilex	-1.527	-0.509	0.081	-0.509	-0.207	0.042	3.903	6.401	-3.026	-0.763
Quercus										
robur&petraea	-5.101	-0.738	0.157	-0.392	-0.203	0.158	7.358	11.220	8.149	4.585
Quercus suber	-4.163	-0.987	-0.008	-0.341	-0.099	0.272	-5.582	7.045	3.298	-1.062
Robinia										
pseudoacacia short-lived	-6.486	-1.134	0.384	-0.153	-0.274	2.188	-2.889	5.937	3.854	-5.392
broadleaves	0.401	-0.355	-0.049	-0.257	-0.162	0.048	3.785	7.499	3.536	1.515
broadleaves	0.716	-0.064	-0.281	-0.217	-0.080	-0.559	3.606	7.355	3.306	0.760
	lead_sp14	lead_sp15	lead_sp16	lead_sp17	lead_sp18	lead_sp19	lead_sp2	lead_sp20	lead_sp3	lead_sp5
Retula snn	-2 045	-3 168	2 700	-2 022	-1 661	0.953	6 777	0 883	2 215	7 768
Castanea sativa	3 927	2 005	2.750	-3 171	-1 199	1 663	3 001	2 344	3 916	5 962
Eucalyptus spp.	0.565	-2.018	5.725	-1.525	-2.699	3.328	7.912	3.332	5.350	13,190
Fagus sylvatica	7.779	4.186	3.939	3.179	-16.004	2.372	5.088	2.011	3.855	8,538
Larix spp.	-0.812	6.005	4.143	7.195	-5.723	5.224	5.534	3.748	2.730	-2.844
Other conifers	7.866	-7.303	1.801	1.970	7.392	-0.625	-3.040	0.016	-1.291	-0.233
Other indigenous										
Pinus	-0.904	-6.110	4.768	5.593	-2.371	2.641	4.633	3.100	2.496	9.593
Picea abies	6.065	3.021	3.501	0.306	-2.744	1.570	3.023	3.191	2.815	6.270
Pinus nigra+mugo	-4.546	5.647	6.151	6.278	9.390	5.571	4.776	4.213	4.340	7.242
Pinus sylvestris	-0.732	-4.145	6.688	3.625	8.974	1.974	-1.981	3.189	-18.357	-2.895
Populus plantations	5.574	1.186	2.104	-1.352	-5.552	1.259	2.448	0.690	1.455	3.789
Pseudotsuga										
menziesii	14.790	5.867	6.228	5.226	-1.440	5.747	5.449	4.672	2.362	-3.152
Quercus ilex	5.634	5.997	1.971	1.174	-3.075	1.326	0.468	2.882	2.083	6.088
Quercus	40.345	7.054	0.000	6.240	0 700	5 220	6 447	5 404	5 260	0.427
robur&petraea	10.345	7.051	8.663	6.340	8.720	5.230	6.41/	5.484	5.260	8.427
Quercus suber	-1.997	2.190	3.602	7.511	8.098	2.493	-2.744	2.328	-3.242	-7.864
RODINIa	0.220	2 776	2 019	2 677	0.700	0.600	0.911	1 446	E 240	1 1 2 5
pseudoacacia	-0.520	-3.770	2.916	2.077	9.790	-0.600	-0.811	1.440	-5.249	-1.125
broadloavor	6 964	2 406	2 749	2 002	C 197	4 510	2 204	2 151	2 205	E 220
long-lived	0.804	3.400	3.740	3.555	0.487	4.515	3.254	3.131	2.303	5.550
broadleaves	7.399	3.241	3.790	4.531	8.454	2.602	2.285	5.305	1.893	5.342
	land and	1	land and	land and	D - dbl	656	CLEDDE			
	lead_sp6	iead_sp7	iead_sp8	iead_sp9	Kean	LEL	SLIPPI	w_INHUI	C_IAREI	w_iviweq1
Betula spp.	3.547	4.523	0.314	6.848	0.448	0.033	-0.189	0.443	-1.086	0.657
Castanea sativa	3.032	1.805	-18.208	4.123	-0.241	0.068	-0.440	1.063	-0.464	1.085
Eucalyptus spp.	5.876	5.839	3.672	-0.642	0.601	0.172	-0.369	0.726	-0.765	0.654
Fagus sylvatica	8.159	6.783	4.542	6.187	0.164	0.151	-0.433	1.040	-0.736	0.605
Larix spp.	7.032	12.520	7.428	10.194	0.265	0.343	-0.526	0.328	-0.983	0.121
Other conifers	2.439	4.091	6.490	4.117	0.030	0.193	-0.307	0.382	-1.461	-0.116
Other indigenous										
Pinus	3.886	6.617	4.257	10.993	0.315	0.449	-0.470	0.650	-1.527	-0.421
Picea abies	3.904	4.223	2.872	4.970	0.361	0.077	-0.345	1.187	-1.119	0.600
Pinus nigra+mugo	5.272	6.224	5.622	-4.037	0.248	-0.018	0.007	0.947	-0.780	0.369
PINUS SYIVESTIS	-2.825	-4./9/	1.333	-2.166	0.260	-0.116	-0.221	1.015	-1.5/0	-0.598
Populus plantations	1.835	0.688	-1.622	1.934	-0.164	0.017	-0.021	0.878	0.204	1.280
rseuuulsuga	6 260	5 5 60	1 955	-0.409	0.250	-0 256	0 222	1 072	-0.755	2 010
Quereus ileu	0.500	3.360	4.655	-0.409	0.250	-0.556	0.355	1.025	-0.755	2.019
Quercus Ouercus	1.927	-7.880	-0.556	5.224	0.200	-0.046	0.307	1.119	-1.333	0.477
robur&petraea	7,105	7,325	6.463	7,970	0.314	-0.069	-0.130	1.245	-0.726	1 035
Quercus suber	3,601	5,855	4,138	7,583	0.312	0.187	-0,278	0.559	-1,102	-0.430
Robinia	5.001	5.655	1.150	7.565	0.012	0.107	0.270	0.000	1.102	0.450
pseudoacacia	-2.230	-4.890	3.593	-1.479	-0.203	-0.185	-0.534	1.200	-0.843	0.841
short-lived										
broadleaves	3.453	4.762	2.358	5.547	0.059	0.040	0.113	0.724	-0.859	0.582
long-lived										
broadleaves	2.626	3.358	2.029	4.225	0.360	0.182	0.045	1.122	-1.156	0.703

	w_MaDR	s_SDmT	c_seaP	c_seaPET	w_SDmR	w_MAXmT	w_MAXmP	w_MINmP
Betula spp.	-0.587	-1.373	-0.689	0.092	-0.525	-0.160	-0.025	-0.235
Castanea sativa	-0.233	-1.061	-0.568	0.237	0.032	-0.962	-0.177	0.186
Eucalyptus spp.	0.173	-2.849	0.037	0.324	-0.279	0.136	-0.679	0.446
Fagus sylvatica	0.145	-1.378	-0.664	0.438	-0.308	0.008	-0.346	-0.442
Larix spp.	0.343	-1.724	-0.222	0.349	-0.321	0.210	-0.543	0.013
Other conifers	0.179	-2.265	-0.453	0.175	-0.291	0.639	0.144	-0.325
Other indigenous								
Pinus	0.225	-1.226	-0.255	0.032	-0.478	0.762	-0.565	0.104
Picea abies	-0.373	-1.551	-0.342	0.475	-0.404	-0.597	-0.374	-0.303
Pinus nigra+mugo	-0.094	-2.489	-1.015	0.582	-0.565	1.100	0.207	-0.465
Pinus sylvestris	0.032	-5.110	-0.428	0.603	-0.385	1.984	-0.204	-0.111
Populus plantations	-0.437	-1.454	-0.754	0.126	0.168	-0.607	-0.399	-0.433
Pseudotsuga								
menziesii	-0.731	-2.120	-0.750	1.107	-0.492	0.928	-0.157	-0.472
Quercus ilex	0.118	-1.401	-0.443	0.712	-0.365	-0.077	-0.473	-0.544
Quercus								
robur&petraea	-0.148	-2.557	-1.042	0.759	-0.141	-0.208	0.034	-0.815
Quercus suber	0.340	-2.615	-0.651	0.351	-0.429	1.232	-0.534	-0.757
Robinia								
pseudoacacia	0.018	-2.216	-0.727	0.411	-0.903	1.843	0.011	-1.164
short-lived								
broadleaves	-0.004	-1.538	-0.413	0.660	-0.167	0.316	-0.360	-0.135
long-lived								
broadleaves	-0.139	-1.501	-0.406	0.410	-0.369	0.008	-0.441	-0.263



Chapter 4

Tree recruitment shifts in European forests

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Abstract

Climate change severely impacts forest ecosystems globally, including European forests, where the effects on tree regeneration, growth, and mortality are increasingly evident. Augmented tree mortality rates raise concerns about the next generation of trees. However, modelling frameworks that investigate future impacts on forest regeneration, particularly at a European scale, are rare and often limited to stand and landscape dynamics. The absence of a standardized and empirically grounded concept for investigating ongoing tree recruitment shifts creates uncertainty regarding the effectiveness of current forest management strategies in promoting resilient and adapted forests. Forest regeneration involves complex processes such as seed production, dispersal, germination, and establishment of seedlings and saplings. This knowledge gap hinders the identification of limitations to the adaptive capacity of European forests under climate change and the development of effective management strategies to ensure their health and sustainable provision of ecosystem services. To address these gaps, this research integrates a dynamic tree recruitment model for European forests into an empirical forest growth model, using a unique dataset of national forest inventories across 17 European countries spanning individual tree data from over 229,000 plots. The study investigates density and compositional changes in tree recruitment and their spatial patterns across Europe under climate change scenario RCP 6.0. To focus solely on examining the effects of climate within the existing forest structure on tree recruitment, the forest dynamic processes of growth and mortality were disabled for the scenario analyses. The findings reveal declining recruitment densities in many parts of Europe, while areas without recruitment are expected to increase under climate change and the current forest structure. The findings revealed a decrease in recruitment densities across Southern, Western, and Central Europe, while areas with limited or no recruitment due to climate change increase. In Northern and Eastern Europe, recruitment densities are expected to increase under climate change. Although the species composition of recruitment aligns with the overstory composition at the European level, significant differences exist at the national and regional levels. At the species level, significant changes are observed. For example, holm oak is expanding into areas where it was previously absent. Conversely, Norway spruce is experiencing considerable losses across nearly all countries, while birch species are gaining. These divergent trends highlight the need for tailored forest management actions to address climate change challenges. By considering both recruitment patterns and existing forest structures, targeted interventions can be implemented to sustain current levels of tree recruitment. These findings have crucial implications for forest management strategies, emphasizing the importance of addressing recruitment dynamics in the context of climate change to ensure the resilience and sustainability of European forests.

1. Introduction

Climate change severely impacts forest ecosystems dynamics around the globe (IPCC, 2022b; McDowell et al., 2020). Changes in temperature, precipitation, and natural disturbances compromise the sustainable supply of ecosystem services such as timber production, carbon storage, clean air and water, and biodiversity (Forzieri et al., 2021; Seidl et al., 2020). European forests are no exception and the impacts of climate change on regeneration, growth and mortality of trees are increasingly evident (Patacca et al., 2023; Vacek et al., 2023). Especially augmented tree mortality rates raises concern about the next generation of trees. Models that investigate impacts on forest regeneration, however, are rare and often constrained to stand and landscape dynamics (e.g. Dobor et al., submitted; Rammer et al., 2021; Reyer et al., 2014). The absence of a standardized and data-based concept to investigate tree recruitment shifts at a European scale creates uncertainty regarding the effectiveness of current forest management strategies in promoting resilient and adapted forests.

Forest regeneration forms the product of complex processes such as seed production and dispersal, germination, and establishment and growth of seedlings and saplings (Price et al., 2001). Due to a lack of empirical data, these processes are poorly understood, even more so in the context of climate change (König et al., 2022). The acquired knowledge has been applied successfully at stand and landscape level projections and shows that tree regeneration plays a crucial role in forest dynamics (Dobor et al., submitted; Thrippleton et al., 2018). Forest dynamic models that operate at larger, continental, or global scales, however, mostly have a strongly simplified representation of forest regeneration that is unlikely to represent realistic climate change impacts (Hanbury-Brown et al., 2022; König et al., 2022). Alternative approaches such as climate envelope and species distribution modelling provide an important basis for the evaluation of potential species distributions (Hanewinkel et al., 2013; Thurm et al., 2018), and recently, valuable efforts have been made at European scale (Mauri et al., 2023; Takolander et al., 2019).

While there is a good understanding of the ecophysiological potential of tree species and how recruitment processes might be affected by climate change at stand and landscape scale, there is a significant lack of knowledge regarding the current state of forest regeneration and actual changes happening at a European scale. This prevents the identification of potential limitations to the adaptive capacity of European forests under climate change and from developing effective management strategies to maintain their health and sustainable provision of ecosystem services. In this study, a recently developed dynamic tree recruitment model for European forests (Chapter 3) is implemented into the empirical forest growth model EFISCEN-SPACE (Nabuurs et al., 2007; Schelhaas et al., 2022; Schelhaas et al., 2018a). The model is applied across 17 European countries using a unique dataset of national forest inventories to realistically represent the current forest state and to investigate the dynamics across the climate change scenarios RCP 6.0.

Here, we examine whether climate change is limiting the adaptive potential of European forests through shifts in tree recruitment. Specifically, we investigate (I) density and (II) compositional changes of tree recruitment and (III) their spatial patterns across Europe until 2100. Tree recruitment densities are expected to decline with increasing temperatures and water limitations from north to south under climate change. Compositional shifts are expected across all forest types through a combination of climate change impacts and changing forest management paradigms. Ultimately, this research applies a uniform concept to investigate shifts in tree recruitment on a pan-European level. This enables the identification of potential limitations of the adaptive capacity of European forests, and contributes to a better understanding of how European forests will change under climate change. Based on this, forest management implications for tree recruitment can be assessed.

2. Methods

2.1 EFISCEN-SPACE

To investigate climate change effects on forest regeneration in Europe the empirical forest growth model EFISCEN-Space was used. The model represents the forest as a collection of 1-hectare model stands, each of which serves as a representative unit for a larger area. The simulated stands are initialized using individual tree observations from stand or plot inventories to realistically represent the current forest state. The distance between the stands is defined by the distance between the inventory plots. Interactions between modelled stands are not considered. One of the key features of EFISCEN-Space is its capability to evaluate the impact of various forest management strategies on forest resources (cf. Schelhaas et al., 2022; Verkerk et al., 2017).

Forest dynamics within each stand are represented as changing numbers of trees per diameter class and tree species. The model distinguishes 40 diameter classes with a width of 2.5 centimetres, starting at diameter class 1 (0-2.5 cm; (Lerink et al., 2023). Corresponding to the most common tree species in Europe, the model considers 20 species or species groups. The transitions to higher diameter classes are determined using species-specific Gompertz growth functions calibrated on an extensive dataset of observed diameter increment data from across Europe. The selection of forest structure, soil, nutrient deposition, and climate variables for the model was performed in two phases for each species. The first phase involved a forward selection procedure using a selection-dataset, where variables were added one at a time and ranked based on the Akaike information criterion (AIC). The best ranking variable was accepted based on an F-test performed on the predicted values from an acceptance-dataset. In the second phase, candidate variables obtained from the first phase were used in a backward selection procedure on the full dataset to finalize the selection of explanatory variables. The selected variables were then used to estimate the coefficients of

the final model using ordinary least squares (OLS) regression (Schelhaas et al., 2018a). Mortality and harvest events are simulated by removing stems from specific diameter classes. These removals are based on fixed, species-specific fractions derived from observations of repeated forest inventories (Schelhaas, et al., 2018a).

The model operates at an annual resolution, producing yearly outputs that capture the forest state, mortality, and harvest. These outputs encompass stem numbers, basal area, and volume, providing information at the stand, species, and diameter class levels. Timber volume is derived from tree diameters using regional allometric volume functions (Schelhaas et al., 2022; Verkerk et al., 2017). These outputs can be combined to provide annual summaries for each individual model stand, as well as for the overall modeled area.

2.2 Implementation of a dynamic tree recruitment model

In EFISCEN-Space, recruitment relied on user-defined estimates of stem numbers per species, which were subsequently incorporated into the smallest simulated diameter class. This simplified approach imposes limitations on the length of model projections, restricting them to a timeframe of 20-40 years and posed a notable constraint for EFISCEN-Space. To overcome this limitation, a dynamic tree recruitment approach has been introduced, as developed in Chapter 3. This approach simulates tree recruitment while considering forest structure, soil conditions, nutrient deposition, and climate, thus allowing for a more comprehensive representation.

The model predicts tree recruitment for 19 out of the 20 simulated species groups in EFISCEN-Space. Due to the lack of observations for Sitka spruce, a species introduced in reforestation programs in the mid-20th century, prevented its parameterization and inclusion in the recruitment model. As a result, the recruitment of Sitka spruce still depends on user-defined parameters. The dynamic tree recruitment model consists of two distinct models that simulate the number and species of recruitment trees from both planting and natural regeneration. First, the number of tree recruits is derived from the mean of a negative binomial distribution. Second, the probability of 19 simulated species groups is calculated using a multinomial logistic regression model (see equations in Chapter 3). The sum of probabilities across the species adds up to 1. Both models were parameterised using recruitment data from forest inventories of 8 European countries and a set of 9 site variables describing the forest structure and soil, and 11 climatic explanatory variables. Climate variables included in the model that affect tree recruitment are Thornthwaite humidity index, total annual actual evapotranspiration, mean temperature of the wettest quarter, mean annual diurnal temperature range, standard deviation of monthly temperature, precipitation seasonality, potential evapotranspiration seasonality, standard deviation of monthly radiation, maximum monthly temperature, maximum monthly precipitation and minimum monthly precipitation. A detailed description of the parameterisation of both models is provided in Chapter 3. Species-specific plot recruitment is then derived through the multiplication of the count predictions from the first model with the species probabilities

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of the second model. Because the predicted probability of a species group being present is never exactly 0, all species would regenerate in every model stand, albeit often with low numbers. We therefore imposed a minimum threshold of 4 recruitment trees per hectare and year, which ensures a match between the average predicted number of species groups per plot with the average observed number of species groups per plot in the parameterisation dataset. In theory, the simulation of plot recruitment can be applied to any desired area and time interval. However, for the purpose of aligning with the simulation of adult trees, a standard configuration of one hectare and an annual time step was chosen. This ensures consistency within the model and facilitates a comprehensive understanding of the overall dynamics of tree growth and development.

2.3 Model setup

2.3.1 Initialization data

Forest inventory data was used to initialise the stands in EFISCEN-Space. The dataset includes data of 17 European countries from over 229,000 plots (Table 1) and covers a large share of European forests (Figure 1). Except for Finland, the data are derived from national forest inventories (NFIs). The Finnish dataset (1985-86 and 1995) comes from the forest health monitoring network, see (Mäkipää & Heikkinen, 2003) for details. Differences in sampling strategies exist in terms of sample grid, sampling strategy, sampled area and size threshold of measured trees. The challenge of combining and using such data in model simulations arises primarily from variations in sampling densities and size thresholds used. Sampling densities may cause variation in the level of uncertainty in the results. Additionally, without harmonization, variations in size thresholds may impact simulation outcomes. However, in this study size thresholds were kept uniform and potential biases arising from spatial variations are investigated and reported.

Country	NFI Census	N Plots
Croatia	2005 - 2009	5,698
Czech Republic	2011 - 2015	13,811
Denmark	2017 - 2021	6,183
Finland	1990 - 1995	315
Flanders	2009 - 2016	2,128
France	2008 - 2012	28,283
Germany	2011 - 2013	50,272
Ireland	2015 - 2017	1,681
Italy	2005 - 2005	6,182
Luxembourg	2008 - 2012	1,642
Netherlands	2017 - 2021	2,826
Norway	2017 - 2021	11,643
Poland	2015 - 2019	28,110
Slovakia	2015 - 2017	1,388
Spain	1997 - 2007	46,686
Sweden	2017 - 2021	11,642
Switzerland	2009 - 2013	2,516
Wallonia	2008 - 2011	1,220
Total		222,226

Table 1 Overview of National Forest Inventory datasets used to initialise EFISCEN-Space. The table shows the census period and the corresponding number of plots for each country.

Figure 1 Map providing a visual representation of the plot locations across Europe.

2.3.2 Climate data

In order to simulate the effect of changing climate on tree recruitment, the static climate and weather variables used in EFISCEN-Space (Schelhaas et al., 2022), variables described in (Schelhaas et al., 2018a) and for estimating the recruitment model parameters (Chapter 3) are replaced by timeseries. The provided timeseries were derived from the Inter-Sectoral Impact Model Intercomparison Project (ISIMIP, Warszawski et al., 2014), using daily data from the earth system model GFDL-ESM2M (Dunne et al., 2012) under the representative concentration pathway 6.0 (Moss et al., 2010). The data can be downloaded from the following link: https://www.isimip.org/gettingstarted/details/51/. The climate and weather variables were calculated following the methodology described in Schelhaas et al. (2018a).

Climate scenarios from different models can deviate in both the absolute value and the time trend. Furthermore, the calculated scenario values at a given location are not exactly the same as the values used in the estimation of the recruitment models. Therefore calculated climate and weather variables were re-calibrated on the values from the original datasets.

$$v_{(t,adj)} = v_{ref} + (v_t - v_{2018})$$

Where $v_{t,adj}$ is the re-calibrated value of variable v in year t. v_{ref} is the reference value of variable v used for model estimation, v_t is the value of variable v in the specific climate scenario for year t and v_{2018} is the value of variable v in 2018 – the year used as reference. As a consequence, only the calculated changes in the climate and weather variables are taken into account.

2.4 Simulations and scenarios analyses

In a normal setup of the model, recruitment would change over time not only due to changes in climate, but also due to changes in forest structure as influenced by growth, mortality, management and recruitment, which in itself are also influenced by climate change. Since we are only interested in the direct effect of climate change on recruitment patterns, we eliminate the other factors by running the simulations only for one year and switching off the growth, mortality and harvest modules. The model was configured to simulate each year from 1990 to 2100 in a separate simulation, using the climate data for the corresponding year from the climate change scenario and initialising the model each simulation again with the plot-level NFI observations.

In the simulations, a common recruitment diameter threshold of 7 cm was applied to all countries to eliminate design-based differences between countries. Simulation results were stored as average density (N ha⁻¹) and composition of recruitment per simulation year, averaged per country but also over a 25 km grid for inspection of further spatial patterns. The average simulation results of the period 1991-2020 were set as a reference level against which changes in tree recruitment densities and compositional shifts were assessed. Compositional shifts of tree recruitment were summarised at the country level. The Bray-Curtis dissimilarity index was used to quantify compositional shifts between the observed overstory tree species composition and predicted recruitment compositions (Legendre & Legendre, 1998). Because the numbers of the overstory and recruitment trees are fundamentally different, species abundances were expressed as proportions. The Bray-Curtis index was calculated as

$$BC_{ij} = \frac{2C_{ij}}{S_i + S_j}$$

where C_{ij} is the sum of the smaller species proportion for species present in the overstory and the recruitment. S_i and S_j are the total sum of the species fractions. The formula can therefore be simplified to $BC_{ij} = 1-2C_{ij}/2$ which equals $1-C_{ij}$.

3. Results

3.1 Recruitment density

In the simulated period, a gradual and consistent decrease in the mean predicted tree recruitment densities was observed (Figure 2A). During the timeframe of 1991-2020, an average of 18.5 trees were recruited per hectare and year across all countries. In the period of 2071-2100, this number declined to 17.2 trees per hectare and year. Simultaneously, the predicted number of plots without tree recruitment increased from 24.5 percent to 27 percent in the same period (cf. Figure 2B). Strong variations can be observed among individual countries concerning the predicted amount of tree recruitment but also the changes over time. The Netherlands, for example, has an average plot recruitment of 23.2 in the period 1991-2020 which declines by 35 percent in the period 2071-2100. Sweden, however, shows an increase of 1 percent in the same period with a high initial average plot recruitment of 22.9 tree per hectare and year. Generally, countries with a high average recruitment density showed lower percentages of plots without tree recruitment.

Investigating the spatial patterns of tree recruitment shifts at sub-country level reveals notable variations even within a single country (Figure 1C and D). Generally, Southern, Western, and Central Europe experience a consistent decline in recruitment densities, accompanied by an increase in plots without tree recruitment. In contrast, Northern and Eastern Europe exhibit contrasting trends, with recruitment densities on the rise. Notably, the south-eastern parts of Germany and Poland stand out by showing a positive trend in recruitment, while the remaining regions within those two countries experience a decline. The findings indicate that forest regeneration across wide areas in Europe is projected to significantly decline under climate change compared to current levels. Additionally, areas where tree recruitment fails to occur at all are expected to increase. These trends suggest that forest regeneration could emerge as a limiting factor for the overall functioning of European forests.



Figure 2 Recruitment density changes across simulated countries. A) Country-wise averages of simulated stand recruitment densities over time. Black line shows the average across countries. B) Country-wise average percentage of plots without tree recruitment. Black line shows the average across countries. C) Proportional change of recruitment densities between the averages of period 1991-2020 and 2071-2100. Recruitment densities were summarised in 25km grid cells. D) Proportional change of number of plots without recruitment between the averages of period 1991-2020 and 2071-2100. Annual, country-wise predictions of tree recruitment and the number of plots without recruitment are recorded in Supplement 1. The number of plots per grid cell are recorded in Supplement 2.

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3.2 Recruitment composition

Across all simulated countries, the species composition of the recruited trees shows minimal deviation from the observed composition of overstory trees (cf. Figure 3). The largest difference arises within the Betula spp. species group. On average, Betula accounts for 18.8 percent of the recruited trees during the period 1991-2020, but in the overstory, its presence is relatively low at 5.7 percent. This is also the main cause for the ratio shift between broadleaved and coniferous species. While the overstory comprises 44 percent of broadleaved trees, the recruitment percentage remains constant at 47 percent during the periods 1991-2020 and 2071-2100. Compositional shifts in the predicted recruitment compositions remain minimal across time and countries. However, within individual countries, these shifts become more pronounced (Table 2).



Figure 3 The outer circle shows the species composition of observed overstory and simulated tree recruitment averaged over the periods 1991-2020 and 2071-2100 across all countries, plot representative areas are not taken into account. The inner circle shows the composition of broadleaved (green) and coniferous (brown) species.

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Abies spp.	3.0	3.7	2.4	0.9	0.8	1.0	10.8	0.0	0.0	0.0	0.0	0.0	2 0.	0.0 0.0	4.	2 1.0	0.7	2.1	0.9	1.1	0.2	0.0	0.0	1.8	2.3	1.7
Betula spp.	0.7	0.4	0.1	3.6	21.2	12.4	6.8	48.8	44.4	12.3	25.9 2	5.9 0.	0 17	.3 11.8	3.5	2.7.6	2.9	4.7	17.6	11.6	5.0	45.7	48.5	0.8	3.7	1.8
Castanea sativa	1.5	0.4	0.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0 1.	4 0.	1 0.2	7.1	5 2.2	2.8	0.2	0.0	0.0	0.0	0.0	0.0	8.7	2.9	3.3
Fagus sylvatica	25.8	7.4	8.0	5.9	2.5	3.4	10.4	2.2	2.5	0.0	0.0	0.0 2.	9.0	2 0.1	- 80	1 2.0	1.7	15.0	5.2	4.8	0.7	0.1	0.0	14.9	2.0	2.2
Larix spp.	0.2	0.0	0.0	3.7	4.4	4.5	3.9	6.4	6.6	0.0	0.0	0.0 1.	7 1.	6 1.4	0.0	7 0.7	0.5	2.0	2.6	2.3	4.7	11.7	10.2	2.2	3.7	3.6
Other conifers	0.6	0.8	0.6	0.4	0.6	0.6	12.9	1.9	1.9	0.2	0.2 (0.2 0.	2 0.	0.0 0.0	0.(5 0.4	0.3	0.5	0.2	0.4	0.69	4.6	4.1	1.0	0.7	0.6
Other indigenous Pinus	1.9	2.1	2.0	0.1	0.1	0.1	0.8	2.2	2.8	0.0	0.0	0.0	5	6 1.2	4.	3 7.5	7.9	0.1	0.2	0.3	0.0	13.1	14.6	3.1	3.5	2.6
Picea abies	1.7	3.0	0.8	49.4	10.0	8.6	17.7	6.2	5.2	13.3	7.8 1	2.9 4.	3	0.0 0.0	4.5	3 1.5	0.2	29.6	5.1	3.3	4.8	3.8	0.5	6.5	1.5	1.0
Pinus nigra+mugo	1.9	1.0	0.9	0.1	0.1	0.2	1.9	2.1	1.8	0.0	0.0	.0 9.	6 4.	5 4.3	2	1 2.0	1.8	0.3	0.4	0.4	0.0	0.3	0.1	3.2	2.6	2.4
Pinus sylvestris	0.6	14.9	11.9	15.4	39.8	42.9	5.7	14.1	15.2	6.69	55.2 5	9.9 21	.0 39	.3 39.6	5.1	5 23.5	22.1	20.8	40.2	44.3	0.8	2.7	2.8	2.2	10.2	9.6
Populus plantations	0.8	0.5	0.4	0.9	0.6	0.5	2.1	0.2	0.2	0.0	0.0	1.0 17	.4 3.	7 4.0	0.0	2 0.1	0.1	0.2	0.1	0.1	0.0	0.0	0.0	1.2	0.3	0.2
Pseudotsuga menziesii	0.1	0.0	0.0	0.0	0.0	0.0	0.8	0.1	0.1	0.0	0.0	0.0	5	0.0 0.0	2.:	3 0.5	0.4	2.2	0.2	0.2	1.9	1.3	0.8	0.3	0.0	0.0
Quercus ilex	1.8	3.4	4.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	5 5.5	ŝ	5 4.3	10.6	0.0	0.0	0.1	0.0	0.0	0.0	5.9	6.7	9.0
Quercus robur&petraea	8.8	3.6	3.4	5.9	0.2	0.3	7.4	1.5	2.5	0.0	0.0	0.0 12	.3 18	.1 17.(14.	7 11.3	10.0	7.6	3.7	4.0	1.0	0.5	0.7	1.2	2.0	1.8
Quercus suber	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0 0.0	0.	2 0.1	0.4	0.0	0.0	0.0	0.0	0.0	0.0	0.9	0.1	0.2
Robinia pseudoacacia	3.9	2.9	5.4	0.7	0.7	1.2	0.0	0.0	0.0	0.0	0.0	0.0	6 0.	2 0.1	1.5	3 0.5	0.9	0.3	0.2	0.2	0.0	0.0	0.0	2.1	2.9	6.1
long-lived broadleaves	40.9	51.4	55.0	8.5	13.2	18.6	12.2	3.1	4.2	0.1	0.0	11 0.0	.2 4.	5 4.9	26.	1 27.1	27.8	10.1	8.9	11.5	4.7	0.8	0.7	35.1	50.5	50.2
short-lived broadleaves	5.7	4.7	4.0	4.5	5.9	5.8	6.7	11.2	12.5	4.2		1.0 16	.3 9.	5 9.8	9.6	3 6.6	5.7	4.1	14.7	15.5	7.1	15.1	16.5	8.4	4.2	3.4
Eucalyptus spp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0 0	0 0.1	0.(0.6	3.2	0.0	0.0	0.0	0.0	0.2	0.5	0.4	0.3	0.3
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Abies spp.	0.4	9.0	0.9	0.2	0.0	0.0	0.0	0.0	0.0	2.7	2.1	2.6 2.	5 10	.0 11.4	1.0.1	1 0.1	0.1	0.1	0.0	0.0	12.3	11.9	10.4	0.2	0.0	0.0
Betula spp.	2.5	23.5	13.2	13.5	25.0	19.4	26.8	42.1	41.1	8.0	16.1 1	3.5 2.	7 7.	5 4.3	0.0	7 0.9	0.3	16.2	32.6	30.5	1.9	12.9	8.8	3.0	13.3	8.1
Castanea sativa	0.0	0.0	0.0	0.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0 0.0	1.	1 0.3	0.4	0.0	0.0	0.0	3.0	2.6	3.4	0.4	0.0	0.1
Fagus sylvatica	19.3	3.7	2.5	4.1	0.5	0.3	0.1	0.0	0.0	4.3	1.1	12 28	.0	8 10.(3.5	2 0.3	0.3	0.4	0.0	0.1	19.3	9.7	11.8	15.0	5.5	4.2
Larix spp.	1.1	0.9	0.5	3.4	5.1	4.6	0.1	0.2	0.4	1.4	1.2	1.4 1.	3 1.	3 1.5	0	1 0.1	0.1	0.2	0.2	0.2	0.0	6.8	7.1	2.4	2.9	2.0
Other conifers	0.1	0.0	0.1	0.8	0.1	0.3	1.3	0.5	0.5	0.0	0.0	0.0	1.0	6 0.6	11	9 2.5	2.1	1.9	0.8	0.9	1.1	0.6	0.6	0.3	0.4	0.5
Other indigenous Pinus	0.0	0.1	0.3	0.2	0.3	0.5	0.0	0.2	0.4	0.0	0.0	0.0	0.	3 0.2	30.	9 29.6	27.3	0.0	0.0	0.0	0.0	0.4	0.8	0.0	0.5	1.0
Picea abies	39.2	1.8	0.4	3.7	0.1	0.0	38.2	35.2	38.1	7.3	2.6	2.6 20	.2	8 8.4	0.0	0.0	0.0	41.0	17.8	19.7	40.7	19.8	10.2	35.7	3.3	0.9
Pinus nigra+mugo	0.2	0.0	0.0	3.5	2.2	2.3	0.0	0.0	0.0	0.0	0.1 (0.1 0.	3 0.	4 0.3	10.	6 9.6	9.3	0.0	0.0	0.0	1.2	1.1	1.2	0.9	0.4	0.2
Pinus sylvestris	1.9	37.0	41.6	22.1	42.0	45.1	21.4	19.4	16.9	57.5	64.9 6	4.0 6.	6 20	.5 19.3	3 16.	9 16.5	15.9	34.1	41.0	40.4	2.5	14.9	21.3	3.0	41.7	49.7
Populus plantations	0.7	0.8	0.9	1.1	0.3	0.3	1.6	0.1	0.1	0.9	0.4 (0.4 1.	0	0 0.8	0.0	0.0	0.0	1.3	0.3	0.3	0.2	0.0	0.0	0.1	0.0	0.0
Pseudotsuga menziesii	4.7	0.1	0.0	4.6	1.1	0.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0	2 0.1	0.1	0.0	0.0	0.0	0.2	0.0	0.0	3.9	0.1	0.0
Quercus ilex	0.0	0.0	0.0	0.0	0.1	1.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	13.	4 22.7	26.4	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.1	1.7
Quercus robur&petraea	15.3	12.2	17.1	18.6	13.3	14.1	1.0	0.0	0.0	0.9	0.2 (7. 7.	0.0	0 0.1	2.5	2 1.5	0.9	0.9	0.1	0.1	1.5	3.3	4.9	0.0	1.4	3.1
Quercus suber	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.4	1 2.6	3.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Robinia pseudoacacia	0.3	0.2	0.3	0.6	0.1	0.1	0.0	0.0	0.0	0.4	0.2 (0.4 2.	3 1.	9 2.8	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.5	1.0	0.2	0.2	0.0
long-lived broadleaves	12.2	11.1	14.7	10.9	2.9	3.5	0.7	0.1	0.1	10.0	6.6 8	3.7 22	.1 29	.5 33.4	1 7.5	3 6.1	5.8	0.5	0.2	0.3	11.9	11.0	13.5	32.0	26.6	25.4
short-lived broadleaves	2.0	7.8	7.5	12.2	6.9	7.3	8.8	2.1	2.5	6.5	4.4 4	1.9 5.	8 7.	5 7.1	5.5	9 2.5	1.8	3.6	6.9	7.5	4.0	4.3	4.8	2.8	3.6	3.2
Eucalyptus spp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.1	5 4.7	5.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0

Chapter 4

For instance, the predicted recruitment of *Picea abies* during the period 2071-2100 in the Czech Republic is, with 8.6 percent, significantly lower compared to the current observed overstory percentage of 49.8 percent. However, in Scandinavian countries, the predicted recruitment share of Norway spruce remains relatively consistent with the overstory (Norway) or exhibits an increase (Finland). Furthermore, several other species display a notable increase in recruitment across various countries. *Pinus sylvestris*, for example, experiences an upward trend in recruitment across almost all countries. Additionally, species such as *Quercus Ilex*, expand into countries where they have not been present yet. *Quercus Ilex*, which is currently present in the overstory of Spain, Croatia, and Italy, emerges as new additions to the recruitment composition during the period 2071-2100 in the Netherlands, Switzerland, Belgium, France, and Germany.

The analysis of compositional differences reveals a slight increase in dissimilarity between the observed overstory composition and the simulated tree recruitment composition over time and across countries (Figure 4 A). Different countries exhibit varying levels of dissimilarity, with the less species-rich Scandinavian forests showing lower dissimilarities. However, dissimilarity trends differ among countries. For example, Switzerland, Slovakia, and Wallonia are expected to undergo stronger species shifts in the future, while levels remain stable in Denmark, Poland, and Italy.

Looking beyond the country level, a closer examination at finer spatial scales provides additional insights (Figure 4 B and C). It becomes evident that not only do absolute dissimilarities vary within countries (Figure 4 B), but dissimilarity also changes across the simulation period (Figure 4 D). For instance, in Norway the dissimilarity levels at the country scale are relatively low. However, there is a notable contrast between the southern and northern regions, with higher dissimilarity observed in the southern areas, which may be attributed to the higher number of species capable of growing in the south compared to the northern regions. Additionally, dissimilarity changes throughout the simulated period occur in the opposite direction. In contrast, Poland maintains consistently low dissimilarity throughout the simulation. In Spain, dissimilarity starts low but increases significantly towards the end of the simulation period caused by abundance shifts of several species (cf. Table 2). Denmark exhibits high dissimilarity, which remains relatively stable throughout the simulation.



Figure 4 Bray-Curtis Dissimilarities between the observed overstory species group composition and the simulated tree recruitment species group composition. A) Country-wise averages of Bray-Curtis Dissimilarities over time. Black line shows the average across countries. B) Bray-Curtis dissimilarity of period 1991-2020. Values were summarised in 25km grid cells. C) Proportional change of Bray-Curtis dissimilarity between the averages of period 1991-2020 and 2071-2100. The number of plots per grid cell are recorded in Supplement 2.
4. Discussion

Evaluation of the simulation results provides valuable insights into the recruitment development across Europe and considerations for forest management. It is crucial to recall the study design, which predefines that absolute recruitment densities and species compositions are influenced by both the existing forest structure and climatic conditions. In these simulations, changes over time, however, are solely driven by subsequent variations in climatic variables, as the simulation assumes a constant forest structure throughout the simulation period, excluding any natural or management-induced alterations. Also, the results are bound to the climate change scenario RCP 6.0.

4.1 Unraveling patterns and shifts of tree recruitment across Europe

The results reveal diverging trends across European regions. Scandinavia and Eastern Europe are experiencing higher recruitment rates under the simulated climate change scenario. Conversely, recruitment densities in large parts of Central, Western and Southern Europe are expected to decline by 20 - 40% or more towards the end of the century (cf. Figure 2). Suchlike shifts in recruitment densities and compositions are already recognized for individual species and regions and have been attributed to climate change (Reich et al., 2022; Richter et al., 2022; Unkule et al., 2022). In North America, for example, the expansion of forests on the northern boundary is not compensating for the declines observed on the southern boundary (Rotbarth et al., 2023). In the context of increasing tree mortality rates in Europe (Neumann et al., 2017) only a viable population of recruiting trees bears the potential to mitigate negative effects on forest functioning by closing gaps and replacing less adapted forest stands. However, the overall decline in recruitment densities, together with the projected increase in forest stands where tree recruitment is unsuccessful, poses a serious threat to the sustainable provision of ecosystem services and goods in large areas of European forests.

The central question is whether the recruited trees come in sufficient quantities and if the species communities are suitable considering the future climatic conditions. The findings of this study highlight the importance of considering both country-level and spatially explicit analyses to gain a comprehensive understanding of the compositional dynamics of tree recruitment (cf. Figure 4). By examining dissimilarity patterns and their temporal variations, we can gain insights into how species compositions evolve and shift across regions. This knowledge contributes to our understanding of the complex interplay between environmental factors and tree recruitment dynamics. Compositional shifts are predicted to be larger in Central and Western Europe compared to the rest of Europe. This phenomenon could be attributed to two factors. Firstly, it is possible that forest management practices in Central and Western Europe have led to overstory species compositions that can only be achieved through intensive regulation, involving initial planting and subsequent species adjustments through thinning. Secondly, in Northern and Eastern Europe, the species pool

capable of thriving is naturally limited by site conditions, making significant compositional shifts in recruitment less likely to occur.

Regionally, there is a notable contrast between the abundance of light-demanding species in the overstory and the recruitment, such as birch and pine species, which may raise suspicions and demands closer examination. The higher abundance of light-demanding species in the recruitment process finds several potential and eventually combined explanations. Ecologically, pioneer species have the tendency to regenerate in large quantities once favorable conditions are present, whereas species that regenerate under the canopy exhibit much lower recruitment rates (Price et al., 2001). Consequently, pioneer species dominate among the recruiting trees, which may explain their high abundance. In summary, more than 80 percent of European forests are actively managed and maintained in a relatively young state. This means that old growth climax forests, which tend to have higher numbers of shade-tolerant species, are rare in Europe. (FOREST EUROPE, 2020). Further, the discrepancy between their abundances in the overstory and recruitment may further be amplified by past management practices that favored species with high expected timber values (Bolte et al., 2009) that encounter limiting factors when recruiting under less intensively managed circumstances. Therefore, it is crucial to evaluate the credibility of the results at the species level. It is not surprising to observe substantial disparities between the overstory and recruitment of Quercus robur, Quercus petraea, and Picea abies as these species have been extensively planted in the past. The low abundance of these species in the recruitment composition can be attributed to changing forest management approaches like shifts towards the use of natural regeneration (FOREST EUROPE, 2020) and in the case of declining oak recruitment, additionally to constraints through browsing (Ramirez et al., 2019). The increasing presence of Pinus sylvestris in countries like Luxembourg and Switzerland, is surprising as current observation are suggesting a decline of the species. In Switzerland, for instance, increased mortality of Pinus sylvestris has been attributed to a combination increasing stand density (due to management changes) and severe drought events (Rigling et al., 2013). Our model, however, indicates higher proportions of Pine trees as the maximum monthly temperature increases. This implies, that the dataset used for the parameterization of the species model either lacks the presence of drought effects on pine recruitment, or that the climatic data did not adequately capture the extremes of drought to detect a constraining impact.

An alternative explanation may be linked to limitations linked to the statistical model used to predict the probability of observing a certain species group among the recruits. Multinomial regression models are not able to account for random effects, such as country-specific forest management effects which are not quantifiable from the NFI data. Further, the parameterization of the regression parameters involves the use of a neural network which may be sensitive to imbalanced categories in the training data and therefore introduce positive biases for individual species and regions (Huang et al., 2022). Also, the resolution of climate variables used in the parameterization may have been too coarse. Particularly in

mountainous areas, significant variations in elevation can lead to distinct climatic conditions on small spatial scales. These differences may not be adequately captured in the climate data utilized in this study, resulting in averaged climatic conditions favoring the recruitment of *Pinus sylvestris* over species like *Picea abies* which requires lower average temperatures and higher precipitation sums to perform well (Bradshaw et al., 2000; Rehfeldt et al., 2002). To clarify these uncertainties, further investigation are required.

The compositional changes across a large part of Europe, however, are relatively modest, suggesting gradual shifts in tree species compositions. The most significant predicted changes are concentrated in regions where extensive forest plantations have been established, such as Sitka spruce in Ireland or exotic conifer species in Denmark (cf. Table 2; Joyce & O'Carroll, 2002; Kjær et al., 2014). Given that approximately two third of the observations used for the parameterization of the species model originated from natural regeneration and lacks observations from such extensively managed plantations (cf. Chapter 3; FOREST EUROPE, 2015), the model lacks the ability to accurately predict tree recruitment. However, the results are generally in agreement with the predictions of climate envelope and species distribution modelling (Brus et al., 2012; Dyderski et al., 2018). For example, silver fir, despite having a broad potential distribution, is predominantly found in central Europe, as indicated in Table 2. Likewise, oak has the potential to occur in Scandinavia but is absent. The limited realization of their potential niche may be strongly influenced by factors such as the availability of seed sources and dispersal distances. (cf. Chapter 3 Supplement 6; Axer et al., 2021).

The range shifts, however, are predicted to occur much slower compared to other approaches (cf. Hanewinkel et al., 2013; Takolander et al., 2019; Thurm et al., 2018). This is likely caused by the incorporation of the current forest structure from the NFIs and may result in more realistic representations of limiting effects on tree regeneration processes such as seed limitations. An empirical recruitment approach may therefore better capture the effects of current forest structure compared to conventional climate envelope and species distribution models. However, a notable exception is the study conducted by Mauri et al. (2023). Here, seed dispersal limitations were taken into account in the used climate envelope model. Their findings reveal a decline in species richness under climate change when recruitment relies solely on natural dispersal. This finding opens the discussion about assisted migration and hence, adaptations of current forest management strategies.

4.2 Implications for forest management and policy

Gaining a comprehensive understanding of recruitment dynamics is crucial for developing tailored forest management strategies that consider the unique characteristics of specific geographic regions. The results presented here emphasize the significance of the geographical context to identify regions where tree recruitment may become a limiting factor in forest ecosystem dynamics under climate change and under the current forest management strategies. In such regions, management interventions need to be adapted and

customized to mitigate the effects of climate change on tree recruitment and sustain viable recruitment levels.

Implementing silvicultural practices that promote diverse natural regeneration, facilitating the establishment of climate-resilient species, and considering assisted migration strategies where necessary and appropriate, are potential approaches to address these challenges (Bolte et al., 2009; Sousa-Silva et al., 2018). Tree species exhibit significant adaptation potential at the species level (Müller-Starck, 1989; Peña et al., 2022). A collapsing old-growth forest does not necessarily indicate that the recruiting population is non-viable. Natural selection allows better-adapted individuals to prevail, potentially forming adapted populations in the next generation (Lindner et al., 2010). Therefore, planting better-adapted provenances or species (assisted migration) may be necessary, unless a viable young recruitment population is expected and in line with forest management goals. Ultimately, the specific strategies should always be conducted at and adjusted to the stand level, taking into account local conditions and developments. For instance, spruce monocultures planted far outside their natural distribution range, may require assisted migration of the new desired species because the stand lacks the desired species in the seed bank.

Identifying suitable management strategies is essential to counteract the negative effects of climate change and achieve desired recruitment outcomes. Thorough scenario analyses may serve this purpose. It is important to recognize that recruitment is just one aspect of vegetation dynamics. A comprehensive understanding requires considering natural tree mortality, forest management practices, and natural disturbances (cf. Schelhaas et al., 2015). By examining the combined influence of these factors, a more complete picture of the forest's adaptive potential emerges, allowing to recognize the need for intervention.

Lastly, this study demonstrates that issues related to forest recruitment extend beyond regional or national boundaries and affect large areas in Europe. As a result, European efforts are necessary to mitigate the negative impacts of climate change on forest functioning. Collaborative initiatives among stakeholders, including forest managers, hunters, researchers, and policymakers, are vital for sharing knowledge and best practices, identifying suitable management actions, and monitoring the effectiveness of interventions.

5. Conclusions

In conclusion, the evaluation of simulation results provides valuable insights into recruitment development across Europe and its implications for forest management. The findings indicate that recruitment densities will decline in large parts of Europe under the studied climate change scenario, while areas without recruitment are expected to increase under climate change and the current forest structure. Although the species composition of recruitment aligns with the overstory composition at the European level, there are notable differences at the national and regional levels. These divergent trends emphasize the need for tailored forest management actions to address climate change challenges. By considering

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both recruitment patterns and existing forest structures, targeted interventions can be implemented to sustain current levels of tree recruitment. The results presented in this study, based on inventory data and scenario analysis, clearly show the limitations and potential of forest recruitment in supporting the required adaptations of forests to climate change. The findings emphasize the need for forest management interventions across large areas in Europe that are tailored to regional and local conditions. Specific measures such as assisted migration or the assessment of new species should be considered as part of these interventions.

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Supplement 1

Country-wise average predicted tree recruitment per hectare and year

	HR	CZ	DK	FI	BE	FR	DE	IE	IT	LU	NL	NO	PL	SK	ES	SE	SW	BE
1001	17.9	11.2	20.8	20.0	(FL)	18.0	11.6	22.0	18.6	11.2	19.9	20.7	10.6	10.0	12/	21.0	15.2	(WA)
1992	17.3	10.4	19.3	35.3	16.0	16.7	10.6	32.7	17.5	10.8	17.4	31.9	9.8	9.0	12.2	22.7	13.4	4.2
1993	20.0	13.7	17.6	29.9	16.3	17.3	12.1	33.0	19.2	11.8	18.1	30.8	11.3	11.7	13.9	21.4	15.6	4.4
1994	20.8	12.7	16.4	30.8	14.4	16.3	10.8	32.9	18.8	11.3	16.2	31.5	10.6	11.8	12.7	21.8	14.5	4.2
1995	21.6	14.4	17.6	33.4	16.4	15.2	11.4	34.6	18.9	11.5	17.2	32.1	11.5	12.6	12.1	23.1	14.6	4.3
1990	18.5	14.7	15.3	30.6	16.2	13.9	10.9	34.9	16.7	11.8	17.7	32.1	12.1	12.6	10.8	20.3	12.5	3.9
1998	17.1	14.8	15.4	30.5	16.5	13.4	11.0	34.7	15.7	10.2	18.6	33.9	11.7	11.7	10.6	21.9	12.2	3.6
1999	18.2	15.0	16.6	29.7	16.0	12.6	11.2	34.5	14.9	9.2	17.9	33.5	12.6	11.3	10.1	22.7	12.6	3.3
2000	19.6	16.4	19.0	29.4	16.2	14.2	11.5	36.0	15.8	9.5	17.9	34.5	13.7	13.6	10.3	21.0	14.9	3.4
2001	10.4	13.0	21.5	35.7	21.5	14.4	10.6	35.8	13.9	9.9	18.7	38.0	11.5	9.9	9.5	22.8	13.2	3.0
2002	14.7	12.7	18.9	31.8	22.0	14.0	11.1	35.4	13.7	8.9	25.2	37.9	11.2	9.1	10.0	20.4	13.3	3.8
2004	16.1	14.0	20.7	32.7	23.3	17.3	12.7	37.4	15.6	9.8	26.8	36.0	12.0	11.5	10.9	20.9	15.1	4.4
2005	17.1	14.4	23.1	31.7	24.9	18.2	13.9	39.2	15.6	10.9	28.0	35.7	11.6	11.5	10.4	22.0	16.8	5.1
2006	18.6	14.4	21.0	32.1	23.8	18.1	12.4	40.3	16.0	10.6	25.1	33.0	11.0	12.0	10.8	19.7	16.9	4.7
2007	17.9	14.5	23.7	34.4	26.1	18.4	12.8	39.5	15.5	11.4	27.1	34.5	10.9	10.9	11.4	21.4	13.5	5.2
2009	19.3	14.6	23.1	31.9	30.0	17.4	14.0	37.3	17.0	12.1	31.2	31.3	12.5	12.8	10.6	21.5	14.4	5.5
2010	20.1	14.9	25.3	27.8	24.3	17.6	13.8	37.8	17.0	12.8	25.6	32.0	13.1	13.5	10.6	21.6	14.9	5.3
2011	20.8	13.5	24.0	30.7	23.4	17.6	13.2	38.3	17.6	14.4	24.3	32.1	12.9	12.0	10.3	21.8	14.1	5.5
2012	19.1	11.8	23.2	27.5	20.2	16.4	12.4	36.2	17.1	12.7	22.0	32.5	11.4	10.8	10.3	21.8	13.3	4.6
2013	17.6	11.9	26.9	32.6	22.2	16.8	13.9	36.3	16.9	14.0	25.4	37.8	13.0	11.3	10.4	26.5	13.6	5.2
2015	17.0	11.8	23.3	33.1	19.8	16.7	13.4	36.3	16.3	15.1	24.0	36.6	13.1	12.0	9.5	25.4	13.8	5.3
2016	15.2	13.0	25.0	36.7	22.5	17.1	15.0	37.7	15.6	16.2	26.5	38.6	13.2	11.9	9.8	26.9	14.4	5.8
2017	16.6	13.9	24.6	34.9	20.6	17.0	14.5	40.4	16.9	14.4	24.7	37.7	13.8	13.3	10.3	25.5	14.8	5.1
2018	19.1	18.6	24.8	39.2	25.0	19.8	17.5	39.7	18.8	14.5	27.4	39.3	14.4	18.3	11.0	27.4	17.4	6.7
2020	21.8	21.9	27.3	37.1	29.8	20.7	18.6	40.7	19.4	19.9	33.0	39.2	17.6	20.0	10.7	27.7	17.5	7.9
2021	21.9	19.6	26.8	34.6	28.2	20.3	17.8	41.8	18.3	18.8	30.8	39.1	16.5	18.2	10.3	28.6	17.6	7.6
2022	22.4	19.2	25.1	36.9	27.7	19.4	17.0	40.1	19.4	18.2	30.3	40.2	16.4	17.9	10.6	26.3	17.4	7.2
2023	23.0	19.9 21.4	25.0 20.5	31.7 29.8	31.4 25.4	20.6 19.7	18.1	39.1 36.4	20.2	18.4	33.2 27.4	42.0 39.4	15.3	17.4	11.0	26.3	18.4	7.9
2025	24.5	20.9	19.8	32.4	24.0	18.3	15.4	34.6	17.9	16.2	25.7	41.4	15.8	18.4	10.1	26.0	16.2	6.7
2026	24.9	20.0	19.7	30.3	25.7	17.9	15.8	35.1	18.3	17.2	27.9	41.1	16.4	18.4	10.0	25.6	17.0	6.8
2027	23.7	16.8	19.0	28.8	21.0	17.0	12.9	34.2	17.2	14.6	23.5	41.1	14.6	16.3	10.0	24.7	15.3	5.6
2028	22.4	15.5	18.0	33.3	17.5	15.8	11.2	31.1	17.3	12.2	19.5	42.3	14.1	16.0	10.1	25.1	15.5	4.7
2025	18.5	15.0	20.9	37.5	14.5	14.1	10.5	31.8	14.6	10.9	16.3	43.4	13.8	14.9	9.0	24.5	13.1	4.4
2031	17.6	14.9	21.8	43.1	14.6	13.0	10.6	31.7	13.9	10.2	16.6	43.1	13.6	14.1	8.8	26.8	12.0	3.9
2032	17.5	11.7	24.1	45.4	15.1	13.7	10.3	31.0	14.6	10.8	17.1	40.7	11.7	12.0	9.7	26.3	12.3	4.1
2033	18.5	10.5	25.5	44.8	15.4	13.7	10.3	30.5	15.8	10.9	17.8	42.6	10.3	11.4	10.1	27.6	12.9	4.1
2034	21.1	11.0	25.9	50.5	14.4	12.7	9.2	31.5	15.1	10.4	18.3	42.5	9.9	11.9	9.3	28.2	12.0	3.9
2036	19.4	11.7	26.9	50.6	16.3	13.7	10.3	34.6	15.2	11.1	18.8	42.5	10.8	12.5	9.4	28.4	14.0	4.0
2037	20.5	11.1	23.4	45.8	16.1	13.5	10.3	34.2	16.4	11.0	18.5	38.3	10.6	12.8	9.9	25.9	14.8	3.9
2038	22.7	11.7	21.0	45.8	15.7	13.7	10.3	33.6	18.3	11.3	17.1	36.8	9.9	11.5	10.3	24.8	17.1	3.8
2039	22.2	11.5	20.2 19.4	44.3 40.9	14.4 16.2	13.6 14.1	9.8 10.5	33.9 34.4	18.7	9.6	15.0 16.5	30.9	10.1	12.2	10.7	23.5	17.4	3.3
2041	22.9	13.1	19.8	42.5	17.1	14.8	11.1	35.6	18.9	10.1	17.2	39.6	11.5	13.9	9.6	23.8	20.6	3.6
2042	23.9	13.7	17.0	40.4	14.8	15.8	10.4	34.2	20.7	10.0	15.0	37.0	11.4	14.3	10.8	22.1	20.0	3.4
2043	21.9	13.9	14.9	34.2	14.1	15.2	10.0	32.8	20.0	9.2	13.9	34.3	10.9	13.9	11.6	18.9	18.9	3.1
2044	20.4 19.8	13.2	15.1	33.1	14.1 15.5	14.2 13.4	97	31.9	19.8	9.3	14.5 16.8	34.7	9.0	12.1	10.9	20.2	18.5	3.2
2045	19.9	13.1	17.8	32.9	16.1	14.6	10.0	32.7	17.8	9.8	17.8	38.3	10.4	13.0	10.5	19.4	15.8	3.4
2047	20.3	12.0	17.3	33.6	15.0	14.1	9.3	31.7	17.3	9.9	17.4	34.8	10.0	12.8	9.9	18.7	14.7	3.5
2048	19.8	12.3	19.2	38.5	15.8	13.0	9.6	31.7	16.6	10.4	17.7	34.2	10.5	12.2	9.2	19.9	13.4	3.6
2049	19.6	14.3	19.3	37.9	15.5	11.6	9.7	30.8	16.6	9.0	17.5	32.6	12.1	13.0	9.4 9.1	18.0	12.3	3.2
2050	20.9	12.0	22.0	41.2	18.4	11.2	10.4	30.9	16.0	9.7	19.3	33.5	10.9	11.9	7.5	20.8	14.3	3.4
2052	25.5	12.8	25.0	43.9	18.6	11.5	11.0	30.9	17.0	9.9	19.4	33.2	11.2	12.3	7.7	21.2	14.0	3.7
2053	27.1	15.4	24.3	45.6	19.1	12.3	11.6	30.9	17.9	10.8	18.7	31.5	12.5	15.1	8.0	19.4	14.7	4.0
2054	27.6	14.6 15.7	24.5	42.3	20.2	12.6	11.8 12 7	30.7	17.8	10.9	20.8	33.1 37 4	12.3	14.2	8.3 g 1	19.6 21 0	14.4 16.7	4.1
2055	23.0	15.9	26.4	30.3	22.0	14.0	14.0	33.4	17.5	11.1	24.2	37.4	12.5	13.7	8.7	22.1	16.2	4.0
2057	20.3	16.1	27.1	30.5	25.9	15.6	14.8	35.4	17.3	12.7	28.2	38.0	12.9	14.8	8.8	23.2	16.1	5.5
2058	17.1	14.3	26.2	31.5	23.6	15.6	15.1	34.9	16.4	12.5	26.7	36.4	12.2	12.1	9.2	23.3	14.8	5.2
2059	14.3	14.0	25.4	30.3	22.6	15.0	14.5	37.5	14.5	12.6	26.4	41.0	12.3	12.8	9.2	23.4	12.9	5.1
2060 2061	13.1	14.5 14 1	26.5 26.9	28.9 28.6	23.8 22.6	15.5 14 5	14.9 14.9	38.3 35.5	13.5 14 7	12.8	27.5	40.5 36.4	13.3	13.2 11 7	9.4 9.4	23.0 24 3	12.5	5.3 4.8
2062	13.3	14.4	26.3	32.2	22.5	14.1	14.6	35.0	14.7	10.7	27.4	34.8	13.2	11.8	9.3	25.4	13.2	4.6
2063	15.3	13.8	27.0	34.9	23.8	14.4	14.0	35.4	15.1	11.2	27.6	33.3	12.8	11.9	9.6	25.3	12.5	4.6

2064	16.9	13.2	24.7	36.7	19.9	13.9	12.5	34.7	15.3	11.5	23.5	34.0	11.8	12.0	8.9	22.8	12.9	4.2
2065	18.8	12.5	24.7	34.8	16.6	12.9	10.7	33.1	15.6	10.5	20.1	33.6	11.9	12.3	8.6	22.7	12.4	3.7
2066	22.9	16.0	24.9	34.3	18.1	12.9	11.3	31.9	17.2	10.3	21.7	34.0	13.4	13.6	8.7	21.6	12.1	3.9
2067	24.2	14.7	26.7	36.5	17.2	12.8	10.7	31.7	17.8	9.0	21.3	32.7	11.8	12.7	8.6	21.8	12.0	3.5
2068	25.2	14.3	26.8	36.5	16.9	12.5	9.9	32.3	18.7	9.0	20.6	34.2	11.8	13.6	8.3	23.0	12.2	3.6
2069	23.9	15.0	25.7	38.2	15.8	12.5	9.6	33.7	17.5	9.2	18.6	38.7	11.6	14.5	8.6	25.4	11.4	3.5
2070	23.6	13.5	24.9	35.9	15.9	12.4	9.5	33.5	16.8	9.8	17.9	38.6	9.7	11.4	8.6	23.2	11.7	3.7
2071	22.1	14.0	23.6	33.6	16.0	11.6	9.9	32.7	16.4	9.0	17.8	38.7	9.7	12.1	8.3	22.5	12.5	3.8
2072	20.7	15.6	22.3	37.0	16.8	11.6	10.4	31.4	16.8	8.8	19.1	37.2	10.7	12.9	8.6	22.5	12.1	3.7
2073	21.0	15.7	19.8	36.9	16.3	12.4	11.2	30.5	17.7	8.6	18.7	35.0	10.0	12.0	9.6	21.4	13.3	3.7
2074	17.9	14.0	18.4	38.2	15.4	13.1	10.7	30.1	17.5	8.7	17.7	35.2	9.9	13.0	10.7	21.1	15.6	3.6
2075	18.2	15.1	17.0	35.5	15.5	12.9	11.1	30.3	18.0	10.2	17.5	35.5	10.3	12.8	10.2	20.9	16.9	4.0
2076	18.1	16.6	15.6	36.7	16.2	13.2	12.3	29.0	18.9	10.3	18.7	34.3	11.5	13.9	10.1	20.3	18.2	4.1
2077	18.7	16.6	18.4	35.9	19.6	13.9	12.7	29.1	19.4	10.2	22.6	35.2	13.5	14.1	9.6	20.9	18.6	4.6
2078	18.3	18.5	18.5	37.5	19.6	14.1	12.6	29.3	19.7	11.1	22.5	34.9	15.1	18.5	9.3	22.6	18.3	4.8
2079	17.8	17.5	18.0	34.9	16.8	13.2	10.6	27.4	19.0	11.0	19.7	36.5	14.3	17.9	9.7	21.3	14.5	4.3
2080	17.7	16.5	21.2	32.3	18.3	14.4	10.5	29.9	18.0	11.3	19.9	39.2	14.3	17.9	10.1	24.1	14.9	4.6
2081	16.0	17.0	23.2	33.0	17.8	13.2	10.0	30.0	16.5	10.7	19.5	43.1	15.0	17.2	9.6	26.3	13.9	4.3
2082	14.3	17.7	24.6	33.6	18.6	12.4	11.2	31.2	15.6	10.8	20.3	44.3	16.2	18.0	8.7	29.4	13.3	4.3
2083	13.9	16.5	26.3	35.0	18.4	12.1	11.6	30.7	14.4	9.9	20.7	45.0	16.8	15.9	9.1	29.2	12.2	4.0
2084	15.1	16.1	26.1	35.6	17.7	11.4	11.1	30.3	14.3	9.7	19.4	43.3	15.7	15.1	9.2	27.9	11.5	3.9
2085	13.0	14.0	23.8	38.0	15.0	10.8	10.4	31.5	12.4	10.3	16.3	40.7	13.4	13.2	8.6	26.9	10.5	3.6
2086	13.4	13.6	24.1	35.6	13.5	11.1	10.3	31.8	12.6	8.6	14.8	42.9	14.4	12.3	9.1	27.5	9.8	3.1
2087	14.2	13.7	22.5	41.0	14.3	11.8	10.9	32.2	12.9	8.8	14.9	39.1	14.9	11.6	8.9	30.1	11.4	3.2
2088	13.4	13.5	20.5	45.9	13.5	11.1	11.4	32.0	12.8	9.4	14.8	34.6	14.2	11.3	8.7	29.1	11.3	3.3
2089	13.8	12.9	19.1	49.9	13.9	12.1	11.2	33.5	13.2	10.2	15.1	32.5	13.2	12.0	8.7	26.5	12.6	3.6
2090	17.8	12.4	18.1	42.7	13.2	12.6	10.2	31.7	14.4	10.3	15.1	29.9	11.8	10.8	9.2	23.8	12.7	3.6
2091	18.0	12.3	16.7	39.9	12.8	11.9	9.3	32.3	14.8	9.8	14.2	28.4	10.6	12.0	9.0	22.6	12.5	3.4
2092	13.8	11.1	18.7	42.9	13.1	11.7	9.3	34.1	12.7	9.9	14.7	31.3	10.5	10.6	8.8	24.8	10.7	3.4
2093	17.1	11.8	18.1	36.7	13.2	11.3	9.1	33.2	14.7	9.4	14.9	30.9	9.7	10.7	9.2	21.6	11.1	3.2
2094	16.1	12.1	17.0	42.3	13.6	10.3	8.9	33.3	13.8	9.6	15.5	29.3	9.3	11.3	8.6	21.1	10.4	3.2
2095	16.4	12.1	18.7	39.7	13.7	10.6	9.2	32.8	14.0	9.7	16.1	32.2	10.0	12.8	8.7	20.3	10.8	3.2
2096	16.7	12.3	19.0	41.8	12.4	10.6	8.5	31.9	14.3	8.6	15.1	36.0	10.3	12.2	9.3	20.2	10.9	2.9
2097	18.2	13.0	20.5	39.4	12.6	10.4	9.0	31.7	15.0	8.4	15.4	39.5	10.0	12.0	8.8	21.8	10.5	2.7
2098	17.9	13.6	23.3	42.5	12.6	10.4	9.3	32.7	14.6	8.3	15.4	42.3	11.2	13.4	8.3	25.6	10.1	2.7
2099	16.7	12.8	25.2	46.8	12.5	10.7	9.4	32.3	14.7	8.5	15.6	43.6	11.3	12.1	8.2	27.8	10.4	2.9
2100	17.4	11.9	22.4	43.4	11.4	10.9	8.1	30.5	15.6	7.8	14.3	39.2	10.6	12.0	8.5	25.1	10.8	2.7

Country-wise average predicted percentage of plots without tree recruitment per year

	HR	C7	DK	FI	BE	FR	DE	IF	ІТ		NI	NO	PI	SK	FS	SE	SW/	BE
		CL.	DI		(FL)					20		110		510	25	52	5	(WA)
1991	21.0	40.2	22.6	0.0	19.6	19.2	36.0	5.4	22.7	43.4	16.7	2.8	29.6	40.1	17.2	8.4	32.9	61.6
1992	22.3	42.0	23.8	0.0	21.9	22.1	38.6	5.3	23.7	43.8	18.0	2.6	32.2	42.4	18.8	7.6	37.6	62.5
1993	18.1	34.4	25.3	0.0	21.7	21.5	34.9	5.4	22.0	42.4	17.2	3.0	27.8	34.5	15.8	8.5	32.8	61.6
1994	17.3	36.8	27.0	0.0	23.8	23.0	38.3	5.3	21.4	43.3	19.2	2.7	29.6	34.4	17.0	8.5	35.2	62.8
1995	17.1	32.7	25.4	0.0	21.2	24.1	36.5	4.9	21.6	43.4	18.1	2.9	27.3	32.1	17.3	7.7	33.3	62.9
1996	19.5	35.0	25.4	0.0	21.6	27.0	37.3	4.9	23.1	42.5	16.8	2.3	26.3	35.2	19.0	7.9	36.2	64.7
1997	20.0	33.2	27.9	0.0	23.2	27.5	38.3	5.1	23.1	42.3	17.8	2.5	25.9	32.7	19.1	9.5	38.7	65.4
1998	21.5	32.8	27.9	0.0	24.0	27.2	38.1	5.0	23.5	45.2	17.7	2.2	27.1	35.6	19.9	8.3	39.1	67.1
1999	20.1	32.8	27.2	0.0	24.4	28.4	38.2	5.2	25.4	47.9	17.9	2.2	25.0	36.5	20.7	7.5	38.7	68.7
2000	18.1	29.9	24.3	0.0	23.5	25.0	37.6	4.7	24.1	47.4	17.9	2.3	22.5	30.5	19.9	8.5	33.7	68.4
2001	21.4	35.7	22.8	0.0	21.5	24.9	39.4	4.3	26.6	46.5	16.7	1.7	27.2	39.8	22.3	7.4	37.2	66.8
2002	24.4	36.1	25.2	0.0	17.7	25.5	38.6	4.5	27.3	47.7	13.6	1.9	28.9	43.0	21.6	8.7	36.8	66.2
2003	25.3	36.8	24.7	0.0	18.0	25.1	36.9	4.3	27.1	49.2	11.6	1.8	28.0	41.6	21.1	9.1	37.2	65.2
2004	22.4	33.8	23.5	0.0	16.4	21.1	34.7	4.3	24.5	47.0	10.9	2.1	25.8	35.4	19.8	8.6	33.4	60.5
2005	20.2	33.5	21.3	0.0	14.6	19.4	31.8	4.3	25.0	45.1	9.8	2.0	27.0	34.5	21.0	7.9	28.5	57.5
2006	18.6	33.5	22.8	0.0	15.2	19.9	34.5	4.0	24.0	45.6	11.5	2.4	28.3	33.1	20.5	9.5	28.2	59.3
2007	19.7	33.5	20.8	0.0	13.6	20.1	34.2	3.9	23.2	43.8	10.5	2.3	28.3	33.4	18.5	8.2	31.8	57.3
2008	20.0	36.3	21.4	0.0	13.7	21.6	34.8	4.0	23.5	43.0	10.0	2.6	28.7	35.6	19.1	7.9	35.7	57.3
2009	18.4	32.9	20.7	0.0	12.1	20.9	32.5	4.3	22.6	42.2	8.4	3.2	24.7	31.1	19.5	8.5	33.6	56.4
2010	17.2	32.6	19.4	0.0	14.9	20.3	31.8	4.3	23.6	39.2	11.4	3.1	23.3	29.7	19.4	8.8	32.5	56.1
2011	17.7	35.0	20.6	0.0	15.0	19.5	32.6	4.4	22.8	34.5	11.7	3.1	23.7	34.1	19.6	8.9	34.2	56.1
2012	18.7	38.9	20.4	0.0	17.9	21.4	34.3	5.1	23.3	37.9	13.6	2.9	26.9	36.7	19.8	8.2	36.4	59.2
2013	20.2	38.8	19.3	0.0	17.8	22.5	34.8	5.0	22.6	37.4	13.0	2.1	25.0	36.1	19.8	7.4	38.1	59.3
2014	22.4	38.9	18.0	0.0	16.5	20.7	31.9	4.9	23.1	36.1	11.6	2.1	23.3	36.5	21.0	5.6	36.3	56.1
2015	22.4	39.3	20.3	0.0	19.0	20.6	33.0	5.0	23.2	35.1	12.3	2.1	23.0	34.9	22.9	6.1	34.8	55.4
2016	25.7	37.1	19.7	0.0	16.6	20.1	29.7	4.9	24.5	32.0	10.5	1.9	23.0	35.0	23.1	5.5	32.1	53.0
2017	23.5	35.5	20.1	0.0	17.8	20.8	30.6	4.3	22.6	36.4	11.1	1.8	21.7	31.1	22.1	5.9	30.3	56.6
2018	20.6	32.4	19.3	0.0	15.9	17.6	27.7	4.2	21.0	36.4	10.0	1.5	20.6	27.2	22.0	5.2	28.9	53.8
2019	18.7	27.4	18.3	0.0	13.9	16.3	25.5	4.5	20.4	33.1	9.0	1.5	18.4	20.8	21.2	4.7	26.4	49.5
2020	16.2	22.4	18.5	0.0	12.1	15.0	23.9	4.0	19.7	27.2	7.9	1.6	16.1	18.1	21.1	5.2	25.5	46.2
2021	15.7	25.6	18.4	0.0	12.9	16.2	24.9	3.9	21.0	30.2	8.9	1.6	17.5	20.6	22.3	4.9	24.7	47.1
2022	15.7	26.0	19.6	0.0	13.1	17.5	25.8	4.2	20.0	30.1	8.7	1.5	17.6	21.5	21.2	5.5	26.7	48.7
2023	15.0	24.6	18.8	0.0	10.4	15.8	23.1	4.3	19.9	28.1	7.7	1.5	17.8	21.3	20.6	5.5	24.5	45.6
2024	12.9	22.7	21.7	0.0	13.3	16.5	26.7	4.7	19.3	33.3	10.0	1.6	18.3	19.8	20.5	6.3	24.6	50.0
2025	13.1	23.4	22.5	0.0	14.4	18.7	28.2	5.3	21.8	31.9	10.4	1.4	18.2	19.7	22.4	6.1	29.1	50.1
2026	12.5	24.1	22.8	0.0	13.3	20.2	27.9	5.1	21.4	32.1	9.2	1.6	17.7	19.3	22.2	6.0	28.8	49.8

2027	12.9	28.7	24.0	0.0	17.3	22.2	33.4	5.2	23.0	37.5	12.1	1.5	20.5	21.9	21.9	6.5	32.3	54.5
2020	12 0	21.2	25.7	0.0	10 0	24.1	27.0	F 0	22.0	40.0	15.2	1 2	21.4	22.5	22.0	6.5	22.5	F0 0
2028	13.0	31.Z	25.7	0.0	19.0	24.1	37.9	5.8	22.9	40.9	15.5	1.5	21.4	23.5	22.0	0.5	32.5	58.9
2029	15.1	29.7	25.9	0.0	22.0	23.1	39.2	6.1	23.5	42.2	17.3	1.2	21.2	22.4	21.5	6.8	34.3	61.1
2030	17.4	32.1	22.9	0.0	23.2	25.4	39.3	5.6	25.9	43.7	19.2	1.2	21.9	24.9	25.4	5.7	35.9	61.9
2021	197	22.6	22.7	0.0	22.1	27 /	20.6	5.6	27.1	12.7	18 /	11	22.2	26.7	25.5	5 5	28.0	62.0
2031	10.7	32.0	22.7	0.0	23.1	27.4	35.0	5.0	27.1	43.7	10.4	1.1	22.5	20.7	23.5	5.5	30.5	03.5
2032	18.8	38.8	20.7	0.0	22.3	25.5	39.7	5.9	26.4	41.3	17.9	1.4	26.2	31.6	22.4	5.7	38.5	63.0
2033	18.0	41.5	19.8	0.0	21.8	25.3	39.9	6.2	24.1	41.6	17.0	1.3	30.2	33.6	21.2	5.6	37.2	62.4
2034	18 3	42.8	19.6	0.0	23.3	26.5	42.8	59	25.5	41 9	18.0	13	31.8	35.8	23.1	56	38.9	65.5
2025	10.0	40.2	17.0	0.0	21.0	20.0	41.0	5.5	24.1	40.0	10.0	1.0	20.2	22.5	22.0	5.0	20.0	C2 0
2035	10.1	40.3	17.0	0.0	21.9	20.0	41.Z	5.7	24.1	40.0	15.9	1.5	29.2	32.5	23.9	5.5	30.0	03.9
2036	17.4	38.4	18.6	0.0	20.9	23.4	39.3	5.4	24.5	39.2	15.7	1.4	28.7	31.1	23.3	5.6	33.3	63.4
2037	16.7	40.1	21.0	0.0	21.2	24.3	38.9	5.4	22.8	38.7	15.7	1.7	29.2	30.3	22.5	6.6	30.8	64.5
2020	15.0	20 7	22.6	0.0	21 6	22.0	20.6	E /	20.0	27 5	17.2	1 7	21.2	22.4	21.2	7 2	27.2	64.0
2030	15.0	30.7	22.0	0.0	21.0	23.0	35.0	5.4	20.5	57.5	17.5	1.7	51.5	55.4	21.5	7.5	27.2	04.5
2039	15.6	39.1	23.1	0.0	23.9	24.7	41.6	5.4	20.5	41.5	19.6	1.9	31.0	32.1	21.4	8.1	27.6	69.2
2040	13.1	33.7	24.8	0.0	21.2	23.6	39.6	5.4	19.6	43.8	17.9	1.5	25.7	26.4	22.5	8.2	25.6	67.8
2041	14 4	36.5	24 3	0.0	19.9	22.0	37 7	51	21.0	41 5	16.3	16	26.9	28.2	24.2	76	23.0	66.2
2042	1 / 1	25.2	27.0	0.0	22.4	20.0	40.1	E /	10 5	42.0	10.0	1.0	27.1	20 6	21.1	0.0	24.1	67.4
2042	14.1	55.5	27.9	0.0	25.4	20.0	40.1	5.4	19.5	42.0	19.0	1.0	27.1	20.0	21.1	0.9	24.1	07.4
2043	16.2	35.3	29.8	0.0	24.5	21.9	41.6	5.7	20.2	44.8	20.7	2.4	28.6	30.0	20.6	10.7	27.9	68.8
2044	18.3	36.6	29.7	0.0	25.2	25.1	41.3	5.7	20.6	44.9	19.3	2.4	30.4	33.7	22.4	10.9	28.5	69.2
2045	18 3	38.8	27.2	0.0	22.6	26.7	42.0	5.8	23.1	45.9	16.6	19	34.4	37 3	23.7	9.6	31.2	69.1
2045	47.5	20.0	27.2	0.0	22.0	20.7	44.4	5.0	20.1	44.0	45.0	2.2	20.0	34.0	23.7	0.0	22.2	67.2
2046	17.5	36.8	26.5	0.0	21.9	24.1	41.1	5.8	23.5	44.2	15.2	2.2	29.9	31.9	24.1	9.6	32.2	67.3
2047	16.6	39.1	27.2	0.0	23.7	24.8	42.5	6.2	23.7	43.7	16.6	2.8	31.3	32.3	24.0	10.1	32.9	66.6
2048	17.1	38.2	23.9	0.0	22.1	27.2	41.8	6.0	24.4	42.8	16.9	3.0	29.9	32.6	25.8	9.2	34.9	65.3
2040	17 2	2/1	24 5	0.0	22.7	21.1	41.0	6.2	24 E	47.0	17 /	2 5	25 4	21 E	25.6	10.0	20.2	60 C
2049	17.5	54.1	24.5	0.0	22.7	51.1	41.9	0.5	24.5	47.0	17.4	5.5	23.4	51.5	25.0	10.8	30.2	00.0
2050	17.3	36.8	22.3	0.0	21.0	32.2	41.9	5.8	26.3	48.4	16.6	3.0	29.0	32.3	29.3	9.9	36.3	67.5
2051	16.1	36.6	20.9	0.0	19.4	31.7	39.6	6.0	26.1	46.6	15.7	2.9	28.3	33.2	30.8	8.6	31.7	65.1
2052	12.9	36.7	18.6	0.0	19.4	31 7	38.2	61	25.1	46 7	15.6	27	28.3	32.1	29.6	83	32.1	65.0
2052	11 1	21.2	10.0	0.0	10.0	20.0	20.5	6.2	22.2	44.1	17.0	2.1	24.7	26.2	20.0	0.7	22.2	c2 2
2053	11.1	31.2	19.2	0.0	18.9	28.8	30.5	0.3	23.7	44.1	17.2	3.1	24.7	20.2	28.2	9.7	32.Z	03.Z
2054	10.9	32.7	19.1	0.0	18.1	27.9	36.1	6.1	23.7	43.4	14.3	2.7	25.5	27.4	26.3	9.2	32.7	62.8
2055	13.1	30.6	17.9	0.0	16.7	25.9	31.9	5.5	23.9	42.9	12.3	2.2	24.9	28.6	28.2	7.9	28.9	60.3
2056	15.2	20.2	17 0	0.0	16.1	25.0	21.2	5.6	22.8	12 5	11 /	2.2	25.7	28.8	25.8	8 2	20.8	58.0
2050	15.5	50.5	17.5	0.0	10.1	25.0	51.2	5.0	23.0	43.5	11.4	2.2	25.7	20.0	25.0	0.5	25.0	58.0
2057	17.8	29.9	17.4	0.0	13.9	21.8	30.0	5.0	23.7	41.2	9.8	2.0	24.0	26.7	25.1	7.6	30.2	55.8
2058	22.6	33.9	17.6	0.0	15.6	20.8	28.5	5.1	23.9	40.1	10.5	2.0	25.6	33.4	24.9	7.4	31.7	56.9
2059	26.3	34.4	19.6	0.0	16.5	21.2	29.9	43	26.3	39.5	10 7	17	25.6	31.3	24.7	71	35.8	58.0
2000	20.0	22.7	10.0	0.0	10.5	20.4	20.1	4.4	27.5	20.2	0.7	1.0	22.0	20.0	24.2	7.1	20.0	50.0
2060	29.0	33.7	10.0	0.0	15.5	20.4	29.1	4.4	27.5	39.2	9.7	1.8	23.2	30.8	24.2	/.1	30.0	57.2
2061	28.6	34.6	17.7	0.0	16.5	22.2	28.6	4.9	25.8	41.2	9.4	2.0	23.2	33.8	24.5	6.6	34.7	59.4
2062	28.4	34.3	18.2	0.0	17.2	24.2	30.1	4.9	26.4	44.8	10.1	2.1	23.2	33.9	23.9	6.1	36.0	59.8
2063	24.2	25.1	17.0	0.0	15.0	24.2	21.0	5 1	25.2	42.0	00	2.2	22.0	22.9	22.2	5 0	27.0	50 7
2005	24.5	25.0	10.0	0.0	10.0	24.0	24.7	5.1	25.2	42.0	12.5	2.2	20.0	22.0	22.5	7.0	26.4	55.7 C2.F
2064	20.8	35.9	19.6	0.0	18.6	24.8	34.7	5.4	25.4	42.0	13.1	2.2	26.2	32.6	24.1	7.0	36.4	62.5
2065	18.8	36.9	19.7	0.0	22.0	26.5	38.5	5.8	24.9	42.6	15.6	2.4	25.9	32.6	25.0	7.6	37.0	66.3
2066	15.1	31.0	20.0	0.0	19.8	27.0	38.3	5.9	23.7	44.8	14.1	2.3	22.5	29.7	24.0	8.4	39.2	63.9
2067	1/1 2	22.7	18.2	0.0	20.4	28.1	40.0	57	22.0	18.2	1/1 1	25	26.1	21.7	25.2	8.2	20.0	65.7
2007	14.2	33.7	10.2	0.0	20.4	20.1	40.0	5.7	22.5	40.2	14.1	2.5	20.1	31.7	25.5	0.5	35.5	05.7
2068	13.4	34.1	19.0	0.0	20.9	28.7	42.5	5.5	21.8	48.7	14.5	2.0	26.2	30.0	25.5	7.1	39.3	65.7
2069	14.4	33.1	20.1	0.0	21.8	29.4	43.4	5.4	23.3	48.1	16.3	1.7	27.0	28.0	24.5	6.1	40.9	66.2
2070	14.9	36.1	20.1	0.0	21.5	28.8	43.4	5.4	23.8	46.5	17.1	1.7	32.3	34.6	25.6	7.4	39.6	64.3
2071	15.2	25.2	21.0	0.0	21 5	20.0	40 E	E /	24.2	10 E	17 1	1 7	22.2	22.7	26.7	7.0	20.0	62.4
2071	15.5	55.5	21.0	0.0	21.5	50.0	42.5	5.4	24.5	40.5	1/.1	1./	52.2	52.7	20.7	7.9	30.9	05.4
2072	16.5	32.7	21.7	0.0	20.2	30.3	40.9	5.7	23.5	47.9	15.9	1.8	28.9	30.3	25.7	7.9	39.0	64.0
2073	16.1	32.7	24.3	0.0	21.1	29.7	39.0	5.9	23.1	49.2	16.7	2.1	31.0	33.1	22.8	8.5	37.4	63.4
2074	18.8	35.0	25.2	0.0	22.4	28.9	40.2	6.4	23.1	49.1	17.8	2.3	31.6	30.7	20.7	9.0	32.6	64.4
2075	10 /	22.1	26.6	0.0	22.2	20.0	20.0	6.7	22.2	44.0	17.0	2.4	20.2	21.2	21 6	0.2	20 5	62.7
2075	10.4	35.1	20.0	0.0	22.2	20.0	50.0	0.2	22.7	44.0	17.9	2.4	50.2	51.2	21.0	9.2	29.5	02.7
2076	18.7	30.7	27.5	0.0	21.4	27.5	35.3	6.7	22.6	43.5	16.5	2.4	26.6	29.8	22.5	9.6	29.3	61.6
2077	18.1	30.6	24.6	0.0	18.0	26.1	34.6	6.5	21.6	45.2	12.8	2.2	22.1	28.7	23.9	8.8	29.1	58.6
2078	17.9	27.2	25.3	0.0	17.8	25.0	34.6	6.5	21.2	42.6	12.9	2.2	19.5	21.0	24.4	7.8	28.3	57.7
2070	10 1	20.2	25.6	0.0	21.2	26.0	20.0	7 /	21.7	12 1	1/1 8	22	21.2	21.6	22.7	87	25.2	61.8
2079	19.1	29.2	25.0	0.0	21.2	20.9	39.0	7.4	21.7	42.4	14.0	2.5	21.5	21.0	25.7	0.7	55.Z	01.0
2080	20.1	30.6	22.2	0.0	19.3	24.4	39.6	6.4	22.8	42.9	15.4	2.0	21.0	21.5	22.2	7.2	33.4	58.8
2081	21.5	29.8	20.7	0.0	20.1	25.4	40.3	6.1	24.0	43.7	15.5	1.6	20.1	23.4	23.0	6.3	34.3	60.8
2082	24.8	28.8	19.9	0.0	18.8	27.4	35.9	5.7	25.1	41.8	14.3	1.4	18.6	21.8	26.3	5.4	35.1	60.8
2002	25.2	20.2	10.0	0.0	10.0	20 5	25.4	F 0	27.2	AA C	14.2	1 4	17.2	25.7	24.0	F 0	20.0	C2 0
2065	25.5	50.2	10.0	0.0	19.0	20.5	55.4	5.0	27.5	44.0	14.2	1.4	17.5	23.7	24.9	5.0	50.0	02.0
2084	23.8	31.0	19.2	0.0	19.9	30.4	37.4	6.1	27.2	44.9	15.9	1.6	19.0	26.4	24.9	6.0	37.1	63.9
2085	27.1	34.5	20.4	0.0	23.7	32.1	39.0	6.1	31.2	42.1	18.2	1.7	23.0	31.2	27.3	6.1	39.3	66.8
2086	26.6	35.1	19.1	0.0	25.7	32.0	40.2	59	30.2	47.2	21.4	17	20.9	33.7	26.7	57	41 3	69.6
2000	20.0	25.1	20.7	0.0	20.7	20.1	20.2	5.5	20.2	47.2	21.7	1.0	20.5	25.7	20.7	47	20.0	CO 0
200/	24.0	55.0	20.7	0.0	24.0	50.1	30.ō	5.8	29.8	40.0	21./	1.0	20.1	55.4	20.1	4./	50.8	00.0
2088	27.2	36.3	22.3	0.0	25.7	32.1	37.8	6.0	30.0	45.1	22.0	2.3	21.4	35.9	27.9	5.0	38.3	67.8
2089	26.8	37.4	23.6	0.0	24.8	29.5	38.4	5.2	29.6	44.4	21.9	2.5	23.3	33.4	28.6	6.0	35.4	65.4
2090	20.1	38.6	24.4	0 0	25 Q	27.7	41 3	5 8	27 9	44.8	22 3	33	26.7	36.0	26.5	71	36 5	65.7
2000	20.1	20.0	27.4	0.0	20.0	20.4	42.3	5.0	27.5	45.0	24.0	3.5	20.7	22.4	20.0	7.1	27.7	CC 7
2091	20.1	38.4	26.9	0.0	20.6	29.1	43.4	5./	27.0	45.9	24.0	3./	29.8	33.4	27.4	7.9	3/./	66.7
2092	25.9	40.6	24.7	0.0	26.2	29.1	42.8	5.2	30.7	44.9	22.8	2.8	30.0	36.4	28.3	6.8	40.9	67.1
2093	21 5	39.0	25 5	0.0	26.1	29.9	43 1	5.4	26.3	45.6	21 9	33	32 5	36.7	26.5	84	40.8	68 5
2004	22.5	20.0	23.5	0.0	20.1	22.5	10.1	E /	27.2	12 7	20.4	2.5	24.4	25.0	20.0	0.2	12 1	60.0
2094	22.5	30.0	27.5	0.0	23.8	32.0	45./	5.4	27.3	45.7	20.4	5.0	54.4	55.0	20.1	9.3	45.4	09.0
2095	21.7	38.3	25.6	0.0	26.4	32.2	42.8	5.4	27.2	43.5	19.1	2.9	32.1	31.8	28.2	9.5	42.5	69.2
2096	21.3	37.2	25.4	0.0	28.8	32.3	44.3	5.6	27.0	46.4	19.5	2.1	31.1	33.6	27.2	9.5	42.4	71.9
2097	19 7	35.5	24 1	0.0	28.8	33.0	43.0	5.8	26.2	46 7	18 7	1.9	31.0	33.6	28.6	82	43 7	72 8
2000	20.1	24 6	21.4	0.0	20.0	22.7	12.0	E 6	26.0	47.0	10.1	1 /	27.2	20.1	20.0	6 A	AE 2	72.4
2030	20.1	34.0	21.4	0.0	20.0	33.7	42.0	5.0	20.0	47.9	19.1	1.4	27.3	5U.1	23.2	0.4	43.3	12.4
2099	22.1	36.5	19.7	0.0	28.9	33.0	42.4	5.7	26.5	48.0	19.3	1.2	27.4	33.2	29.0	5.6	45.4	71.0
2100	21.6	37.9	21.5	0.0	31.3	33.5	46.8	6.2	25.0	50.6	21.2	1.6	29.4	33.2	27.4	7.0	46.3	71.6

Number of NFI plots per 25km grid cell for the mapping of recruitment density and Bray-Curtis dissimilarity index across Europe. The left figure shows the number of plots per grid cell where recruitment was simulated corresponding to Figure 2. The right figure contains less plots per grid cell because it only includes plots where recruitment was predicted corresponding to Figure 4.





Chapter 5

General Discussion

General Discussion

1. The role of forest regeneration

Climate change effects on European forest dynamics are inevitable. Changes in species distributions, tree growth, mortality and frequency of natural disturbances have been observed (Lindner et al., 2010: Patacca et al., 2023) and are expected to increase in magnitude (McDowell et al., 2020; Seidl et al., 2020) reducing the climate change mitigation potential of forests (Nabuurs et al., 2022). Reacting to those trends, forest managers aim to increase forest resilience in order to prevent and buffer potential negative impacts (Bolte et al., 2009; Lindner et al., 2014). To cope with the high level of uncertainty under climate change, it is essential to recognise the pivotal role of regeneration in long-term stand dynamics, and subsequently nurture dense and diverse recruitment to enable a large set of potential pathways for future stand development. This thesis aimed to provide a quantitative description of forest regeneration in relation to local site conditions and forest management to, ultimately, enable realistic forest resource projections across Europe that include species change, and that can be used to identify suitable forest management strategies under climate change. The question therefore was whether the anticipated tree recruitment in Europe will be adequate, or if adaptation to forest management practices are required to avert the decline of forest functioning under climate change.

Given the complex factors influencing forest functioning, models of forest dynamics (MFDs) provide a suitable means to assess potential trajectories and guide decision-making in forest management and forest policy (Schou et al., 2015). To examine future forest resource availability and develop appropriate management strategies on a European scale, it is crucial to incorporate a dynamic representation of tree regeneration in models of forest dynamics. In Chapter 2, various potential approaches to modelling tree regeneration are reviewed, taking into account the detailed ecological processes involved in forest regeneration. The knowledge gained from this review was then applied in Chapter 3, where statistical models were used to isolate and quantify the environmental effects on tree recruitment on a European scale. In Chapter 4 the quantified dynamics were integrated into EFISCEN-Space, a large-scale forest resource model, to simulate tree recruitment given the current forest structure under the climate change scenario RCP 6.0. In this chapter both quantitative and compositional shifts in European tree recruitment were evaluated.

In this general discussion I synthesize the key findings and insights from the previous chapters to derive integrated implications for promoting the long-term sustainability of European forests. By incorporating knowledge about tree recruitment processes and incorporating them into modelling, the discussion aims to provide practical advice for sustainable forest management strategies and policy formulation. The goal is to facilitate the resilience of European forests and their continued provision of essential ecosystem services. Given the significance of forest dynamics models in guiding management decisions, the general discussion is divided into two parts. The first part of the discussion delves into the implications of forest growth modelling, specifically addressing the challenges of forest

regeneration modelling. It examines factors that should be taken into consideration, identifies shortcomings of the presented approach, and explores potential solutions to address existing issues. The second part focuses on the implications for the forest ecosystem, particularly European forest resources, and its management. This second section highlights key concerns such as the interpretation of predicted changes in tree recruitment, the implications for forest management practices, and the necessary policy-level actions to ensure forest functionality in the face of climate change.

2. Modelling forest regeneration

2.1 The trade-off between generality, accuracy and realism in modelling forest regeneration

The choice of the appropriate modelling approach poses a significant challenge when it comes to forest regeneration. Most Models of Forest Dynamic (MFDs) have considered this aspect during their initial development. For instance, MFDs focusing on studying natural forest dynamics require a more comprehensive integration of regeneration processes, such as seed production, dispersal, and germination (Price et al. 2001). However, adjustments and refinements are often necessary as new discoveries emerge or to enhance existing approaches. Examples of this can be found in LandClim and LPJ. In LandClim, the incorporation of competition between ground vegetation and seedlings for water resources improved model accuracy (cf. Schumacher et al., 2006; Thrippleton et al., 2016). Applied by many research groups, LPJ has been modified with several modules that allow it to represent agricultural land-use types, fire dynamics and plant phenology (cf. Schaphoff et al., 2018; Sitch et al., 2003). Nevertheless, MFDs oriented towards forest resource management initially overlooked natural forest regeneration, assuming that forests would be managed and replanted after harvesting (Chapter 2). This poses an additional challenge in developing an appropriate forest regeneration model, as it must align with the existing structure of the underlying MFD. After all, most forest resource models were not developed to study the impacts of climate change but use chronosequences under presumed stable climate to simulate forest dynamics. Furthermore, the availability of ecological data for parameterizing specific processes is often limited, which, in combination with other constraints, leads to the choice of a modelling approach that may not be optimal but remains the best available option.

A wide range of approaches exists for modelling forest regeneration, resulting in the development of numerous tree regeneration and tree recruitment models. Tree regeneration models aim to capture the complex processes of tree reproduction, encompassing seed production, dispersal, and germination. In contrast, tree recruitment models take a simplified perspective, focusing on predicting the number of seedlings or saplings that surpass a specific threshold without explicitly considering earlier stages of development. Climate envelope models, while not strictly classified as forest regeneration models, allow for identifying geographic regions where tree species can successfully

regenerate based on climatic constraints (Brandt et al., 2017; Chakraborty et al., 2021). When constructing ecological models, the primary goal is to maximize accuracy, realism, and generality. Accuracy focuses on ensuring agreement between model predictions and observations. Realism involves accurately representing ecological processes in the model. Generality pertains to the applicability of the model's assumptions across a wide range of conditions. To further support the selection of an appropriate forest regeneration modelling approach, it is useful to map the desired forest regeneration model accordingly. While Leven's hypothesis of a trade-off among these three requirements has been disproven in some contexts (Mahnken et al., 2022; Orzack & Sober, 1993), it seems to holds true for forest regeneration models (Figure 1). Tree regeneration models achieve a high level of realism by incorporating detailed ecological processes that hold true in various settings (Generality), whereas tree recruitment models sacrifice realism in favour of accuracy and general applicability. Climate envelope models, on the other hand, offer the greatest generality but lack accuracy and process realism. Considering these factors, along with the intended purpose of the forest regeneration model, should facilitate the selection of appropriate approaches.



Figure 1 Mapping of general forest regeneration approaches after Leven's scheme for model development.

In the case of the model developed in this thesis the selection of the appropriate approach was rather straight forward. EFISCEN-Space, the MFD for which the forest regeneration model was developed, aims to inform about forest resources at European level and to project them into the future under climate change and altered forest management strategies. Therefore accuracy and generality had highest priorities. Further constraints were given by the structure of the MFD. The growth functions of EFISCEN-Space were based on forest inventory data and only valid for trees above a certain size threshold. Generally, the model was tailored to simulating the development of national forest inventory plots utilizing their extensive and systematic spatial coverage. Given the ambition to simulate forest

resources at pan-European scales, National Forest Inventories data was the most suitable source that provided sufficient coverage for the parameterization of a forest regeneration model. All these points together made it inevitable that the right choice for a regeneration model of EFISCEN-Space had to be a tree recruitment model. This doesn't imply that process realism was considered unimportant. In fact it is very much desired, as not only environmental conditions are changing but also forest management which makes natural regeneration and therefore natural processes more important. Nonetheless, it is important to acknowledge that the use of NFI data and the adoption of a tree recruitment model impose certain limitations.

2.2 Limitations and shortcomings of the presented recruitment model

2.2.1 Methodological constraints

The model presented in Chapter 3 has certain constraints that need to be taken into account when interpreting the results. One limitation is that the tree recruitment approach, by not considering the detailed ecological processes involved in tree regeneration, may not capture dynamic changes adequately. This is a common trade-off between accuracy and realism in mostly empirical models (cf. Figure 1). Consequently, the presented model may not accurately simulate fundamental changes in regeneration dynamics that can occur under climate change. For example, if climatic changes no longer fulfil the chilling requirements for certain species to germinate, the recruitment model will fail to replicate this factor. As a result, such empirical models, including the one presented in this thesis, are not suitable for forecasting forest dynamics over extended periods, as regeneration models do (cf. Hasenauer, 2006; Price et al., 2001; Vanclay, 1994). To mitigate the risk of missing changes in recruitment dynamics, it is crucial to update and adjust the model as new data becomes available.

2.2.2 Data limitations and statistical issues

Using existing NFI data from seven countries and eight different forest surveys with different sampling strategies has posed significant challenges for the statistical modelling and parameterizing the tree recruitment model. The combinations of sample plot area, time intervals between plot observations, and diameter thresholds for recruitment trees have prevented the incorporation of random effects, which would otherwise account for random variation at survey-level. As a result, misfits may arise, as evidenced by the discrepancy between predicted and observed recruitment counts in Flanders (Chapter 3, Supplement 4) or the unexplained increase in pine abundance in Switzerland (Chapter 4, Table 2).

Time is another crucial aspect when analysing tree recruitment. It is unknown to which degree the NFI data used in this study did already capture tree recruitment responses to climate change. The uncertainties are further amplified by the imperfect overlap in the data used for parameterizing the model, as well as the variations in census intervals, which represents the time between two plot observations (cf. Chapter 3, Table1). With longer

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General Discussion

intervals, tree recruitment is more likely to be affected by natural mortality or management impacts, introducing undesired biases in the model parameters. Additionally, the substantial differences in sampled tree populations based on diameter thresholds indicate possible effects of forest management on tree recruitment. For example, in Switzerland, where the diameter threshold is 12 cm, the tree population has likely undergone tending and thinning measures, contrasting with the population observed in Sweden, where the diameter threshold is 4 cm. Consequently, recruitment trees may have been removed before they could be measured, directly impacting the distribution of recruitment counts and potentially species compositions. While the quantifiable effect of these removed trees may be unknown, further research on recruitment modelling should be aware of potential forest management effects. It is crucial to recognize these limitations and discrepancies when interpreting and comparing data across different regions or countries.

Lastly, it should be noted that the National Forest Inventory (NFI) data utilized in this study do not distinguish between trees that have naturally regenerated and those that have been planted. This lack of information regarding the source of recruitment introduces an additional layer of uncertainty in the tree recruitment model. While the specific focus of the model was not to differentiate between these two types of regeneration, it is essential to recognize their fundamental differences, as they can significantly influence recruitment densities and compositions. Natural regeneration tends to follow established patterns that can be inferred from stand structural variables, whereas planting practices are often influenced by factors such as national or regional forest subsidies, local preferences, and individual choices (cf. Ross-Davis et al., 2005; Rvan, O'Donoghue et al., 2022; Yousefpour & Hanewinkel, 2015). Furthermore, the proportion of naturally regenerated trees compared to planted ones has undergone significant shifts over the past decades and varies considerably across different regions (FOREST EUROPE, 2015; Girdziušas et al., 2021). For instance, in South-West Europe, the percentage of forests resulting from planting and seeding is as low as 11 percent, whereas in Central-East Europe, this number rises to 42 percent. Unfortunately, the presented model lacks the ability to account for these differences, which highlights the need for further research and consideration of the various factors influencing recruitment densities and species compositions.

2.2.4 Factors ignored

Several factors that significantly affect tree recruitment have not been considered in this study. While tree recruitment is treated as a stochastic process, it is actually a complex combination of various ecological processes occurring over time. Many of these processes are directly influenced by micro-site quality. For example, small-scale variations in soil properties and the litter layer can impact seedling survival by affecting water and nutrient availability and competition with the herb layer (Kroiss & HilleRisLambers, 2015; Nopp-Mayr et al., 2012; Ohlson & Zackrisson, 1992). Shading from nearby adult trees can mitigate the negative effects of drought (Frost & Rydin, 2000). The availability of dead wood not only

protects young trees from browsing (Marzano et al., 2013; Wild et al., 2014) but also provides moisture for seed germination (Orman & Szewczyk, 2015).

However, due to the multitude of factors that can potentially influence the ecological processes driving tree recruitment and the difficulty in measuring them, it is reasonable to treat tree recruitment as a stochastic process and use proxy variables. Climate variables are often used as such proxies, but they have the limitation of not being directly observed at the plot level and instead rely on gridded datasets.

2.3 Ways forward for tree recruitment modelling

In tree recruitment modelling, numerous issues and limitations are present. However, viable solutions are available to address these challenges and improve the effectiveness of the models. The composition of forest surveys for the parameterisation of tree recruitment drivers comes with both challenges and opportunities.

1) The inconsistencies between survey methods regarding the time between the measurements, plot area and the measured tree sample (defined by the diameter threshold) evidently influences the amount of tree recruitment (cf. Chapter 3, Table 3 & 6). While the assumption of a proportional relationship between the measured plot area and the number of recruitment trees is reasonable, for time it likely only holds true under the premise that the values are not too widely distributed. More practically, given an observation of two recruitment trees on 250 m², it is acceptable to assume four recruitment trees on 500 m². Similarly, observing two recruitment trees in a five year interval and assuming four recruitment trees in ten years is also acceptable. With increasing time between the measurements and subsequent proceeding stand development, however, it becomes more likely that some of the recruitment trees have been subject to harvesting or natural mortality. Hence, if the time intervals become too extreme, the assumption of a proportional relationship between time and the number of recruitment trees is increasingly compromised. The time intervals in this study were, with few exceptions, within ten years around the mean. Therefore plot area and time interval were both modelled as offsets. If the time interval between two observations becomes more extreme and the assumption of a proportional relationship no longer holds true, it should be modelled as a covariate (Feng, 2022). The challenge hereby lies in the collinearity with the diameter threshold applied in the different forest surveys (cf. Table 3). In general, many NFIs have moved to shorter census intervals during the last inventory cycle. Together with more common equal time spans time-spans in between this problem may be solved already.

2) Taking the diameter thresholds of the different forest surveys into account constitutes a bigger challenge. There are various options to deal with changing diameter thresholds but there is little evidence in the scientific literature. Käber et al. (2021) presents the only study that investigated the performance of dynamic tree recruitment models across forest surveys. They fitted a separate model for each diameter threshold and found that it did not

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substantially affect the parameter estimates of the environmental covariates. An alternative approach could be to harmonise the diameter thresholds across the countries by applying the largest observed threshold (12cm). However, that would not only result in tremendous loss of tree observations but also compromise observation errors caused by the artificial change of sampling designs which are sensitive to the combination of plot area and diameter threshold (Král et al., 2010). New approaches to account for differences in sampling designs are being developed that allow computation and comparison of forest structural estimates between different types of sample plots (e.g. fixed-area, concentric circles, angle count) and specific plot designs (e.g. radii, diameter thresholds, basal area factor; Suvanto et al., in prep.).

A more promising alternative to solve the issues described under 1) and 2) could be the application of non-discrete probability distributions after harmonising tree recruitment observations over time interval and plot area. The two major advantages are the prevention of collinearity issues between sampling variables and, with preceding interpolation, the ease of assumptions on plots where no recruitment was observed. While observed zeros stay always zeros, independent from the harmonisation method, interpolated recruitment rates stay within the limits of known plot areas and time intervals, in contrast to extrapolated rates. More practical, while it is unlikely that an observed zero on a 50 m² plot remains a zero if one hectare was observed, it is plausible and supported by the actual observation that it stays a zero on one square metre. Preceding interpolation to annual recruitment rates per square metre (or minimum observed time intervals and plot areas) would therefore provide more realistic recruitment rates and reduce the discrepancies between unharmonized recruitment distributions. Further rescaling of recruitment rates would, for example, allow the application of beta regression techniques which can be extended, similar to discrete probability distributions, to zero-inflated distributions. Lastly, by eliminating sampling design factors, it would be possible to incorporate random effects into the model which could further improve model fits by eradicating regional misfits.

3) Further, worth exploring in future research is the integration of micro-site effects into tree recruitment modelling. Forest structural variables derived from plot-level observations can provide more precise indicators of micro-site conditions relevant to tree recruitment. A potential approach to better comprehend microclimate conditions within a forest is to consider the locations of trees within a plot. The underlying concept is that adult trees in the southern part of a plot may exert a greater impact on essential resources for tree regeneration compared to those in the north. However, it should be noted that plots are typically small in size, making it challenging to fully capture microclimate variations. Additionally, the influence of trees outside the plots may have significant effects, and this information is not available in the NFI data. Conducting tests at the national level may provide more comprehensive insights into micro-site effects, as international setups may encounter challenges due to differences in sampling designs, potentially leading to an unequal qualitative description of forest structure as a proxy for micro-site effects.

4) Lastly, this thesis serves as a proof of concept regarding the opportunities that arise by combining existing NFI data across large geographical ranges. Such dataset allow to further our understanding of forest dynamics and the development of more effective forest management strategies under climate change. Collecting such data sets requires great efforts, from the people who measure in the field, to the researchers who ensure the quality of the data, to those who use it for analysis and applications. This must be accompanied by long-term visions as acquiring forest inventories is yet a challenging endeavour (cf. Nabuurs et al., 2007; Nabuurs et al., 2010). The data more than 400,000 permanent sample plots that are currently measured by European countries (Lawrence et al., 2010) could be made available, at least for research purposes. Further, countries could be encouraged to harmonise their NFI sampling strategies to reduce the challenges encountered through variations in plot area, size thresholds, and time intervals between the observations. In the context of forest regeneration, permanent measurements of trees below the diameter threshold may allow a better understanding of the detailed processes affecting tree recruitment. Today, most NFIs measure trees below the size threshold only temporarily.

3. Implications for forest management and policy

3.1 Considerations for forest regeneration

Presumed increases of climatic extremes under climate change give reason for concern. The projected precipitation shifts (Casanueva et al., 2014) in combination with increasing occurrence and severity of extreme summer temperatures (Jacob et al., 2014; van der Linden & Mitchell, 2009) cause a decline in recruitment densities and result in substantial shifts of species composition across a large part of Europe (cf. Chapter 4. Figure 2 and Figure 4). However, the effects of climate change are regionally specific and may not in all regions cause dramatic effects on forest recruitment. While boreal forests are expected to experience the strongest increase in temperature within Europe (Fleig et al., 2015), this also holds for precipitation in summer (Maraun, 2013) which may buffer drought effects on tree recruitment. In Mediterranean and Central European forests however, climate change effects may be stronger as extreme temperatures are expected to increase more drastically (Fischer & Schar, 2010) while summer precipitation declines (Lindner et al., 2010). Speciesspecific range shifts have already been observed due to a number of factors such as growth decline and increased occurrence of natural disturbances. In combination with failing recruitment, forests in the Mediterranean are at risk to turn into shrublands (de Dios et al., 2007).

The results of Chapter 4 show that tree recruitment densities are declining under climate change in large parts of Europe. Especially in Southern, Western and Central Europe, the regeneration phase may hamper long-term forest functioning in the future (cf. Chapter 3 Figure 3 C & D) and cause a decline in the provisioning of ecosystem functions in the future. This in combination with the results of Chapter 3, where strong effects of forest structure on the density and composition of tree recruitment were shown (Chapter 3 Table 5 &

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Supplement 6), provides a solid ground for forest management to actively promote tree recruitment success. By controlling the stand basal area through harvesting, for instance, recruitment densities but also the composition of recruiting species can be actively steered towards resilient forest regeneration. Further, clear advantages of mixed forests over monocultures have been proven with regard to productivity, biodiversity, resilience (cf. Coll et al., 2018; Felton et al., 2010) and microclimate regulation (Richter et al., 2022). This study affirms that benefits of structurally diverse mixed forests also apply to forest regeneration. Mixed forests tend to recruit not only more trees but also more diverse species mixtures with assumed subsequent positive effects on forest resilience (Chapter 3 Figure 3 & 4). In addition, increasing the amount of deadwood could further improve the success of forest regeneration (cf. Liira et al., 2011; Svoboda et al., 2010), although this was not investigated in this study. Lastly, even though the present study did not reveal a direct effect of forest structural diversity on tree recruitment, diverse structures have been linked to increased productivity (Pedro et al., 2017; Zeller & Pretzsch, 2019) and higher resilience to natural disturbances (Dobbertin, 2002) and hence may improve recruitment conditions in the long run.

Forest managers can influence the number and composition of tree recruitment through targeted management interventions. However, the local site conditions may substantially influence the results. Models of forest dynamics that are tailored to specific regions may further assist in defining and validating appropriate strategies for local forest management.

3.2 Assisted migration or natural regeneration?

Due to the absence of information regarding the origin of tree recruitment in the dataset used in this thesis, direct assessment of whether natural regeneration will provide desired recruitment patterns for resilient forests under climate change is not possible. However, considering that over two third of European forests are regenerated naturally (FOREST EUROPE, 2015), we can discuss this issue by evaluating whether the existing forest structure and management practices as represented in the statistical model would lead to the establishment of desired recruitment densities and composition through both planting and natural regeneration. The findings presented in Chapter 4 highlight that forest regeneration could become a limiting factor under climate change, particularly in relation to the current forest structure and management approaches. This raises important questions regarding the potential need for assisted regeneration methods.

Tree species possess an inherited adaptive capacity that allows them to adjust to changing environmental conditions. Various evolutionary mechanisms contribute to genetic adaptation, operating at different hierarchical levels. At the individual level, these mechanisms involve individual heterozygosity, acclimation, and epigenetic responses. Natural selection, on the other hand, acts at the population level, while at the species level, local adaptation is facilitated by gene flow and the colonization of new sites (Lindner et al., 2010).

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Although the adaptive capacity of species is widely recognized as a vital component of forest dynamics, it remains poorly understood. One plausible explanation for this knowledge gap is the existence of a strong observation bias regarding adaptive capacity. Adaptations at the individual level are often imperceptible to the eve. The recognition of a tree's adaptation to environmental conditions throughout its lifetime is challenging since these adaptations are not directly visible. Instead, only when an individual tree fails and exhibits signs of growth decline, or dies, is it identified and labelled as "not adapted". Yet, evidence of heterozygosity and acclimation at the individual tree level has been demonstrated for several species (cf. Bush & Smouse, 1992; Gunderson et al., 2010; Sendall et al., 2015), suggesting that the impacts of climate change on forest productivity and species distribution may be less severe than currently assumed. Furthermore, similar observation biases may also be present at the population level. For example, recently increased mortality in mature beech stands across Europe has been attributed to a combination of drought and site conditions (Archambeau et al., 2020; Frei et al., 2022; Leuschner, 2020). However, hastily concluding that the species lacks the capacity to cope with climate change may be premature. The beech populations currently experiencing high mortality rates may not have undergone natural selection for more drought-tolerant individuals, as drought has not been a limiting factor for the population until now. In the next generation of trees, however, natural selection at the population level may lead to an overall increase in drought tolerance (Jump et al., 2006).

In certain cases, assisted migration may become the only viable option for maintaining a healthy tree population. A notable example is the European ash, which has experienced widespread dieback throughout Europe due to a pathogenic fungus. While a small portion of trees naturally inherit resistance against the infection, the majority of trees, including those lacking natural resistance, are still capable of reproduction. Consequently, ill-adapted trees persist in the ecosystem, albeit without fulfilling other important ecosystem services such as timber production and aesthetics (McKinney et al., 2014). The European ash scenario underscores the potential necessity of forest restoration through assisted migration to restore a balance between desired ecosystem functions. Over time, the collection and breeding of resistant trees can enhance the overall resistance of the species to the fungus by directing gene flow within the population. Preserving the ash species in European forests and re-establishing its commercial significance requires a governance framework that encompasses the identification of resistant genotypes, as well as regional, national, and international integration, while ensuring the preservation of genetic variation. Failure to do so could result in a genetic bottleneck, leading to maladaptation and reduced vigour of the species. Hence, effectively addressing this challenge necessitates a high level of coordination and governance.

In general, forest genetics deserve more attention when evaluating forest management strategies and modelling forest dynamics (Alía et al., 2021). Currently, only a few models incorporate natural adaptation processes (e.g. Kramer et al., 2008). Ideally, MFDs would include recruitment, growth, and mortality functions specific to different life stages and

populations to account for varying levels of natural adaptation to environmental changes (e.g., Hülsmann et al., 2016). However, limited understanding and data constraints currently impede the incorporation of species-level adaptation in models. Therefore, most modelling frameworks, including EFISCEN-Space, fail to give profound advice on whether to assist migration of species or not. In conclusion, fostering the establishment of dense natural regeneration is promotes successful natural adaptations. Site-level assessments are necessary to determine if in-situ adaptive responses can maintain healthy tree populations. Where this is not expected, assisted migration of better adapted individuals or provenances should be considered.

3.3 The importance of reinforcing international collaboration in monitoring, management expertise and forest policies

The challenges associated with forest regeneration in Europe have become more apparent, necessitating increased policy attention to ensure the long-term sustainability of forest ecosystems. To effectively address these issues, international forest policies should emphasise the following six key points:

1) Effective Collaboration and Knowledge Exchange:

Dealing with the challenges of forest regeneration necessitates strong collaborations between forest practitioners, scientists, and policymakers. These collaborations should facilitate the exchange of knowledge and experiences regarding successful regeneration strategies. By sharing best practices and lessons learned, stakeholders can collectively work towards identifying effective approaches that promote healthy forest regeneration across Europe.

2) Preservation of Genetic Resources:

Preserving genetic resources is paramount to ensure the resilience and long-term viability of European forests. Networks like the European forest genetic resource programme (EUFORGEN, Alía et al., 2021) facilitate knowledge sharing, coordinate and monitor conservation of forest generic resources, and promote its appropriate use, to ultimately enhancing the genetic diversity and adaptability of forest species.

3) Establishing a European-wide monitoring program:

Expanding European-wide monitoring programs for forest dynamics is urgently required. While current efforts focus on utilizing remote sensing technologies (Buras et al., 2021; Loozen et al., 2020; Mallinis et al., 2004), such as satellites images, these methods are limited in their ability to observe the dynamics of tree regeneration beneath the forest canopy. Facilitating the harmonisation of existing permanent ground-based monitoring networks across Europe (NFIs) would provide valuable data on forest regeneration processes, enabling researchers to better understand and model forest dynamics.

4) Recognizing the Impact of ungulate Species:

An often-neglected factor hindering natural regeneration is the high population levels of ungulate species throughout Europe. These ungulates, although an integral part of the ecosystem, can exert significant pressure on young tree seedlings, inhibiting their growth and survival. The impact of ungulates on forest resilience needs to be recognized as an international threat to forest health. Urgent action is required to develop effective strategies that address ungulate populations while maintaining a balanced ecosystem.

5) Balancing consideration of ecosystem services:

Policy decisions should emphasise the recognition of the broad range of ecosystem services provided by forests. Forest ecosystems cover a substantial 43 percent of the European land surface and contribute to various vital goods and ecosystem services, including regulating climate and water resources, protecting biodiversity, mitigating drought effects, and recycling precipitation (Ellison et al., 2017; FOREST EUROPE, 2020). While carbon storage is a crucial service recognized by international policies, a sole focus on maximizing carbon storage potential, can pose a severe threat to forest ecosystems. Under climate change, limitations related to water and nutrient availability (Hungate et al., 2003; Norby et al., 2010), along with reduced tree longevity (Bugmann & Bigler, 2011), and increasing frequency and severity of natural disturbances (Reyer et al., 2017; Seidl et al., 2017), could transform forests into carbon sources rather than sinks, as observed already today in some countries (Cienciala & Melichar, in review). It is crucial to set aside areas to protect biodiversity and understand natural dynamics, but promoting adaptive forest management in the majority of forests may provide a more effective strategy to maintain and balance the desirable functions.

6) The need for policy commitment:

Policy decisions must prioritize the conservation and sustainable management of European forests. Currently, the European Union dedicates less than 700 million Euro to support forest management through the European Agricultural Fund for Rural Development (EAFRD, Haeler et al., 2023; European Union, 2013), while agriculture receives over 50 billion in subsidies (European Parliament, 2021). Allocating more funding to forests is essential, given the magnitude of their ecosystem functions, including contributions to food safety through precipitation recycling (Teuling et al., 2017). The high level of uncertainties surrounding forest dynamics necessitates conservative strategies that prioritize ecosystem functioning over short-term policy goals. Emphasizing the utilization of natural potential wherever possible and providing funds to sustain diverse and resilient forest ecosystems are crucial steps towards long-term sustainability. Policies should consider all ecosystem services and forest functions, focusing on the dynamics that influence these services rather than solely focusing on specific targets or stocks. By adopting a holistic and sustainable approach,

policymakers can generate effective support for the long-term functioning of forest ecosystems.

4. Concluding remarks

Extensive efforts have been made in forest dynamic modelling to integrate recognized ecological mechanisms and address the diverse ecological and climatic factors that influence regeneration success. However, certain processes crucial for forest regeneration remain insufficiently understood and quantified, thereby restricting our ability to accurately forecast forest dynamics under changing climatic conditions. The increasing utilization of natural regeneration in European forests mandates the incorporation of dynamic recruitment models into common forest resource models. Effectively supporting forest management strategies in the face of climate change involves understanding fundamental processes like regeneration, establishing a connection between primary production and dynamics of species populations, and informing adaptive forest management through comprehensive assessment of regeneration options.

Modelling recruitment remains a complex task with room for improvement. It is important to recognize that when modelling at large spatial scales, regional limitations in representing the recruitment dynamics of individual regions may arise. The integration of existing forest surveys across large geographic areas in the presented modelling approach offers valuable insights into the influence of climatic factors on tree recruitment, making it a valuable contribution to forest research and management.

The challenges revealed in this thesis highlight the potential limitations of forest regeneration across large areas in Europe, raising concerns about the future sustainability of forest ecosystems. To promote adaptive capacity, forest managers need to assess whether climate-resilient species mixtures will successfully establish naturally. In cases where environmental constraints hinder natural establishment, assisted migration of better adapted species and provenances becomes necessary. The anticipated shifts in recruitment densities and species compositions may lead to a decline of forest functioning and pose significant challenges for forest management.

In conclusion, the regeneration phase of forests offers substantial opportunities for forest management to shape and guide the future development of adapted ecosystems. The results reported in this thesis provide valuable insights for long-term projections and aid our understanding of sustainable and adaptive forest management practices under changing environmental conditions. By prioritizing collaborative efforts, knowledge exchange, and comprehensive policies, we can enhance the resilience and adaptive capacity of European forests and ensure their long-term viability.

Chapter 5



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References



Summary

Summary

European forests are essential for delivering a range of ecosystem goods and services to local and regional communities as well as playing a critical role in safeguarding biodiversity. Climate change has significantly affected European forests, necessitating adaptations to ensure their continued functioning. At the same time, there is a growing demand for goods and services from forests, posing additional challenges for forest management. The regeneration phase offers the best opportunity to adapt forests to changing environmental conditions. During this phase, the forest structure and species composition can be adjusted to increase resilience. Forest managers are faced with the task of determining the most effective approaches, as uncertainties remain regarding the speed and extent of climate change impacts and shifts in societal demands.

The regeneration phase of a forest comprises a sequence of complex ecological processes, many of which are not fully understood. Tree regeneration is the product of successful flowering and pollination of mature trees, seed production and eventually dispersal. In order to germinate and establish, seeds require specific environmental conditions linked to light, temperature, soil moisture and nutrients. After germination, seedlings are vulnerable to drought, browsing and competitions for resources, resulting in the highest tree mortality rates throughout stand development. Considering the influence of site conditions and forest management on forest regeneration processes, the key questions addressed in this thesis were:

To what extent can the present and anticipated forest regeneration provide the basis for necessary adaptation to meet future demands on forests? How can this be assessed, considering the intricate interplay between ecological processes, forest management, and effects of climate change?

Given the entanglement of factors affecting forest dynamics, simulation modelling offers a practical tool to guide decision-making in forest management and policy. Considering the impact of climate change on European forests and the need for adaptation of forest management, understanding how forests regenerate becomes essential. However, existing models of forest dynamics often oversimplify forest regeneration and its changes under adaptive forest management and climate change. This thesis aims to provide a quantitative description of forest regeneration in relation to local conditions and management practices, based on observed regeneration throughout Europe. The goal was to enable realistic projections of forest resources in Europe, including species changes, and allow the identification of suitable forest management strategies under climate change. To find the appropriate level of detail regarding the quantitative description of forest regeneration, regeneration approaches of existing models of forest dynamics were explored in Chapter 2. This was integrated in the development of a dynamic tree recruitment model in Chapter 3. In Chapter 4 the recruitment model was implemented within a large-scale forest resource model to investigate the effects of climate change on forest regeneration under the current forest conditions through scenario analyses. Chapter 5 synthesizes results from previous chapters to draw conclusions for tree recruitment modelling and the implications for forest management.

More detailed. Chapter 2 summarizes the main ecological processes involved in tree regeneration, investigates how they have been formulated in 29 existing dynamic forest models and evaluates their ability to represent climate change impacts on forest regeneration. We distinguished between ecological-based and empirical-based approaches of forest regeneration. The fundamental difference lies in their application and thus required representation of forest regeneration. Ecological-based approaches are generally found in model frameworks that investigate natural forest dynamics and hence seek generality and realism in specific model formulations. The represented processes of forest regeneration are much more detailed compared to empirical-based approaches. Empirical-based approaches evolved in the context of prognosis and projection of forest resources. In the latter case, the focus in the specific formulation of forest regeneration has been on accuracy rather than generality or realism, driving empirical approaches to a simpler representation of forest regeneration. In general, a large variety of forest regeneration modelling approaches has been developed. The conclusions of Chapter 2 highlight that ecological processes involved in tree recruitment and incorporated in ecological-based models are neither fully understood nor sufficiently quantified, thus limiting the ability to accurately predict forest dynamics under climate change. The empirical approaches investigated mostly focus on the effects of forest structure on forest regeneration, but these approaches are bound to specific environmental conditions, including forest management, and are therefore limited in capturing the dynamic changes associated with climate.

Based on the conclusions of chapter 2, an empirical-based approach was developed in **Chapter 3** to simulate forest regeneration in EFISCEN-Space, a large-scale forest resource model. Given the overall model objective to quantify future availability of forest resources, a dynamic tree recruitment modelling approach was considered sufficient. A more detailed representation of forest regeneration across tree species and large spatial scales is restricted by the availability of data.

Tree recruitment was defined as the trees that grow above a predefined size threshold between two observations in a forest survey. Those trees have successfully passed the most vulnerable stages of tree regeneration, hence, the process of tree recruitment is the result of all previous processes of tree regeneration and therefore highly stochastic in nature. In Chapter 3, a dynamic tree recruitment model was developed using forest survey data from eight European countries, including nearly 138,000 individual tree recruitment events. The model was applied to investigate the influence of forest structure, soil characteristics, and different groups of weather and climate variables on both the quantity and species of recruiting trees. The climatic groups covered different aspects, including average annual conditions, within-year averages, annual variability, extreme events within a year, and combinations of these groups. The combination of climate and weather variables yielded the

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best performance among the tested groups. The findings revealed distinct climatic effects on tree recruitment, with stable climatic conditions and high precipitation benefiting recruitment while high maximum temperatures had a negative impact. The lead species in a plot played a significant role in determining the recruited species. Forest structure was also identified as an important factor in tree recruitment, with multi-species stands showing advantages over single-species stands in terms of recruitment quantities and species compositions.

While the ecophysiological potential of tree species and regeneration processes are relatively well studied at both stand and landscape levels, there is currently a gap in European assessments that adequately consider the impact of the existing forest state. This knowledge gap hampers the identification of limitations to European forests' adaptive capacity under climate change and the implications for management and policy.

In Chapter 4 the dynamic tree recruitment model developed in Chapter 3 is implemented into EFISCEN-Space. A comprehensive dataset from national forest inventories across 17 European countries was utilized to provide a detailed description of the current forest structure under the climate change scenario RCP 6.0 until 2100. The study investigated density and compositional changes in tree recruitment and their spatial patterns under a climate change scenario. The findings indicate a decline in recruitment densities in Southern, Western, and Central Europe, primarily attributed to climate change and the current forest structure. As a result, an increase in areas without recruitment is anticipated in these regions. Conversely, in Northern and Eastern Europe, recruitment densities are expected to increase in response to climate change. While the species composition of recruitment aligned with the overstory composition at the European level, significant variations existed at national and regional levels. In Spain, for instance, the similarity between recruitment and the overstory compositions is quite high, but becomes increasingly dissimilar under climate change. Contrasting Denmark, where the species compositions are already quite different and the changes remain low. At the species level, movements are observed, with Holm oak predicted to be successfully recruited in five countries where it has not been present in the overstory towards the end of the century. Norway spruce, however, experiences a strong decline across most countries and will, for instance, not be part of the forest regeneration in Flanders. These divergent trends emphasized the need for customized forest management approaches to tackle climate change challenges. By considering both recruitment patterns and existing forest structures, targeted interventions can be implemented to sustain tree recruitment levels.

In **Chapter 5** the key findings and insights of the previous chapters were synthesized, with the aim of deriving integrated implications for the long-term sustainability of European forests. The general discussion was divided into two parts, focusing on the implications of forest growth modelling and the forest ecosystem and its management.

While significant progress has been made in integrating ecological mechanisms and addressing diverse factors influencing regeneration success, certain crucial processes remain insufficiently understood and quantified, restricting accurate predictions of forest dynamics under changing climatic conditions. The increasing use of natural regeneration in European forests necessitates the incorporation of dynamic recruitment models into common forest resource models to support effective forest management strategies in response to climate change. Modelling recruitment at large spatial scales poses challenges, as regional limitations in representing recruitment dynamics may arise. However, the integration of existing forest surveys across large geographic areas in the presented modelling approach provides valuable insights into how climatic factors influence tree recruitment, thereby contributing to enhanced forest management practices. The decline in recruitment densities and future species compositions, underscore the potential limitations of forest regeneration across large areas in Europe, raising concerns about the future sustainability of forest ecosystems. To enhance adaptive capacity, forest managers need to assess whether climateresilient species mixtures can establish naturally. In cases where environmental constraints hinder natural establishment, assisted migration of better-adapted species and provenances becomes necessary. Anticipated shifts in recruitment densities and species compositions may lead to decline in forest functioning and pose significant challenges for forest management.

In conclusion, the regeneration phase of forests presents significant opportunities for forest management to shape and guide the development of adapted forest ecosystems. The results presented in this thesis offer valuable insights for long-term projections and contribute to our understanding of sustainable and adaptive forest management practices under changing environmental conditions. By prioritizing collaboration, knowledge exchange, and comprehensive policies, we can enhance the resilience and adaptive capacity of European forests, ensuring their long-term viability.



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As a kid, I spent most of my time outside exploring new things, an activity I wanted to continue as a grown-up. Scouting surely amplified my fascination with nature and forests. So, I purposefully pursued my dream, but not without support:

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As the first PhD candidate appointed in the Vegetation, Forest and Landscape Team, I enjoyed a very stable work environment. Funds for traveling, publishing, books or simply the finest office equipment was never a discussion. Bas, we were the oldest young researcher in the Team and I can say that it was always a pleasure working with you. Thank you for the outstanding assistance using EFISCEN-SPACE, you are a true expert. Ajdin, a man not shy to get his hands dirty. Emergency assists became sort of standard. Thanks for you selfless efforts to help me out on the last strip of my project. Paul, Joukje, Joop, Nils, Silke, Sietse, Sara, Sandra, Sven, Inge, Seppe, Judith2, Pieter and the many others, thank you for the pleasant work environment, I felt welcome from the beginning till the end. Igor and Geerten, the programming and statistic experts, thank you for the time spent on explaining me complex modelling concepts, providing and discussing ideas but also the support at hand.

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Short Biography

Louis Andreas König was born in Ehningen, Germany, on March 1, 1991. He studied Forest



Engineering in Freising at the University of Applied Sciences Weihenstephan-Triesdorf in 2011. He made his first contacts with science during a five-month internship at the Norwegian Institute for Bioeconomy Research, where he conducted productivity studies on steep slope harvesting systems on the west coast. In his bachelor's thesis, he investigated the growth performance of four economically important tree species in Upper Franconia, Germany, using dendrochronology. During and after his B.Eng. studies, he worked as a private contractor performing the full range of manual forestry work.

In 2016, Louis moved to the Netherlands to study Forest and Nature Conservation as part of the master's program at Wageningen University. As part of a field stay during his master's thesis project, he spent three months in Brazil, where he used travel grants from the Albert Mennega Stichting and Fona Conservation to study factors for successful reforestation of former mine lands. During his master's internship, he analysed a Dutch Douglas-fir provenance trial for its productivity and susceptibility to drought.

After completing his master's degree, Louis worked as a junior researcher at Wageningen Environmental Research for six months before starting his PhD project at Wageningen Environmental Research and the Forest Ecology and Forest Management Group at Wageningen University. With funding from the Graduate School for Production Ecology and Resource Conservation, he investigated the drivers of tree recruitment in Europe. Using data from national forest inventories, he parameterized a dynamic tree recruitment model for the pan-European forest resource model EFISCEN-SPACE to enable long-term projections of forest resources.

In early 2023, he started a four-year postdoctoral position at ETH Zurich in Switzerland. The goal of his research is to understand the effects of forest management on sediment production and flooding in alpine watersheds using an established forest landscape model.

Outside of university, Louis spends most of his time with his friends gardening, fishing, or, when time permits, brewing or distilling.

List of Publications

König, L.A., Medina-Vega, J.A., Longo, R.M., Zuidema, P.A., Jakovac, C.C.. (2022) Restoration success in former Amazonian mines is driven by soil amendment and forest proximity. Phil. Trans. R. Soc. B 10.1098/rstb.2021.0086, in Phil B Special Issue: Understanding forest landscape restoration: reinforcing scientific foundations for the UN Decade on Ecosystem Restoration

König, L.A., Mohren, F., Schelhaas, M.-J., Bugmann, H., Nabuurs, G.-J.. (2022) Tree regeneration in models of forest dynamics – Suitability to assess climate change impacts on European forests. Forest Ecology and Management, Volume 520.

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PE&RC Training and Education Statement

With the training and education activities listed below the PhD candidate has complied with the requirements set by the C.T. de Wit Graduate School for Production Ecology and Resource Conservation (PE&RC) which comprises of a minimum total of 32 ECTS (= 22 weeks of activities)



Review/project proposal (10.5 ECTS)

- Climate change impacts and adaptive measures in European forests
- Regeneration approaches in models of forest dynamics
- Climate smart forestry long term impacts of climate change on European forests, its forest management adaptation and subsequent wood supply from European forests

Post-graduate courses (10.5 ECTS)

- Conflicting demands in European Forests; PE&RC (2018)
- Machine learning for spatial data; WGS (2019)
- Dynamic modelling in R; WGS (2020)
- Introduction to zero-inflated models; WGS (2021)
- European forest management; PE&RC (2021)
- Introduction to GAM and GAMM; WGS (2023)

Laboratory training and working visits (2.1 ECTS)

- Machine learning and tree mortality; University of Birmingham (2020)
- Tree ingrowth modelling; Swiss Federal Institute for Forest, Snow and Landscape Research (2021)

Invited review of journal manuscripts (1 ECTS)

 Land Degradation & Development: changes in floristic and vegetation structure throughout a tropical forest chrono sequence on abandoned gold-mining lands

Competence strengthening/skills courses (3.4 ECTS)

- Efficient writing strategies; Wageningen into Languages (2021)
- Intensive writing week; Wageningen into Languages (2021)
- Scientific publishing; PE&RC (2022)
- Introduction to LaTeX; WGS (2022)

Scientific integrity ethics in science activities (0.6 ECTS)

- Scientific integrity; WGS (2021)

PE&RC Annual meetings, seminars and the PE&RC weekend (1 ECTS)

- PE&RC Symposium drought, plant hydraulics and vegetation modelling (2018)
- PE&RC/FEM PhD workshop: identifying and tackling stress (2022)
- PE&RC Last year retreat (2022)

Discussion groups/local seminars or scientific meetings (6.5 ECTS)

- CLIMO CLImate smart forestry in mountain regions symposium (2019)
- I-Maestro Innovative forest management strategies for a resilient bioeconomy under climate change and disturbances workshop (2019)
- FEM Journal club (2019-2021)
- KNBV Alternative tree species under climate change workshop (2020)
- TreeMort workshop (2020)
- ALTERFOR Alternative models and robust decision-making for future forest management symposium (2020)
- FEM R Club (2021)

International symposia, workshops and conferences (4.8 ECTS)

- FORMASAM Forest management scenarios for adaptation and mitigation workshop and conference; Grenoble, France/Zvolen, Slovenia (2019/2020)
- Adapting forests to climate change symposium; Toulouse, France (2020)

Societally relevant exposure (0.3 ECTS)

 Interview with the Wageningen University and Research resource magazine about forests of the future (2021)

Lecturing/supervision of practicals/tutorials (6.3 ECTS)

- Resource dynamics and sustainable utilization (2019-2021)
- Restoration ecology (2020)
- Strategic planning in forest and nature conservation (2021)
- Forest resources (2021-2022)

BSc/MSc thesis supervision (3 ECTS)

 Forest regeneration in the Netherlands: comparing random forest options to predict ingrowth from forest inventory data The research described in this thesis was financially supported by the C.T. de Wit Graduate School for Production Ecology and Resource Conservation (PE&RC). Financial support from Wageningen University for printing this thesis is gratefully acknowledged.

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