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Tamm reviews

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,

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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 and 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., 2012; 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 and Tome, 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

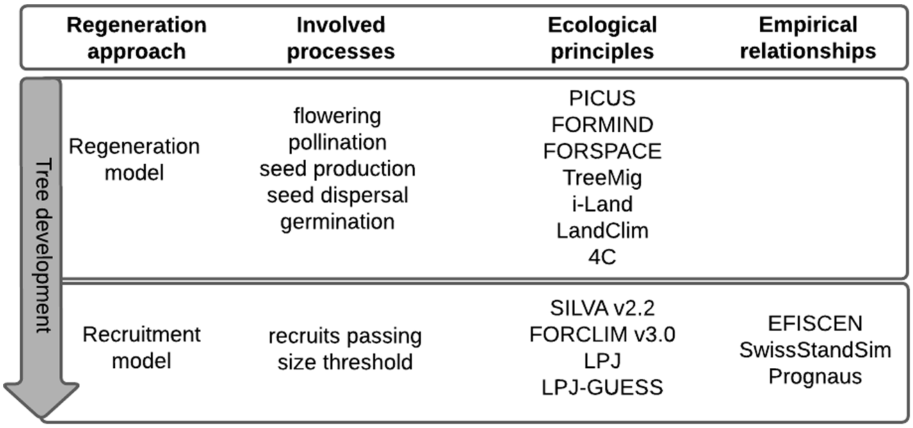
We reviewed 29 MFDs of which we selected 14 to discuss in greater detail. The selection was based on their approach with regard to spatial and temporal structure (Table 1) as well as their tree regeneration approach and the main model purpose (Fig. 1). The models contain typical approaches or new developments, 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.

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 (Fig. 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 (Fig. 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 structure	Temporal structure	Tree 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., 2012	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	Recruitment model
	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	
	PROGNAUS	Ledermann, 2002	stand	individual	5 year	
	SwissStandSim	Zell et al., 2019, p.c.	empirical	individual	5 year	
	EFISCEN	Sallnäs, 1990, Nabuurs et al., 2010	stand	stand	5 year	



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

Fig. 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.

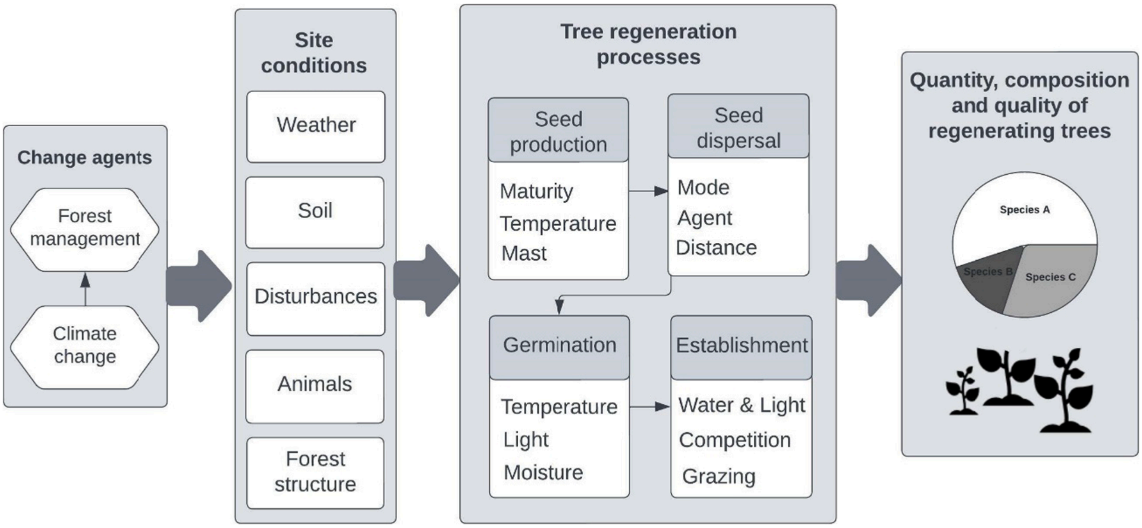


Fig. 2. Depiction of tree regeneration processes and its influencing biotic and abiotic factors. Some of the processes are incorporated in regeneration models in quite some details, while recruitment models generally aggregate those processes. Climate change affects next to the site conditions also forest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

3. 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 (Fig. 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 years 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 type- and 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 (Muller-Haubold et al., 2015) and altered mast year cycles (Fig. 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 (Bogdziewicz et al., 2017). For an improved representation of 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.

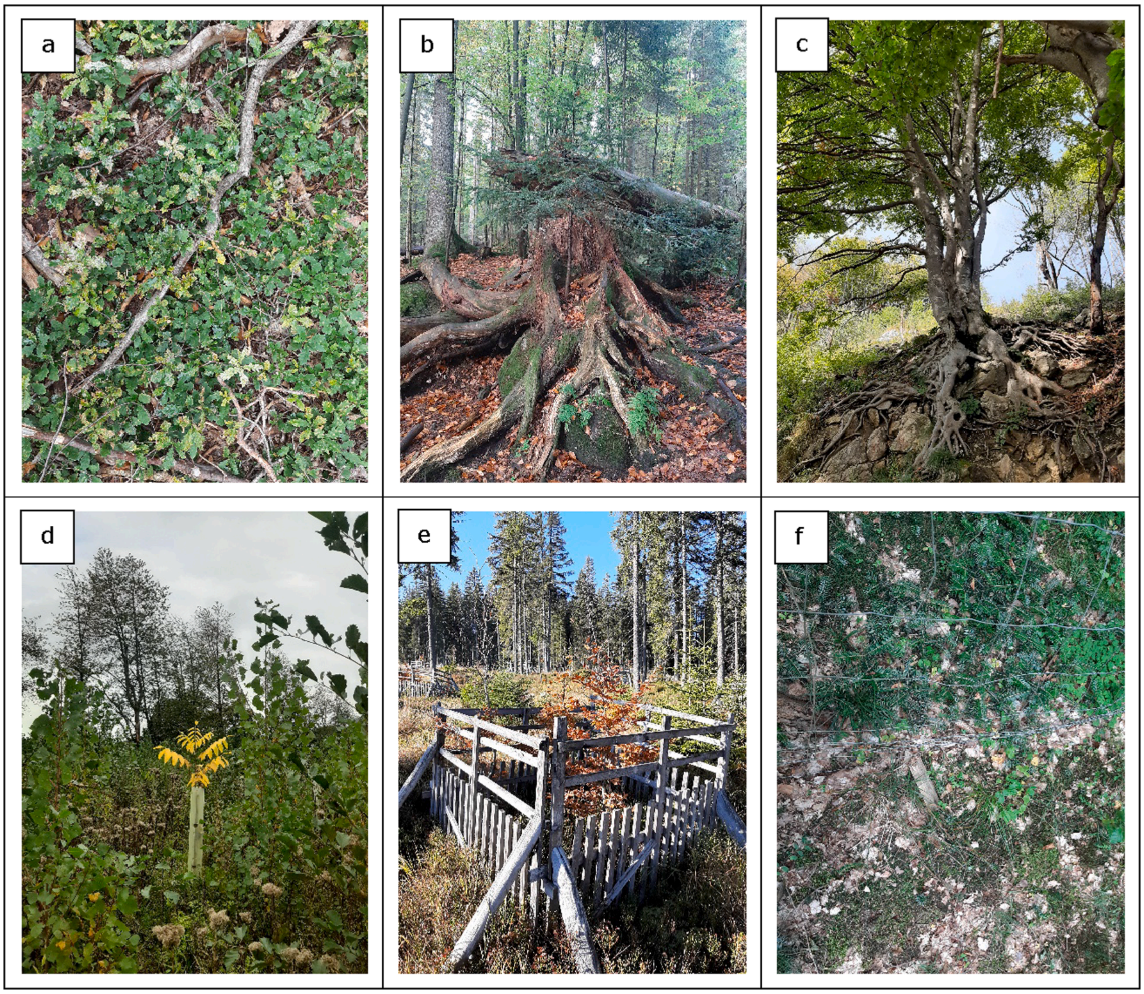


Fig. 3. Examples of forest regeneration: a) 2-year-old oak saplings after full mast b) silver fir regenerating on old trunk in a natural forest reserve c) rare case of resprouting beech in mountain coppice d) assisted migration of walnut in between natural poplar regeneration e) beech enrichment planting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

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., 2012), 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., 2012). 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 et al., 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.

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 (Iida & 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., 2012; 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 and 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., 2012). **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.

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 × 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 (Fig. 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 (Fig. 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 (Fig. 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).

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; Härkönen 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 land–atmosphere 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 yield models (hereafter G&Y; cf. model based on empirical relationships in Fig. 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 yield 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., 2012). 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 et al., 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), 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; Koven 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 (Penuelas et al., 2007) but more influential may be management shifts towards increasing the forests' adaptive capacity by introducing new, hitherto unobserved species (Fig. 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. Koven et al., 2020; Nabel et al., 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.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary material

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