



## Tree regeneration in models of forest dynamics: a key priority for further research

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Key words/phrases:	tree regeneration, tree recruitment, tree establishment, forest dynamics, models, landscape, stand, global, ingrowth, climate change
Abstract:	<p>Tree regeneration is a key process in forest dynamics, particularly in the context of forest resilience and climate change. Models are pivotal for assessing long-term forest dynamics, and they have been in use for more than 50 years. However, an assessment of their ability to accurately represent tree regeneration is lacking. We assess how well current models capture the overall abundance, species composition, and mortality of tree regeneration.</p> <p>Using 15 models built to capture long-term forest dynamics at the stand, landscape, and global levels, we simulate tree regeneration at 200 sites representing large environmental gradients across Central Europe. The results are evaluated against comprehensive data from unmanaged forests. <small>Please drop the word "comprehensive". it would have been comprehensive if the dataset contained information on all aspects of the regeneration process, but it only provides you with a means of evaluating recruitment past a 7 cm diameter threshold.</small></p> <p>Most of the models overestimate regeneration levels, which is only compensated in some models by high simulated mortality rates in the early stages of individual trees dynamics. Simulated species diversity of regeneration matches the observed ranges. Models simulating higher species diversity at the stand level do not feature higher regeneration diversity. The effect of light availability on regeneration levels is captured better than the effect of temperature and soil moisture, but patterns are not consistent across models. Increasing complexity in the tree regeneration modules of the models is not related to higher accuracy of simulated tree regeneration. Furthermore, individual model design is more important than scale (stand, landscape, global) and approach (empirical, process-based) for accurately capturing tree regeneration.</p> <p><small>I don't think your analyses support the argument that models capture essential feature.</small> Despite considerable mismatches between simulation results and data, it is remarkable that most models capture the essential features of the highly complex process of tree regeneration, while not having been parameterized with such data. We conclude that much can be gained by evaluating and refining the modeling of regeneration processes. This has the potential to render long-term projections of forest dynamics under changing environmental conditions that are much more robust.</p>

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# ***Tree regeneration in models of forest dynamics: a key priority for further research***

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**OPEN RESEARCH STATEMENT:** This submission uses novel code, both the data and code are provided in an external repository to be evaluated during the peer review process. The repository can be downloaded from [this figshare private link: https://figshare.com/s/100857ba67d2351dcb15](https://figshare.com/s/100857ba67d2351dcb15). The protocol is available at Díaz-Yáñez, Käber, and Bugmann (2022) ([with link: https://osf.io/czdxp/](https://osf.io/czdxp/)). We will make publicly available the code and data if the manuscript is accepted.

**Keywords:** tree regeneration | tree recruitment | tree establishment | forest dynamics | models | landscape | stand | global

# 1 Abstract

Tree regeneration is a key process in forest dynamics, particularly in the context of forest resilience and climate change. Models are pivotal for assessing long-term forest dynamics, and they have been in use for more than 50 years. However, an assessment of their ability to accurately represent tree regeneration **is lacking**. We assess how well current models capture the overall abundance, species composition, and mortality of tree regeneration.

Using 15 models built to capture long-term forest dynamics at the stand, landscape, and global levels, we simulate tree regeneration at 200 sites representing large environmental gradients across Central Europe. The results are evaluated against **comprehensive** data from unmanaged forests.

Most of the models overestimate regeneration levels, which is only compensated in some models by high simulated mortality rates in the early stages of individual trees dynamics. Simulated species diversity of regeneration matches the observed ranges. Models simulating higher species diversity at the stand level do not feature higher regeneration diversity. The effect of light availability on regeneration levels is captured better than the effect of temperature and soil moisture, but patterns are not consistent across models. Increasing complexity in the tree regeneration modules of the models is not related to higher accuracy of simulated tree regeneration. Furthermore, individual model design is more important than scale (stand, landscape, global) and approach (empirical, process-based) for accurately capturing tree regeneration.

Despite considerable mismatches between simulation results and data, it is remarkable that most models capture the essential features of the highly complex process of tree regeneration, while not having been parameterized with such data. We conclude that much can be gained by evaluating

69 and refining the modeling of regeneration processes. This has the potential to render long-term  
70 projections of forest dynamics under changing environmental conditions that are much more robust.

For Review Only

## 2 Introduction

Forests provide a wide range of products and services of vital importance to humankind (FOR-  
EST EUROPE 2020). Under the pressure of climate change, increasing disturbance impacts and  
changing societal demands on forest ecosystem services, it is becoming ever more important to un-  
derstand how forest structure, composition and function will change, and to evaluate forest capacity  
to adapt to or be resilient after disturbance (Lindner et al. 2010; Seidl and Turner 2022). A wide  
range of models of forest dynamics were developed over the past decades considering the impacts  
of climate (Bugmann and Seidl 2022). From these studies, it is evident that we have a reasonably  
good understanding how to model tree growth (J. K. Vanclay and Skovsgaard 1997; Bugmann et  
al. 1996), and substantial efforts have been dedicated to improving the representation of tree mor-  
tality (Bugmann et al. 2019; Cailleret et al. 2017). In contrast, tree regeneration is a much less  
studied process that is often represented rather coarsely in models (Walck et al. 2011; Leishman et  
al. 1992; Price et al. 2001). Which is a clear research gap in the context of climate-induced forest  
disturbances and forest resilience.

Tree regeneration arises from multiple processes including such as pollination, fruit maturation, seed produc-  
tion, dispersal, germination, juvenile growth and survival (Price et al. 2001; Vacchiano et al. 2018).  
All these processes are difficult to assess, and some of them are scarcely understood and thus ap-  
pear highly stochastic (Bogdziewicz et al. 2021). Identifying the appropriate level of complexity  
for the mathematical formulation of the key factors that are leading to successful tree regeneration  
is challenging. Currently, tree regeneration processes in dynamic forest models are handled in a  
multitude of ways (König et al. 2022; Bugmann and Seidl 2022): from 1) entirely ignoring it (as  
done in classical forest growth models, e.g., Pretzsch et al. 2002), across 2) the use of a few simple

environmental filters, as done in most forest “gap” models (Shugart 1984) and Dynamic Global Vegetation Models (e.g., Hickler et al. 2012; Smith, Prentice, and Sykes 2001a), to 3) complex approaches that incorporate local feedback from the canopy, multiple ecological processes and often also short time steps (e.g., Seidl et al. 2012; Wehrli et al. 2006), or 4) field-based statistical parameterizations, which however are not easy to extrapolate in space and time (e.g., Ribbens, Silander, and Pacala 1994).

Particularly given your conclusion that the models are poor at predicting regeneration processes, should we now return to statistical parameterisation afresh and find better ways of extrapolation/interpolation across space/time?

Overall, models are needed to (1) synthesize existing empirical data and explore their relationships, (2) assess future tree regeneration e.g. in the context of global change scenarios, and (3) identify the most important processes that are shaping ecological patterns. Given the current strategies that are used in models of forest dynamics to represent tree regeneration, model behavior often is prone to problems, such as very high levels of tree regeneration that necessitate excess mortality at early stages of tree life to simulate correct stand structure and composition. Also, inadequately high species diversity in tree regeneration may be simulated, which is characteristic of “classical” forest gap models (Gutiérrez, Snell, and Bugmann 2016), at least as long as the simulation set-up comprises a multitude of species. Some models use calibration against local canopy-level data to constrain simulated regeneration levels, which is likely to hamper the general applicability of these models e.g. under scenarios of climate change. Furthermore, correctly capturing the species composition in tree regeneration as a function of the presence of seed trees in the canopy is often a particular challenge, potentially leading to unrealistic successional drift in the model, which must be corrected by factors that are hard to parameterize (e.g., Lischke and Löffler 2006). A related issue is the excessive reduction of species diversity due to positive feedback effects, such that eventually just single-species stands remain. This is sometimes corrected by the incorporation of a low level of



seed influx of all species at all times ([Schumacher et al. 2006](#)) or by restricting the number of seeds per species in the seedbank ([Lischke and Löffler 2006](#)). However, simulated species composition is usually exceedingly sensitive to assumptions about seed availability, whereas the parameters of such functions are poorly constrained by field data. Lastly, there is often a problem with insufficient observational constraints on parameter values for models that start from very small tree sizes (e.g., 10 cm of height or even seeds) and track tree development in a process-oriented manner by considering a multitude of ecological influences, rather than emphasizing tree regeneration into a larger size class (e.g., [Wehrli et al. 2006](#)).

Thus, a focus on the modeling of tree regeneration processes is sorely needed and overdue ([Price et al. 2001](#); [Walck et al. 2011](#)) if we are to make reliable projections of future forest dynamics, i.e., when the models need to be operated in extrapolation mode, as well as from a fundamental ecological point of view for increasing systems understanding. Also in empirical ecology, tree regeneration has not received a lot of attention ([Hanbury-Brown, Ward, and Kueppers 2022](#)), although many sub-processes have been studied in detail ([Miina, Eerikäinen, and Hasenauer 2006](#)). Yet, little data are available that covers all the processes within one species along environmental gradients, let alone for a vast suite of species. Thus, the available data are fragmented, which constitutes a major problem for model building ([Clark et al. 1999](#)). On the one hand, monitoring on permanent plots (such as National Forest Inventories) often measures tree regeneration ([Zell et al. 2019](#)), however with a design that captures the rate after the stand initiation phase ([Hallsby et al. 2015](#)). Data from permanent plots, although available across regions, are highly heterogeneous, rendering their use difficult in a modeling context ([Käber et al. 2021](#)). On the other hand, targeted studies to measure tree regeneration on experimental sites are often limited in spatial extent, species

studied, or the sub-set of processes that are targeted (Berdanier and Clark 2016; Collet and Chenost 2006).

In the present study, for the first time, a large number of forest models commonly used to assess forest dynamics under climate change are evaluated against a continental-scale, multi-species harmonized dataset on tree regeneration (Käber et al. 2023). By tree regeneration, we refer to the passing of trees across a specific diameter threshold (“ingrowth”). We included models that are based on a range of “philosophies”, from models operating at the stand to the global scale as well as the range of models from empirically derived to “process-based” (e.g., Bugmann et al. 1996; M. Fabrika and Ďurský 2012; Lexer and Hönninger 2001; Reyer et al. 2014). Due to the large variability in tree regeneration patterns in nature and the large number of factors driving this process — including some that are not incorporated explicitly in most models, such as deer browsing — we do not aim for a detailed statistical evaluation of each model. Instead, we aim to evaluate the general regeneration patterns and magnitudes simulated by the models, and benchmark the simulated regeneration niche of multiple species against empirical data along a wide environmental gradient of temperature, moisture, and light availability (Grubb 1977).

More specifically, we aim to answer the following questions: (1) Are models of forest dynamics capturing accurately tree regeneration levels, initial tree species diversity and mortality in the regeneration? (2) Do model traits explain differences in model performance? (3) How well do the models capture total regeneration and individual species regeneration niches across environmental gradients of light availability, temperature, and soil moisture?

## 3 Material and methods

### 3.1 Models

Fifteen models of forest dynamics (including two models featuring model variants) were used to simulate forest dynamics at the stand, landscape or global scale (Table 1). The approaches used for model construction and their origin differ strongly, with most of the models featuring a largely “process-based” approach, whereas two models are based on formulations derived from the statistical analysis of inventory data (SIBYLA and xComp). Some of the models largely rely on the original approach underlying forest gap models (e.g., ForClim 1), whereas some are based on plant ecophysiological processes (e.g., FORMIND and iLand). The different approaches underlying the models have strongly influenced the formulation of tree regeneration processes.

The regeneration models can be differentiated into ‘regeneration’ and ‘recruitment’ approaches (Jerome K. Vanclay 1994; König et al. 2022). *Regeneration models* include processes such as flowering and pollination, seed production, seed dispersal, germination, and seedling growth, which ultimately lead to the simulated number of established trees. *Recruitment models*, in contrast, introduce a number of new trees with certain characteristics such as biomass or diameter, without explicitly considering earlier development processes. We can further distinguish models that feature a feedback in the regeneration, i.e., where the level and species composition of regeneration is influenced by the existing adult tree community via the production of seeds, seedlings or saplings, from models that do not contain such a feedback.

The starting point for tree regeneration in the models differs as well, ranging from seedbank, seed or seedling to sapling (i.e., trees much larger than 10 cm height, often ca. 2-3 m tall). Models

that start from seed need to include a larger number of ecological processes such as germination and survival of young seedlings, whereas models that start from saplings have to aggregate via parameterizations several ecological processes that are not treated explicitly. This latter approach reduces model complexity but comes at the cost of blurring process representation.

In the models used here, the overall complexity in the regeneration modules varies considerably. Following Bugmann and Seidl (2022), we can classify seven models (iLand, PICUS, LandClim, ForCEEPS, LPJ-GUESS, ForClim and TreeMig) as having rather high complexity in their regeneration modules (mean regeneration formulation complexity across all processes  $>0$ , Table 1). Two models, ForClim and ForCEEPS, were used here with two alternative variants of regeneration. ForClim variant 1 (Bugmann et al. 1996) is based on a recruitment module that adheres closely to the concept introduced by Botkin, Janak, and Wallis (1972), whereas ForClim variant 11 is adopting a different approach where individual species properties and their relation to the environment are important (Huber, Bugmann, and Lafond 2020). These two model variants allow us to evaluate a more process-based and complex module (variant 11) against a simple module (variant 1), while the rest of the model structure is identical. Similarly, the two ForCEEPS variants allow us to isolate the importance of the canopy feedback (i.e., simulated actual composition and relative abundance of species in the plot) via seed trees for the quantity and quality (e.g., diversity and composition) of simulated regeneration, as one variant includes this feedback whereas the other does not.

## 3.2 Observed data

Some of the large forest inventories include small seedlings and saplings in nested plots, which are a step in the right direction

Regeneration data covering a wide range of environmental conditions are hard to obtain, and this is one of the reasons why most models of forest dynamics have never been confronted with a dataset

covering such gradients over a large number of sites, to evaluate how well regeneration is captured.  
I don't feel "novel and unprecedented" adds anything to this sentence. There are plenty of networks outside Europe providing this sort of data

The observations used here are derived from a novel and unprecedented network of sites in forest reserves that represent the range of environmental gradients in temperature and precipitation in Central Europe as compiled in the framework of the EuFoRIa network (EuFoRIa 2019) (Figure 1). These forests have been unmanaged for at least 10 years prior to their designation as reserves, and most of them provide time series of natural forest dynamics over multiple decades and up to ca. 80 years. The census periods range from 3 to 37 years, with an average of 14 years. The data provide information at the tree level, thus allowing for the sequential comparison of processes such as individual-tree regeneration and death between the measurements.

COOL  
We selected 200 sites from this network as the benchmarking dataset for the simulation to be representative of the environmental variation contained in the data. This was achieved by applying k-means clustering to define 200 clusters of plots from the original set of 869 plots along the environmental dimensions of temperature, climatic water balance, soil quality and exposition (i.e., unfamiliar term to me slope and aspect). Each of these sites featured at least two consecutive measurements. Regeneration minimum size threshold? thresholds for these sites differed between diameters of 0 and 10 cm. For our study, we defined stem two datasets where one included 165 sites with a diameter threshold of 7 cm or lower, and the other OK, so we're talking about v large trees here included another 35 sites with diameter thresholds between 7 and 10 cm.

Plot size ranged from 0.02 ha to 5.52 ha, and the data were further processed and aggregated following Käber et al. (2023) to provide regeneration rates per ha and per decade. The observations so they are trees.... used in this study featured 30,900 newly established trees. Regeneration rates per site, sample and decade ranged from zero to 1246 trees, with a mean of 56 trees. Adult species composition was also available for each plot. For more details on this not so unique unique dataset and the detailed regeneration

in review and not available

information, cf. Käber et al. (2023).

### 3.3 Simulation protocol

The overarching goal of the <sup>simulation</sup> experiments was to assess ~~the~~ tree regeneration as it arises from empirical data against its representation in a wide range of models of forest dynamics. We define <sup>I suggest "tree recruitment" not "tree regeneration" here.</sup> ~~tree regeneration as the passing of a breast height diameter threshold of 7 or 10 cm,~~ <sup>??</sup> respectively (synonym: ingrowth). To this end, each modeling group was provided with a detailed protocol (Díaz-Yáñez, Käber, and Bugmann 2022) with instructions how to perform the simulations, <sup>provided with</sup> providing input variables on climate and soil conditions, and the list of expected output variables. <sup>These were "blind trials": modelling group were not provided with site information ...</sup> Neither were further site information (except for the data specified below) nor any data on tree regeneration or forest stand features provided prior to the simulation. ~~That is, the models were run in "blind flight" mode.~~

The input variables were collected from different data sources and aggregated to be adapted to the needs of the different models. Time series of climatic variables from 1981 to 2018 were provided in hourly (Era5-land data, Muñoz Sabater 2019), daily and monthly resolution (CHELSA data, Karger et al. 2021). Some variables required for some models, such as relative humidity or vapor pressure deficit, were calculated from these variables. The final instructions for using the climate data were slightly different in each model, based on the approach that best suited the model (Table 1). Soil <sup>?hydrological quality?</sup> quality data were provided as continuous values between 1 and 5 (Soilgrids dataset, Hengl et al. 2017). The protocol also provided the elevation, slope and aspect for each of the 200 sites (ASTER Science Team 2019), but no other spatial information such as coordinates, with the exception of iLand and aDGVM2, which required blurred coordinates to derive highly detailed soil data.

The simulations were run in the absence of natural disturbances. Only the model LPJ-GUESS had to include a background disturbance to increase chances of shade-intolerant species to establish. The simulations were set up to sample species-specific regeneration rates per decade and per ha in the equilibrium state of the model, typically entailing a “spin-up” run (as we did not provide any forest data). The modeling teams decided on the simulated area and how they derived these samples. The exact length of the simulation was also decided by the modeling teams (Table 1). Further details on how each modeling team prepared the simulations and the outputs are available in Supplementary Material 1.

The absence of disturbance and running to equilibrium set quite specific conditions; suggest this is emphasised more in abstract / intro / discussion.

The simulations were run in the absence of management to a simulated equilibrium (“Potential Natural Vegetation”) with the current climate, as the ultimate goal was to evaluate tree regeneration under comparable and near-equilibrium conditions. This entails the assumption that (1) the observations from the forest reserves reflect no traces of forest management, and (2) there is an equilibrium between forest dynamics and climate. While the former might be starting to be visible in many of the EuFoRIA reserves, the latter may be more debatable. However, in the absence of detailed data on the history of each plot in the EuFoRIA network, some broad assumptions had to be made. Both the width of the regeneration niche (i.e., in environmental space) as well as the intensity of the regeneration process (i.e., the number of ingrowth trees per area and per unit of time) were of interest.

The simulations were run for mixed-species forests (not multiple single-species simulations) using mixtures of eleven species or genera for which regeneration data of sufficient quality were available from EuFoRIA: *Fagus sylvatica* L., *Picea abies* L., *Abies alba* Mill., *Carpinus betulus* L., *Tilia cordata* Mill., *Acer pseudoplatanus* L., *Betula* spp. L., *Fraxinus excelsior* L., *Quercus* spp. L.,

264 *Alnus glutinosa* L., *Pinus sylvestris* L. The same set of species was used at all 200 sites. Two  
 265 models included their standard set of species for the simulations, which is much larger (i.e., ForClim  
 266 1, ForClim 11, TreeMig). In three models, fewer than these eleven species were simulated (4C,  
 267 xComp, LPJ-GUESS) (Table 1). In 4C only *Fagus sylvatica*, *Picea abies*, *Betula* spp., *Quercus* spp.  
 268 and *Pinus sylvestris* are parameterised. xComp simulations did not consider *Fraxinus excelsior*  
 269 due to a depreciated species parameterisation. In LPJ-GUESS, *Acer pseudoplatanus* and *Alnus*  
 270 *glutinosa* are not parameterized and therefore these species could not be included in the simulation.  
 271 Finally, the model aDGVM2 does not simulate individual species. Rather, community assembly  
 272 processes and trait filtering generate plant communities that are adjusted to the biotic and abiotic  
 273 conditions, and the simulated plants can be classified into ecological strategies based on their trait  
 274 values in a post-processing step.

regeneration number = number of "recruits" entering the 7-cm size class?

275 Each of the models reported the regeneration number by sampling 200 times in a 10-year interval  
 276 for each species and per ha for each of the 200 sites. Multiple samples per site were used to bet-  
 277 ter understand the simulated variation within each site. This was done using different strategies,  
 278 depending on the model, including (1) sampling simulated data from the same 1 ha plot in the equi-  
 279 librium over time, (2) sampling several 1 ha plots from the simulated forest at one specific point in  
 280 time (in the equilibrium) or (3) a combination of (1) and (2). This resulted in 880,000 observations  
 281 per model that simulated the 11 species included in the protocol (200 sites, 200 samples per site,  
 282 11 species and two diameter thresholds). For the models that simulated additional species, their  
 283 regeneration rates were aggregated as “others”.

284 Two models did not provide results from all the simulated samples or sites to avoid unrealistic re-  
 285 sults, as follows. In the model 4C, a threshold of a maximum basal area of  $90 \text{ m}^2 \text{ ha}^{-1}$  was used



to avoid unrealistic stand basal area data, and therefore not all the samples and sites were reported. The reason for this is that 4C is not suitable for long-term simulations without management, due to misrepresentations in density-dependent mortality processes in long-term simulations and assumptions of tree geometry that lead to unrealistic single tree dimensions of very old individuals. LPJ-GUESS had 2% of the sample outputs without tree regeneration, and these were considered as zero stand basal area and zero regeneration for all the tree species simulated; one site produced grassland rather than a forest and was not included in the results.

### 3.4 Data analysis

The simulation results were analyzed regarding (1) regeneration levels (i.e., ingrowth number per unit time and space), (2) regeneration species diversity, (3) regeneration mortality, (4) the relationship between model performance and model traits, and (5) ingrowth gradients along the regeneration niches. We evaluated species diversity across the models and in relation to the observed data by calculating the Shannon index  $H$  based on the relative proportion of the species in terms of basal area. It was calculated for the regeneration ( $H_{R_n}$ ) (Equation 1) and at the stand level ( $H_{S_{n,s}}$ ) (Equation 3). The higher the value of the index, the higher the species diversity at a particular site and sample.

not convinced these formulae need to be shown as the Shannon index is very well known. Consider converting the Shannon index to the effective number of species, by taking the negative of the SI and exponentiating it. This is gaining ground in ecology as it's more intuitive to interpret than SI (see paper by Jost).

$$H_{R_n} = - \sum_{i=1}^s p_{R_n,i} \ln(p_{R_n,i}) \quad (1)$$

$$p_{R_n,i} = \frac{r_{BA_{n,i}}}{TotalR_{BA_n}} \quad (2)$$

$$H_{S_n} = - \sum_{i=1}^s p_{S_n,i} \ln(p_{S_n,i}) \quad (3)$$

$$p_{S_n,i} = \frac{BA_{n,i}}{Total_{BA_n}} \quad (4)$$

where  $s$  is the total number of species present and that have a basal area larger than zero in sample  $n$ ;  $p_{R_{n,i}}$  is the proportion of species  $i$  in sample  $n$  calculated as the regeneration basal area ( $r_{BA_{n,i}}$ ) for that species  $i$  relative to total recruited basal area ( $TotalR_{BA_n}$ ) of the sample  $n$ ;  $p_{S_{n,i}}$  is the proportion of species  $i$  calculated as the basal area of all trees ( $BA_{n,i}$ ) of that species  $i$  relative to total basal area ( $TotalR_{BA_n}$ ) of the sample  $n$ . Species diversity was not assessed for aDGVM2 as this model does not simulate individual species.

now I understand the 7 and 10 cm thresholds mentioned earlier; please clarify earlier mention.

of recent recruits

Mortality in tree regeneration was assessed based on the ratio of regeneration between the 7 and 10 cm diameter thresholds. We used the Reineke self-thinning rule (Reineke 1933; Hans Pretzsch and Biber 2003) as a reference to estimate whether the ratio of regeneration between the 7 and 10 cm diameter thresholds were above or below the expected theoretical rate. The Reineke self-thinning rule is usually calculated for even-aged, single species stands and assumes a fixed relationship between the number of stems and the quadratic mean diameter in fully stocked pure stands. The value used in our comparisons was 1.77 (i.e., we expect stem numbers at 7 cm to be 77% higher than at 10 cm), calculated using Equation 5.

Suggest writing N7 / N10

$$Reineke = \frac{7}{10}^{-1.605} \quad (5)$$

Given my comment above, is there a strong justification for the -1.605 exponent? Or just keep it at one?

We assessed model performance in relation to model traits focusing on (1) model complexity as defined by Bugmann and Seidl (2022), (2) model type (empirical or process based), (3) the presence or absence of a canopy feedback for regeneration, and (4) the scale of application of the model (stand, landscape or global). We tested for significant differences using two-sided t-tests by considering each of these model features regarding the observed and simulated regeneration levels and species diversity, respectively.

Total regeneration and the regeneration niches of the individual species were evaluated across the environmental gradients of light availability, temperature, and soil moisture. Stand basal area (the basal area of all the trees in each sample including tree regeneration) was used as a proxy for light availability at the forest floor, the annual degree-day sum (Allen 1976; Fischlin, Bugmann, and Gyalistras 1995) as a proxy for growing season warmth, and the climatic water balance as a proxy for soil moisture (Speich 2019). Regeneration values were calculated as the mean across the 200 samples per site. The observed data were modeled using a Generalized Additive Model (Wood 2011) with a negative binomial distribution and restricted maximum likelihood to better understand the relationship between the environmental gradients and the levels of observed regeneration, relative to the simulation results per model.

In order to analyze the regeneration niches across the climatic gradients, we focused on five common tree species or genera: *Abies alba*, *Fagus sylvatica*, *Picea abies*, *Pinus sylvestris*, and *Quercus* spp. For these species, we calculated the share in the regeneration basal area per site as the mean across the available samples per site:

$$\bar{R}_{BA_{share_{t,i}}} = \frac{\bar{r}_{BA_{t,i}}}{\sum_{i=1}^s \bar{r}_{BA_{t,i}}} \quad (6)$$

where  $s$  is the total number of species simulated, and  $\bar{r}_{t,i}$  is the mean basal area in the regeneration (subsequently referred to as “regeneration basal area”) of species  $i$  per site  $t$  across the available samples at that site. Furthermore, regarding the share in the regeneration basal area per species ( $\bar{R}_{BA_{share_i}}$ ), we categorized this as zero when the regeneration basal area of that species ( $\bar{r}_{BA_{t,i}}$ ) was zero, but also when both the regeneration basal area of that species ( $\bar{r}_{BA_{t,i}}$ ) and the total regeneration basal area ( $\sum_{i=1}^s \bar{r}_{BA_{t,i}}$ ) equaled zero.

## 4 Results

### 4.1 Regeneration levels

Simulated regeneration levels varied strongly across the 15 models and typically did not match the levels found in the forest reserve data (Figure 2). Regeneration was overestimated in most models for both the 7 and 10 cm diameter thresholds, with the exception of the empirical stand model SIBYLA, the landscape model Landis-II and the global model aDGVM2, which estimated regeneration levels at the lower end of the plausibility interval of the observed data (Figure 2). The models with the largest overestimation were the stand model PICUS and the landscape model TreeMig. For most models, the variability of simulated regeneration levels across the 200 sites (visible from the interquartile range in the box plots of Figure 2) was similar to or smaller than observed, with the notable exception of PICUS, where simulated regeneration variability was much larger.

Both the observations and the simulated data had no regeneration in some samples and at some sites (for details, cf. Table S1). The observed data had 4% of the samples with no regeneration. Only

three models had a larger proportion of no regeneration (4C, Landis-II and aDVM2). Two models always simulated regeneration for both the 7 and 10 cm threshold (xComp and TreeMig), i.e., they did not feature any zero values. The other ten models had a very low percentage of samples with no regeneration (0.01% - 2.39%), i.e., they had distinctly fewer occurrences of zeros compared to the observations.

## 4.2 Tree species diversity of regeneration

Most models matched the level of diversity of the observed data quite well (Figure 3). Five models overestimated regeneration diversity: ForCEEPS, ForClim 1, PICUS, TreeMig and LandClim, the latter particularly for the 7 cm diameter threshold. The model 4C is a special case, as it simulated five species only, i.e., its diversity values are not directly comparable to those of the other models, nor to the observations. Only one model, Landis-II, consistently underestimated regeneration diversity.

In most models, there were only small but significant differences in the species diversity of regeneration between 7 and 10 cm across sites (Tables S2). Four models (iLand, Landis-II, TreeMig and LPJ-GUESS) maintained the regeneration diversity between the 7 and 10 cm thresholds (i.e., the differences between them were not significant, see Table S2), and the same was evident from the observed data.

For both the observed and the simulated data, and both regeneration thresholds, species diversity in the regeneration compared to stand-level diversity did not feature clear patterns across the models (Figures S1 and S2). Most models captured reasonably well or overpredicted species diversity at the stand level (Figure 4A, left and center; cf. Figure S3), but a characteristic feature was that

the simulations had a much lower variability of diversity compared to observations. Models overpredicting species diversity included ForClim1, ForClim 11, FORMIND and TreeMig (Figure 4A, left). Several models underpredicted species diversity, i.e., LPJ-GUESS, ForCEEPS(f) and 4C (Figure 4A, right).

The majority of the models overpredicted regeneration diversity; as already observed in Figure 3, only two of them underestimated it (4C and Landis-II) (Figure 4B and Figure S4). Both the models with feedback and those without feedback from the adult trees to regeneration (via seed production) overestimated, underestimated or captured reasonably well regeneration species diversity compared to the observations. Again, simulated diversity had considerably lower variability than observed diversity in the regeneration.

### 4.3 Mortality in tree regeneration

There were strong differences among the models regarding the mortality rate between 7 and 10 cm (Figure 5). Most of the models featured a mortality rate significantly larger than the observed data, thus at least partially compensating for the general overestimation of regeneration levels (Figure 2 and Table S3); six models did not feature a significant difference compared to the observed data (ForCEEPS, FORMIND, ForClim 1 and 11, iLand and aDGVM2). Four models (xComp, PICUS, LandClim and TreeMig) featured very high mortality rates (i.e., well above the Reineke self-thinning line), which compensated for the strong initial overestimation of regeneration (cf. Figure 2). Interestingly, two models that underestimated overall regeneration levels (SIBYLA and Landis-II; cf. Figure 2) featured mortality rates that were close to but still above the self-thinning line (Figure 5).

The fact that some models (and observed data) featured lower mortality than expected by Reineke's self-thinning rule may point to facilitation, or simply a higher mortality rate before the trees had reached 7 cm diameter. Yet, the case of models such as xComp, PICUS and TreeMig, whose mortality was well above the self-thinning line, indicates that they feature higher regeneration mortality in mixed-species forests compared to even-aged, single-species forests. Some models yielded a mortality rate of regeneration that is broadly compatible with the self-thinning rule (e.g., 4C and LandClim).

The three models with the largest overestimation of the proportion of regeneration at the 7 cm threshold featured the highest mortality between the 7 and 10 cm thresholds (Figure 6A). The other models that overestimated regeneration had mortalities lower than the expected self-thinning ratio, with the exception of LandClim (Figure 6B). It is noteworthy that most of the models that featured a low ratio of regeneration between 7 and 10 cm (i.e., ForCEEPS, ForClim 1, ForClim 11 and iLand) had only a small overestimation of regeneration at the 7 cm threshold (Figure 5). aDGVM2 was the only model that underestimated regeneration at the 7 cm threshold while featuring a low mortality between the two thresholds (Figure 6C), and only a few models were close to the correct regeneration levels at 7 cm while also being close to the Reineke line (SIBYLA, Landis-II; cf. Figure 6D; and 4C as well as LandClim).

Lastly, some models that had a low number of individuals at the 7 cm threshold also had a smaller decrease of regeneration between 7 and 10 cm (ratio 7-10 cm) (Figure S5). In these models, competition and self-thinning are either not pronounced or must have occurred before the trees had reached 7 cm. However, this pattern was not consistent across models (Figure S5). It is noteworthy that there is a relationship between the regeneration levels at 7 cm and the mortality rate (Table

S4): most of the models showed a positive effect (higher regeneration at 7 cm is coupled to an increase of the mortality between 7 and 10 cm). While some models showed a negative effect, the linear trend was not pronounced and not always significant regarding the slope.

#### 4.4 Model performance and model traits

There was no significant relationship between the mean complexity of the regeneration module (Table 1) and the overestimation proportion at a diameter threshold of 7 cm (Figure S6). All the models except 4C had significant differences between the observed and simulated mean regeneration values. Therefore it was not possible to differentiate in terms of performance between models type (empirical or process based), or their scales (stand, landscape or global) (Table S5). The values of regeneration species diversity simulated by each model were also assessed against the observed data to see if there was a difference between models that include a feedback compared to those that did not; all the models except ForCEEPs(f) and FORMIND had significant differences (Table S6). It is noteworthy that for the model ForCEEPS the pattern changed from the overprediction of species diversity in the regeneration to a diversity level that is closer to observations when the recruitment module included feedback (ForCEEPs(f)).

#### 4.5 Regeneration gradients on regeneration niches

When evaluating regeneration levels along key gradients of light availability (basal area), temperature (degree-days) and soil moisture (climatic water balance), distinct features emerged: the models reproduced the effect of basal area in both its magnitude and patterns (Figure 7 and S7) considerably better than the effects of the climatic gradients, where they featured varying patterns.



In the observed data, regeneration levels decreased clearly with increasing stand basal area (Figure 7a). This trend was captured by the Landis-II model only, albeit at much lower values of basal area than in the observations. The other models featured distinctly different trends, such as (1) an increase in regeneration levels with increasing total basal area followed by the absence of regeneration at high values of basal area (ForCEEPS, ForCEEPS(f), FORMIND, TreeMig and LPJ-GUESS), (2) almost constant regeneration levels with basal area (ForClim 11, xComp, LandClim and aDGVM2), or (3) an increase of regeneration up to a certain value of stand basal area followed by a decrease at even higher values of stand basal area, with model-specific thresholds (4C, ForClim 1, PICUS, SIBYLA and iLand).

The observed regeneration did not change much across the climatic water balance gradient, and showed a slight increase with temperature. The models did not match the observed regeneration patterns across the gradients of soil moisture and temperature (Figure 7b,c and S7), and neither was there a clear pattern across models. Regarding the soil moisture gradient, a group of models featured decreasing regeneration with increasing soil moisture (4C, ForClim 1, ForClim11, SIBYLA, xComp, PICUS, LandClim, TreeMig and iLand), while a few models showed the opposite trend (ForCEEPS(f), FORMIND and LPJ-GUESS). Across the temperature gradient, all the models that featured a decrease in regeneration levels with increasing soil moisture showed the opposite trend (i.e., more regeneration with increasing temperature), except for 4C. The other models did not feature a clear pattern.

Silver fir (*Abies alba*), beech (*Fagus sylvatica*), Scots pine (*Pinus sylvestris*) and oak (*Quercus* spp.) were the species observed most frequently in the EuFoRIa data. Most models captured well the share of basal area in the regeneration of these five species compared to the observed data along the

two major climatic gradients (Figure 8, cf. Figure S8). However, the models differed considerably in the way in which they simulated these climatic niches.

First, some models overestimated regeneration across the entire gradients of at least one of the five main tree species (Figure 8, e.g., ForCEEPS, ForCEEPS(f), LandClim or LPJ-GUESS), while other models overestimated regeneration of more than one species for a large part of the climate gradients, such as xComp, PICUS, SIBYLA or LPJ-GUESS (cf. red colors in Figure 8). These trends were consistent for both regeneration thresholds, although the exact changes in the share of the regeneration basal area were different (Figure S8).

Second, there was some congruence in the simulation results by species across the models. The share in the regeneration of Silver fir (*Abies alba*) was captured well across the gradient by most models except for xComp, PICUS, and LandClim, which overestimated the regeneration share of this species. There were also some peculiarities evident for some models, such as 4C that did not simulate *Abies alba*. The patterns across models for *Fagus sylvatica* regeneration were more complex, as its regeneration was underestimated by many models across the environmental gradients featuring negligible regeneration at most sites, while others overestimated it in different parts of the environmental space. Most models overestimated the share of *Picea abies* regeneration in the cold-wet part of the gradients. *Pinus sylvestris* and *Quercus* spp. represented a small share of the regeneration in the observed data mostly at warm-dry sites. Many models, however, erroneously featured regeneration for these two species along most of the climatic gradients, although with a low share of basal area. Five models (4C, FORMIND, SIBYLA, xComp, and LandClim) had almost no regeneration of *Pinus sylvestris* and *Quercus* spp., or did not feature any regeneration of these species at all.

Lastly, there is no model that performed well across the five species regarding the species-specific regeneration levels in the environmental space (Figure 8). Some models (e.g., ForClim11, PICUS) tended to consistently overestimate the regeneration share of all five species, but most models overestimated the regeneration share of some species while underestimating the share of others (e.g., ForCEEPS, LPJ-GUESS).

## 5 Discussion

Tree regeneration is a fundamental process in forest dynamics. Correctly capturing tree regeneration in dynamic models is fundamental to, for example, evaluate post-disturbance dynamics and potential long-term recovery trajectories as it will define the forest state in the first decades (Seidl and Turner 2022). If this initial phase is not captured well, we can not properly assess aspects such as forest resilience or the timing, magnitude and progression of carbon sequestration. In this study, for the first time, projections of tree regeneration from multiple models of forest dynamics were confronted with a unique dataset from unmanaged forest reserves across a large environmental gradient in Europe.

I think there are plenty of other datasets that could be used and have better information on smaller trees than EuFoRIa, so suggest a more nuanced sales pitch here.

The EuFoRIa data (Käber et al. 2023) are exceptional, particularly with respect to the number of records (number of sites and repeated measurements), which is essential for capturing a highly ‘noisy’ process such as tree regeneration. The use of this dataset for model benchmarking provided novel insights on the ability of state-of-the-art models to accurately simulate regeneration levels, species composition, and mortality in an early stage of tree life, i.e., between a tree diameter of 7 and 10 cm. Overall, by adopting this approach a much broader understanding resulted than if we

had used these data for model calibration: it is primarily from the shortcomings of the models that we can gain ecological insights (cf. [Trugman 2022](#)).

## 5.1 Regeneration levels

Most of the models overestimated tree regeneration levels. This has potentially far-reaching implications, e.g., regarding biomass (and thus carbon) turnover, with a potential overestimation of the capacity for forest carbon sequestration ([Pugh et al. 2019](#); [Pan et al. 2011](#)). Yet, we focused on one specific stage, i.e., regeneration into the 7 and 10 cm diameter classes. Trees at this size contribute little to carbon sequestration, and if the excess regeneration at this stage is compensated – in the models – soon thereafter by higher mortality, overall simulated regeneration may still yield trustworthy results at the level of stand structure and related forest attributes such as basal area or biomass.

From a modeling point of view, excess regeneration inevitably requires excess mortality rates in a later stage, either – as observed for some models – between the 7 and 10 cm diameter thresholds, or soon after the 10 cm threshold has been crossed. In any case, correcting at early stages for the expected forest densities at later stages is equivalent to compensating for a first error (excess regeneration) by a second error (excess mortality). It is highly likely that biased projections will result, because the two errors are unlikely to be perfectly linked and thus will not always compensate each other. Hence, this structural problem of most models investigated here is problematic particularly if the models are to be used under novel conditions such as under climate change (e.g., [Huber et al. 2021](#)) or in a decision support context (e.g., [Thrippleton et al. 2021](#)).

Regeneration levels define the structure and composition of future forests, but it is equally important

to correctly identify areas where regeneration is lacking (Rammer et al. 2021). There are multiple constraints to the regeneration niche of tree species (Price et al. 2001), and therefore the absence of regeneration is likely to be common (Fortin and DeBlois 2007), even over larger areas such as the one-hectare plots used here. Tree regeneration data are characterized by zero-inflation. This was clearly evident from the EuFoRIa dataset, but some of the models did not produce zeros at all, or featured a very low proportion of zero data. This substantial difference may be due to the fact that the simulation results were drawn from equilibrium forests, whereas in reality many of the forest reserves are recovering from past management activities and have become denser over the past decades (e.g., Heiri et al. 2009), leading to less regeneration than in an equilibrium situation.

But also --- browsing, establishment sites, competition with herb layer all reduce recruitment

## 5.2 Species composition of regeneration

Correctly capturing species composition in tree regeneration is important to assess the future functional diversity of a forest, e.g., its sensitivity to drought or resilience to disturbances (Redmond et al. 2015; Seidl and Turner 2022). In the simulations, overall species diversity levels in the regeneration were well within the observed range for half of the models (7 out of 14). Thus, while most of the models are facing difficulties to quantitatively match regeneration levels (cf. above), their performance is better when it comes to matching the composition of regeneration as a function of abiotic and biotic conditions. Most models maintained or even decreased regeneration diversity between the 7 and 10 cm thresholds, and the same is visible from the empirical data, but the differences were not significant. Diversity variations may be explained by the way the individual models consider regeneration processes (König et al. 2022), e.g., without considering the feedback from adults, regeneration can be linked to either seed rain from dispersal or a seed/seedling bank; neither

process is incorporated across many models studied here, however.

The species diversity of the entire stand was captured better by the models than the diversity of tree regeneration, and only a few models overpredicted stand-level diversity. Defining regeneration composition as being proportional to adult abundance, regardless of productivity, might be a simple and conservative assumption to safely maintain relative species abundances (Hanbury-Brown, Ward, and Kueppers 2022), although this may be simplistic. Furthermore, based on the simulation results, there is no evidence that models with feedback from the canopy captured better the species diversity of the regeneration than those without feedback, with the exception of ForCEEPS that significantly improved regeneration species diversity with the model version that included feedback (ForCEEPS(f)). The similar performance of models with and without feedback is likely because the models put more weight on the regeneration niche arising from abiotic and biotic filters, than from the habitat niche of the adult trees (Grubb 1977).

### 5.3 Regeneration mortality

There are several factors that lead to mortality during the regeneration phase, such as competition (Casper and Jackson 1997) and multiple abiotic factors (Schmid et al. 2021; Cunningham et al. 2006). As mentioned above, it is reasonable to expect that models that overestimate regeneration may have a particularly high mortality between the 7 and 10 cm thresholds. However, this was not consistently evident from the simulations. This implies that these models must have an excess mortality in later stages, if we assume that all models were able to capture the structure and composition of the adult stands along the EuFoRIa gradient; this however was not tested here.

Higher mortality towards the adult phase has important implications for forest dynamics and the

goods and services provided by forests. On the one hand, mortality in later stages may erroneously enhance the share of less shade tolerant species in the models (Klopčič, Simončič, and Bončina 2015), therefore shifting the species composition. Unrealistic high stem densities for a longer period of time may overestimate the role of tree regrowth in carbon sink dynamics (Pugh et al. 2019). Given our set of simulations and analyses, we cannot conclusively assess what is happening in the models, and further studies are required that focus on a wider range of tree sizes and the fate of tree regeneration along such a size continuum.

#### 5.4 Model performance and model traits

In spite of the critical considerations above, it is remarkable that most models did not deviate exceedingly from the observations with respect to simulated regeneration levels – after all, few if any of the models' regeneration routines are sufficiently constrained by data, with the exception of the empirical models xComp and SIBYLA. It is noteworthy that in spite of their empirical basis, these two models did not match empirical regeneration levels, in a similar magnitude as the other models and even in opposite directions (SIBYLA: underestimation; xComp: overestimation). It appears that using empirical data of limited geographical scope and constrained to managed forests, as done in these models, leads to extrapolation problems already under current climatic conditions. For the other models, whose regeneration modules are not strongly constrained by empirical data, the degrees of freedom that are available for modeling regeneration (König et al. 2022) could have implied that model performance would be much worse than what we found.

Surely more complex models WOULD be better if they captured the relevant processes! Arguing for simple vs complex models is a distraction here... we need models that are as simple as possible but not too simple..

Our study showed that increasing complexity in the regeneration modules is not linked with a higher accuracy of the projections of regeneration levels, species composition or mortality at early tree

stages, as there was no significant relationship between model performance and model complexity. Increasing complexity in regeneration modules has been motivated by better process understanding and enhancing of model accuracy (Bugmann and Seidl 2022). However, more complex models do not necessarily lead to better projections and rather to a reduced transparency and lower predictive power (Franklin et al. 2020). Thus, the question of what level of detail is appropriate and parsimonious for modeling tree regeneration processes remains open (König et al. 2022; Bugmann and Seidl 2022).

## 5.5 Regeneration gradients on regeneration niches

Competition for light as a strong filter for tree regeneration has been widely documented (Messier et al. 1999; Collet and Chenost 2006; Berdanier and Clark 2016), but the models examined here did not reproduce this expectation. However, it is difficult to measure light availability at large spatial and temporal scales. We used total stand basal area as a proxy for light availability (cf. Schmid et al. 2021). However, we were unable to consider light availability restrictions caused by ground vegetation, which may be an important filter for some EuForIa stands (Woltjer et al. 2008). We found pronounced differences in the stand basal area ranges simulated by the models, but also between models and observations. This made it impossible to evaluate the regeneration for the extremes of the stand density ranges in some models. For example, regeneration levels at low stand densities are relevant to assess how well forests are recovering e.g. after gap creation due to disturbance (Seidl and Turner 2022; Grubb 1977). At the level of the simulated one-hectare samples, average basal area is typically not very low as long as no larger disturbances occur, which was explicitly excluded in our simulation protocol. Towards the other end of the spectrum, i.e., with



increasing stand basal area, it would be reasonable to expect that the regeneration of the different species would become sparser and drop out entirely under low-light conditions (Klopčič, Poljanec, and Bončina 2012; Zell et al. 2019). However, few models showed this trend, thus indicating that the relation between regeneration and light availability is not yet captured correctly in most models. Yet, several of the models that did feature an increase of regeneration with increasing basal area include a feedback between seed production of mature trees and regeneration. Thus, it seems that higher light competition does not sufficiently compensate for increased seed availability with higher basal area due to a higher abundance of mature trees.

There were pronounced differences how the main tree species were represented by the models along the environmental gradients, in particular the dominant species *Abies alba*, *Fagus sylvatica* and *Picea abies*. The regeneration levels were sampled from simulations in the equilibrium, and in this state it is expected that non-climax species such as *Pinus sylvestris* or *Quercus* would be of minor importance, or absent (Klopčič, Simončič, and Bončina 2015). Most models captured this low abundance, which is also found in the empirical data. Thus, although the broad patterns are matched by many models, improvements in the quantification of the regeneration niche of the species are needed, but this cannot be done in the absence of robust datasets across multiple

## 5.6 Methodological considerations

The EuFoRIa data as used here are unique and well suited to better understand tree regeneration. However, three aspects of these data may represent considerable limitations. First, we made a comparison of tree regeneration in an equilibrium state, but we cannot assess how close the forests included in the EuFoRIa dataset were to such a state. The data were collected in forest reserves

where no management has taken place for long periods of time. This makes our assumption of an equilibrium between forest properties and environmental drivers more reasonable than it might appear at first sight. In an analysis of primeval forests at demographic equilibrium, Brzeziecki et al. (2021) found higher regeneration rates than the ones observed in the EuFoRia data. Thus, the overestimation of regeneration rates by the models may not be so problematic. Second, the data were collected for regeneration above a 7 cm threshold, thus limiting the assessment of tree regeneration to a holistic viewpoint. This constituted a hard limit based on which we can understand only some aspects of tree regeneration, which in its entirety often comprises a rather long period since seed production (Price et al. 2001). In reality, many environmental constraints are acting on young trees (Käber et al. 2021) that we were unable to assess. Yet, regeneration data with lower thresholds are simply not available in a harmonized manner across large environmental gradients. Third, the empirical data were collected from rather small plots, while we sampled simulated regeneration levels from 1 ha areas, which may lead to an incorrect representation of space. Even though the strategy we adopted is not ideal, it represents a common challenge when harmonizing diverse data sources originating from varied sampling strategies (Portier et al. 2022). It would have been extremely challenging for such a variety of models to follow a protocol where the spatial sampling size was different at each of the 200 sites, and it would have introduced additional uncertainty in the results. Ultimately, we need to acknowledge that the observed data represent just a snapshot of an extremely complex and stochastic reality. This may at least partly explain e.g. the lack of clear patterns in the simulation results along the gradients of climate water balance and degree-days.

The design of our sampling protocol did not include spatial aspects such as seed dispersal or detailed soil data. While we considered a wide range of models of forest dynamics, from stand to global

scales, the simulation setup was limited to 1 ha regeneration values. This lack of consideration of spatial scale is appropriate for stand-scale models, but it potentially puts the landscape models at a disadvantage, as they have been built to be accurate at the landscape level. Without spatial context, we are limiting regeneration to the seed influx from the stand itself, unless the model has a background seed input. Yet, the global models should not be at a disadvantage due to the limited spatial considerations (but cf. Snell et al. 2018; or Lehsten et al. 2019), as they are usually lacking dispersal between cells and are based on a strong abstraction of horizontal space (Hanbury-Brown, Ward, and Kueppers 2022). Lastly, detailed data on soil conditions were not available from the observed data, and independent, admittedly rather coarse data for soil and climatic water balance had to be used instead. It is noteworthy that many models represent drought based on detailed indicators based e.g. on soil water holding capacity, which had to be derived from a rough soil quality measure. This may at least partially explain the unsatisfactory performance of many models along the drought axis (i.e., climatic water balance).

## 5.7 Research recommendations

With our study, we have demonstrated that models of forest dynamics need a focus on tree regeneration modules to make them more robust. It remains uncertain what level of detail is required to model regeneration processes, and this must be addressed in future research. We recommend that the improvement of the regeneration modules is implemented as additional features that can be traced back, as done here for the variants of ForClim and ForCEEPS, and that model complexity and structure must always be connected with modeling objectives (Albrich et al. 2020). If it should be necessary to include more detail in the regeneration models, this will come with higher param-

673 eterisation efforts. This will most likely lead to lower generalization because the required data  
674 will have to be collected from specific locations, as currently there is no general, comprehensive  
675 regeneration dataset available.

676 Therefore, we further recommend that more effort should be invested into collecting harmonized  
677 [regeneration in what sense? Seedlings/ ground layer/ .... What is really needed?](#) datasets on tree regeneration. We emphasize that datasets such as EuFoRIa are invaluable and  
678 should be expanded in both their spatial extent (e.g., towards boreal and Mediterranean conditions)  
679 as well as in time (e.g., continuing the monitoring into the future). Such data will allow for a better  
680 evaluation of forest models and help to reduce the uncertainty in their projections, which is crucial  
681 when they are used as tools for predicting e.g. the impacts of anthropogenic climate change.

682 In the present study, we have considered tree regeneration in the equilibrium state only. It is equally  
683 important to understand how these models project tree regeneration after changes in forest structure  
684 by disturbances ([Seidl and Turner 2022](#)), or under different management strategies ([Lindner, Lasch,  
685 and Erhard 2000](#)). However, this will require an entirely [more akin to data already available in national inventories I think](#) different set of observed data, and poten-  
686 tially not all models of forest dynamics would be able to assess the relationship of these aspects on  
687 tree regeneration, e.g. due to the lack of disturbance or appropriate management modules.

688 We recommend to investigate in detail the implications of the current modeling strategies for tree  
689 regeneration and, ultimately, simulated forest stand structure. This applies particularly to the er-  
690 roneous patterns of excess tree regeneration and later excess mortality, by focusing on a wider  
691 range of tree sizes and the related regeneration dynamics. We also recommend, especially for the  
692 landscape-level models, the inclusion of explicit spatial considerations regarding tree regeneration  
693 ([Beckage and Clark 2003](#)); this, however, is a serious challenge regarding appropriate datasets, as  
694 inventory data have wide coverage, but by definition do not allow for the assessment of spatial

695 interaction effects.

Definition of blind flight "To do something based on guesswork, intuition, or without any help or instructions"....is that what you mean?

696 Exercises like the one presented here, where the models are operated in “blind flight” mode, i.e.,  
697 without the possibility of being tuned towards capturing the expected patterns, should be repeated.  
698 Such benchmarking exercises should next focus on aspects such as specific model traits and the  
699 ecological formulations of particular (sub-)processes, to better understand the implications of the  
700 assumptions on which the models are based. Furthermore, the inclusion of a wide range of models  
701 with different scales, type, population structures, tree regeneration modules and complexity will  
702 ensure a wider benefit to the whole modeling community.

## 703 **5.8 Conclusions**

704 Models of forest dynamics are important tools in science and decision support, and the formulation  
705 of tree regeneration has strong implications for simulated forest properties. The 15 models and  
706 variants used here are facing similar challenges in their representation of tree regeneration: they  
707 generally overestimate tree regeneration levels, and the simulated regeneration niche is not always  
708 captured accurately as a function of biotic (light) and abiotic (temperature and moisture) factors.

709 However, most models properly capture the diversity of the initial tree community, and differences  
710 between model formulations, e.g., the presence or absence of feedback from the adult trees, did not  
711 have a strong effect for capturing the species composition of regeneration.

712 Regarding mortality in the early phase of tree life, many models that feature a particularly high  
713 overestimation of regeneration levels are compensating for this by a larger tree mortality. Often,  
714 this compensation is not sufficient to reduce the high regeneration levels to realistic values. Overall,  
715 there is no clear mortality pattern across all models.

When capturing tree regeneration, the specific design decisions taken in the development of any model are more important for its behavior (accuracy) than scale (stand, landscape, global), modelling approach (empirical vs. process-based), and complexity. Having both empirical and process-based models in our set, the empirically-based models could have been expected to have a better performance, as they were calibrated with inventory data, but this was not the case. Similarly, higher model complexity does not represent an improvement for capturing tree regeneration.

Even though the regeneration routines of most of the models investigated here have never been sufficiently constrained by robust data, the regeneration projections are not overly off. This indicates that a lot can be gained by a focus on the modeling of regeneration processes. The representation of forest dynamics in these models would become much more robust particularly in the face of climate change and post-disturbance dynamics, thus strongly reducing the uncertainty in long-term projections of future forest dynamics.

## 6 Author contributions

O. Díaz-Yáñez and Y. Käber contributed equally and share the first authorship. H. Bugmann, Y. Käber, and O. Díaz-Yáñez developed the study design. All authors contributed to preparing the simulations with their respective models. O. Díaz-Yáñez led the data analysis with contributions during the workshop from Y. Käber, T. Anders, K. H. Braziunas, J. Bruna, S. M. Fischer, J. Hetzer, T. Hickler, H. Lischke, M. Mahnken, P. Mairota, K. Merganičová, T. Mette, X. Morin, W. Rammer and D. Scherrer H. Bugmann. O. Díaz-Yáñez and H. Bugmann led the writing of the manuscript. All authors participated in the revision of the manuscript and approved its submission.

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## 8 Conflict of interest statement

The authors declare no conflicts of interest.

## 9 References

- Albrich, Katharina, Werner Rammer, Monica G. Turner, Zak Ratajczak, Kristin H. Braziunas, Winslow D. Hansen, and Rupert Seidl. 2020. "Simulating Forest Resilience: A Review." Edited by Thomas Hickler. *Global Ecology and Biogeography* 29 (12): 2082–96. <https://doi.org/10.1111/geb.13197>.
- Allen, Jon C. 1976. "A Modified Sine Wave Method for Calculating Degree Days<sup>1</sup>." *Environmental Entomology* 5 (3): 388–96. <https://doi.org/10.1093/ee/5.3.388>.
- ASTER Science Team. 2019. "ASTER Global Digital Elevation Model V003. 2019, Distributed by NASA EOSDIS Land Processes DAAC, <https://doi.org/10.5067/ASTER/ASTGTM.003>. Accessed 2022-11-18." <https://lpdaac.usgs.gov/products/astgtmv002/>.
- Beckage, Brian, and James S. Clark. 2003. "SEEDLING SURVIVAL AND GROWTH OF THREE FOREST TREE SPECIES: THE ROLE OF SPATIAL HETEROGENEITY." *Ecology* 84 (7): 1849–61. [https://doi.org/10.1890/0012-9658\(2003\)084%5B1849:SSAGOT%5D2.0.CO;2](https://doi.org/10.1890/0012-9658(2003)084%5B1849:SSAGOT%5D2.0.CO;2).
- Berdanier, Aaron B., and James S. Clark. 2016. "Divergent Reproductive Allocation Trade-Offs with Canopy Exposure Across Tree Species in Temperate Forests." *Ecosphere* 7 (6): e01313. <https://doi.org/10.1002/ecs2.1313>.
- Bogdziewicz, Michał, Andrew Hacket-Pain, Dave Kelly, Peter A. Thomas, Jonathan Lageard, and Andrew J. Tanentzap. 2021. "Climate Warming Causes Mast Seeding to Break down by Reducing Sensitivity to Weather Cues." *Global Change Biology* 27 (9): 1952–61. <https://doi.org/10.1111/gcb.15560>.
- Bohn, Friedrich J., Karin Frank, and Andreas Huth. 2014. "Of Climate and Its Resulting Tree Growth: Simulating the Productivity of Temperate Forests." *Ecological Modelling* 278 (April):



9–17. <https://doi.org/10.1016/j.ecolmodel.2014.01.021>.

Botkin, Daniel B., James F. Janak, and James R. Wallis. 1972. “Some Ecological Consequences of a Computer Model of Forest Growth.” *The Journal of Ecology* 60 (3): 849. <https://doi.org/10.2307/2258570>.

Brzeziecki, Bogdan, Stanisław Drozdowski, Kamil Bielak, Marcin Czacharowski, Jacek Zajączkowski, Włodzimierz Buraczyk, and Leszek Gawron. 2021. “A Demographic Equilibrium Approach to Stocking Control in Mixed, Multiaged Stands in Białowieża Forest, Northeast Poland.” *Forest Ecology and Management* 481 (February): 118694. <https://doi.org/10.1016/j.foreco.2020.118694>.

Bugmann, Harald. 1996. “A Simplified Forest Model to Study Species Composition Along Climate Gradients.” *Ecology* 77 (7): 2055–74. <https://doi.org/10.2307/2265700>.

Bugmann, Harald, and Rupert Seidl. 2022. “The Evolution, Complexity and Diversity of Models of Long-Term Forest Dynamics.” *Journal of Ecology* 110 (10): 2288–2307. <https://doi.org/10.1111/1365-2745.13989>.

Bugmann, Harald, Rupert Seidl, Florian Hartig, Friedrich Bohn, Josef Brůna, Maxime Cailleret, Louis François, et al. 2019. “Tree Mortality Submodels Drive Simulated Long-Term Forest Dynamics: Assessing 15 Models from the Stand to Global Scale.” *Ecosphere* 10 (2): e02616. <https://doi.org/10.1002/ecs2.2616>.

Bugmann, Harald, Xiaodong Yan, Martin T. Sykes, Philippe Martin, Marcus Lindner, Paul V. Desanker, and Steve G. Cumming. 1996. “A Comparison of Forest Gap Models: Model Structure and Behaviour.” *Climatic Change* 34 (2). <https://doi.org/10.1007/BF00224640>.

Cailleret, Maxime, Steven Jansen, Elisabeth M. R. Robert, Lucía Desoto, Tuomas Aakala, Joseph A. Antos, Barbara Beikircher, et al. 2017. “A Synthesis of Radial Growth Patterns Preceding

- 801 Tree Mortality.” *Global Change Biology* 23 (4): 1675–90. <https://doi.org/10.1111/gcb.13535>.
- 802 Casper, Brenda B., and Robert B. Jackson. 1997. “Plant Competition Underground.” *Annual*
- 803 *Review of Ecology and Systematics* 28 (1): 545–70. [https://doi.org/10.1146/annurev.ecolsys.](https://doi.org/10.1146/annurev.ecolsys.28.1.545)
- 804 [28.1.545](https://doi.org/10.1146/annurev.ecolsys.28.1.545).
- 805 Clark, J. S., B. Beckage, P. Camill, B. Cleveland, J. HilleRisLambers, J. Lichter, J. McLachlan,
- 806 J. Mohan, and P. Wyckoff. 1999. “Interpreting Recruitment Limitation in Forests.” *American*
- 807 *Journal of Botany* 86 (1): 1–16. <https://doi.org/10.2307/2656950>.
- 808 Collet, C., and C. Chenost. 2006. “Using Competition and Light Estimates to Predict Diameter and
- 809 Height Growth of Naturally Regenerated Beech Seedlings Growing Under Changing Canopy
- 810 Conditions.” *Forestry* 79 (5): 489–502. <https://doi.org/10.1093/forestry/cpl033>.
- 811 Cunningham, Catherine, Niklaus E Zimmermann, Veronika Stoeckli, and Harald Bugmann. 2006.
- 812 “Growth Response of Norway Spruce Saplings in Two Forest Gaps in the Swiss Alps to Ar-
- 813 tificial Browsing, Infection with Black Snow Mold, and Competition by Ground Vegetation.”
- 814 *Canadian Journal of Forest Research* 36 (11): 2782–93. <https://doi.org/10.1139/x06-156>.
- 815 Díaz-Yáñez, Olalla, Yannek Käber, and Harald Bugmann. 2022. “Regeneration Workshop Proto-
- 816 col.” *OSF*. <https://doi.org/10.17605/OSF.IO/CZDXP>.
- 817 EuFoRIa. 2019. “European Forest Reserves Initiative. Link: <https://www.wsl.ch/de/Projekte/Euforia.html#tabel>
- 818 Tab2.”
- 819 Fabrika, M. 2005. “Simulátor Biodynamiky Lesa SIBYLA, Koncepcia, Konštrukcia a Programové
- 820 Riešenie.” *Zvolen, Slovakia, Habilitačná Práca, Technická Univerzita Vo Zvolene*.
- 821 Fabrika, M., and J. Ďurský. 2012. “Algorithms and Software Solution of Thinning Models for
- 822 SIBYLA Growth Simulator.” *Journal of Forest Science* 51 (No. 10): 431–45. [https://doi.org/](https://doi.org/10.17221/4577-JFS)
- 823 [10.17221/4577-JFS](https://doi.org/10.17221/4577-JFS).

- Fischer, Rico, Friedrich Bohn, Mateus Dantas de Paula, Claudia Dislich, Jürgen Groeneveld, Alvaro G. Gutiérrez, Martin Kazmierczak, et al. 2016. “Lessons Learned from Applying a Forest Gap Model to Understand Ecosystem and Carbon Dynamics of Complex Tropical Forests.” *Ecological Modelling* 326 (April): 124–33. <https://doi.org/10.1016/j.ecolmodel.2015.11.018>.
- Fischlin, Andreas, Harald Bugmann, and Dimitrios Gyalistras. 1995. “Sensitivity of a Forest Ecosystem Model to Climate Parametrization Schemes.” *Environmental Pollution* 87 (3): 267–82. [https://doi.org/10.1016/0269-7491\(94\)P4158-K](https://doi.org/10.1016/0269-7491(94)P4158-K).
- FOREST EUROPE. 2020. “State of Europe’s Forests 2020.” [who's the publisher?](#)
- Fortin, Mathieu, and Josianne DeBlois. 2007. “Modeling Tree Recruitment with Zero-Inflated Models: The Example of Hardwood Stands in Southern Québec, Canada.” *Forest Sciences* 53 (4): 529–39. <https://doi.org/10.1093/forestsience/53.4.529>.
- Franklin, Oskar, Sandy P. Harrison, Roderick Dewar, Caroline E. Farrior, Åke Brännström, Ulf Dieckmann, Stephan Pietsch, et al. 2020. “Organizing Principles for Vegetation Dynamics.” *Nature Plants* 6 (5): 444–53. <https://doi.org/10.1038/s41477-020-0655-x>.
- Grubb, P. J. 1977. “THE MAINTENANCE OF SPECIES-RICHNESS IN PLANT COMMUNITIES: THE IMPORTANCE OF THE REGENERATION NICHE.” *Biological Reviews* 52 (1): 107–45. <https://doi.org/10.1111/j.1469-185X.1977.tb01347.x>.
- Gutiérrez, Alvaro G., Rebecca S. Snell, and Harald Bugmann. 2016. “Using a Dynamic Forest Model to Predict Tree Species Distributions: Predicting Tree Species Distribution.” *Global Ecology and Biogeography* 25 (3): 347–58. <https://doi.org/10.1111/geb.12421>.
- Hallsby, Göran, Kristina Ahnlund Ulvcrona, Anders Karlsson, Björn Elfving, Hans Sjögren, Thomas Ulvcrona, and Urban Bergsten. 2015. “Effects of Intensity of Forest Regeneration Measures on Stand Development in a Nationwide Swedish Field Experiment.” *Forestry* 88

- (4): 441–53. <https://doi.org/10.1093/forestry/cpv010>.
- Hanbury-Brown, Adam R., Rachel E. Ward, and Lara M. Kueppers. 2022. “Forest Regeneration Within Earth System Models: Current Process Representations and Ways Forward.” *New Phytologist* 235 (1): 20–40. <https://doi.org/10.1111/nph.18131>.
- Heiri, C., A. Wolf, L. Rohrer, and H. Bugmann. 2009. “Forty Years of Natural Dynamics in Swiss Beech Forests: Structure, Composition, and the Influence of Former Management.” *Ecological Applications* 19 (7): 1920–34. <https://doi.org/10.1890/08-0516.1>.
- Hengl, Tomislav, Jorge Mendes de Jesus, Gerard B. M. Heuvelink, Maria Ruiperez Gonzalez, Milan Kilibarda, Aleksandar Blagotić, Wei Shangguan, et al. 2017. “SoilGrids250m: Global Gridded Soil Information Based on Machine Learning.” Edited by Ben Bond-Lamberty. *PLOS ONE* 12 (2): e0169748. <https://doi.org/10.1371/journal.pone.0169748>.
- Hickler, Thomas, Katrin Vohland, Jane Feehan, Paul A. Miller, Benjamin Smith, Luis Costa, Thomas Giesecke, et al. 2012. “Projecting the Future Distribution of European Potential Natural Vegetation Zones with a Generalized, Tree Species-Based Dynamic Vegetation Model: Future Changes in European Vegetation Zones.” *Global Ecology and Biogeography* 21 (1): 50–63. <https://doi.org/10.1111/j.1466-8238.2010.00613.x>.
- Huber, Nica, Harald Bugmann, Maxime Cailleret, Nicolas Bircher, and Valentine Lafond. 2021. “Stand-Scale Climate Change Impacts on Forests over Large Areas: Transient Responses and Projection Uncertainties.” *Ecological Applications* 31 (4). <https://doi.org/10.1002/eap.2313>.
- Huber, Nica, Harald Bugmann, and Valentine Lafond. 2020. “Capturing Ecological Processes in Dynamic Forest Models: Why There Is No Silver Bullet to Cope with Complexity.” *Ecosphere* 11 (5). <https://doi.org/10.1002/ecs2.3109>.
- Käber, Yannek, Christof Bigler, ..., and Harald Bugmann. 2023. “Sheltered and Suppressed: Tree

Regeneration in Unmanaged European Forests (Under Revision).” *Journal of Ecology*, December.

Käber, Yannek, Peter Meyer, Jonas Stillhard, Emiel De Lombaerde, Jürgen Zell, Golo Stadelmann, Harald Bugmann, and Christof Bigler. 2021. “Tree Recruitment Is Determined by Stand Structure and Shade Tolerance with Uncertain Role of Climate and Water Relations.” *Ecology and Evolution* 11 (17): 12182–203. <https://doi.org/10.1002/ece3.7984>.

Karger, Dirk N., Stefan Lange, Chantal Hari, Christopher P. O. Reyer, and Niklaus E. Zimmermann. 2021. “CHELSA-W5E5 V1.0: W5E5 V1.0 Downscaled with CHELSA V2.0. ISIMIP Repository. <https://doi.org/10.48364/ISIMIP.836809>.”

Klopčič, Matija, Ales Poljanec, and Andrej Bončina. 2012. “Modelling Natural Recruitment of European Beech (*Fagus Sylvatica* L.).” *Forest Ecology and Management* 284 (November): 142–51. <https://doi.org/10.1016/j.foreco.2012.07.049>.

Klopčič, Matija, Tina Simončič, and Andrej Bončina. 2015. “Comparison of Regeneration and Recruitment of Shade-Tolerant and Light-Demanding Tree Species in Mixed Uneven-Aged Forests: Experiences from the Dinaric Region.” *Forestry* 88 (5): 552–63. <https://doi.org/10.1093/forestry/cpv021>.

König, Louis A., Frits Mohren, Mart-Jan Schelhaas, Harald Bugmann, and Gert-Jan Nabuurs. 2022. “Tree Regeneration in Models of Forest Dynamics – Suitability to Assess Climate Change Impacts on European Forests.” *Forest Ecology and Management* 520 (September): 120390. <https://doi.org/10.1016/j.foreco.2022.120390>.

Langan, Liam, Steven I. Higgins, and Simon Scheiter. 2017. “Climate-Biomes, Peco-Biomes or Pyro-Biomes: Which World View Explains the Tropical Forest-Savanna Boundary in South America?” *Journal of Biogeography* 44 (10): 2319–30. <https://doi.org/10.1111/jbi.13018>.

- 893 Lasch-Born, Petra, Felicitas Suckow, Christopher P. O. Reyer, Martin Gutsch, Chris Kollas, Franz-  
894 Werner Badeck, Harald K. M. Bugmann, et al. 2020. "Description and Evaluation of the  
895 Process-Based Forest Model 4C V2.2 at Four European Forest Sites." *Geoscientific Model  
896 Development* 13 (11): 5311–43. <https://doi.org/10.5194/gmd-13-5311-2020>.
- 897 Lehsten, Veiko, Michael Mischurow, Erik Lindström, Dörte Lehsten, and Heike Lischke. 2019.  
898 "LPJ-GM 1.0: Simulating Migration Efficiently in a Dynamic Vegetation Model." *Geoscientific  
899 Model Development* 12 (3): 893–908. <https://doi.org/10.5194/gmd-12-893-2019>.
- 900 Leishman, Mr, L Hughes, K French, D Armstrong, and M Westoby. 1992. "Seed and Seedling  
901 Biology in Relation to Modelling Vegetation Dynamics Under Global Climate Change." *Australian  
902 Journal of Botany* 40 (5): 599. <https://doi.org/10.1071/BT9920599>.
- 903 Lexer, Manfred J, and Karl Hönninger. 2001. "A Modified 3D-Patch Model for Spatially Explicit  
904 Simulation of Vegetation Composition in Heterogeneous Landscapes." *Forest Ecology and  
905 Management*, 23.
- 906 Lindner, Marcus, Petra Lasch, and Markus Erhard. 2000. "Alternative Forest Management Strategies  
907 Under Climatic Change – Prospects for Gap Model Applications in Risk Analyses." *Silva  
908 Fennica* 34 (2). <https://doi.org/10.14214/sf.634>.
- 909 Lindner, Marcus, Michael Maroschek, Sigrid Netherer, Antoine Kremer, Anna Barbati, Jordi  
910 Garcia-Gonzalo, Rupert Seidl, et al. 2010. "Climate Change Impacts, Adaptive Capacity, and  
911 Vulnerability of European Forest Ecosystems." *Forest Ecology and Management* 259 (4):  
912 698–709. <https://doi.org/10.1016/j.foreco.2009.09.023>.
- 913 Lischke, Heike, and Thomas J. Löffler. 2006. "Intra-Specific Density Dependence Is Required to  
914 Maintain Species Diversity in Spatio-Temporal Forest Simulations with Reproduction." *Ecological  
915 Modelling* 198 (3-4): 341–61. <https://doi.org/10.1016/j.ecolmodel.2006.05.005>.

- Messier, Christian, René Doucet, Jean-Claude Ruel, Yves Claveau, Colin Kelly, and Martin J Lechowicz. 1999. “Functional Ecology of Advance Regeneration in Relation to Light in Boreal Forests” 29: 12.
- Mette, Tobias. 2014. “Modelling Patagonian Lenga-Forest Dynamics (*Nothofagus Pumilio*) in Chile. Final Report, DFG Project ME 3568/2-1, Bonn, Germany.”
- Miina, Jari, Kalle Eerikäinen, and Hubert Hasenauer. 2006. “Modeling Forest Regeneration. In: Hasenauer, h. (Eds.), Sustainable Forest Management. Growth Models for Europe (Pp. 93–110).” In.
- Morin, Xavier, Harald Bugmann, François Coligny, Nicolas Martin-StPaul, Maxime Cailleret, Jean-Marc Limousin, Jean-Marc Ourcival, et al. 2021. “Beyond Forest Succession: A Gap Model to Study Ecosystem Functioning and Tree Community Composition Under Climate Change.” Edited by Julia Koricheva. *Functional Ecology* 35 (4): 955–75. <https://doi.org/10.1111/1365-2435.13760>.
- Muñoz Sabater, J. 2019. “ERA5-Land Hourly Data from 1981 to Present. Copernicus Climate Change Service (C3S) Climate Data Store (CDS). (23.01.2022).” [doi:10.24381/cds.e2161bac](https://doi.org/10.24381/cds.e2161bac).
- Pan, Yude, Richard A. Birdsey, Jingyun Fang, Richard Houghton, Pekka E. Kauppi, Werner A. Kurz, Oliver L. Phillips, et al. 2011. “A Large and Persistent Carbon Sink in the World’s Forests.” *Science* 333 (6045): 988–93. <https://doi.org/10.1126/science.1201609>.
- Portier, Jeanne, Florian Zellweger, Jürgen Zell, Iciar Alberdi Asensio, Michal Bosela, Johannes Breidenbach, Vladimír Šebeň, Rafael O. Wüest, and Brigitte Rohner. 2022. “Plot Size Matters: Toward Comparable Species Richness Estimates Across Plot-Based Inventories.” *Ecology and Evolution* 12 (6). <https://doi.org/10.1002/ece3.8965>.
- Pretzsch, Hans, and Peter Biber. 2003. “A Re-Evaluation of Reineke’s Rule and Stand Density

- Index.” *Forest Sciences* 51 (4): 304–20. <https://doi.org/10.1093/forestsience/51.4.304>.
- Pretzsch, H., P. Biber, and J. Ďurský. 2002. “The Single Tree-Based Stand Simulator SILVA: Construction, Application and Evaluation.” *Forest Ecology and Management* 162 (1): 3–21. [https://doi.org/10.1016/S0378-1127\(02\)00047-6](https://doi.org/10.1016/S0378-1127(02)00047-6).
- Price, David T, Niklaus E Zimmermann, Manfred J Lexer, Paul Leadley, Irma T M Jorritsma, Jörg Schaber, Donald F Clark, et al. 2001. “Regeneration in Gap Models: Priority Issues for Studying Forest Responses to Climate Change” 51: 34.
- Pugh, Thomas A. M., Mats Lindeskog, Benjamin Smith, Benjamin Poulter, Almut Arneth, Vanessa Haverd, and Leonardo Calle. 2019. “Role of Forest Regrowth in Global Carbon Sink Dynamics.” *Proceedings of the National Academy of Sciences* 116 (10): 4382–87. <https://doi.org/10.1073/pnas.1810512116>.
- Rammer, Werner, Kristin H. Braziunas, Winslow D. Hansen, Zak Ratajczak, Anthony L. Westerling, Monica G. Turner, and Rupert Seidl. 2021. “Widespread Regeneration Failure in Forests of Greater Yellowstone Under Scenarios of Future Climate and Fire.” *Global Change Biology* 27 (18): 4339–51. <https://doi.org/10.1111/gcb.15726>.
- Redmond, Miranda D., Neil S. Cobb, Michael J. Clifford, and Nichole N. Barger. 2015. “Woodland Recovery Following Drought-Induced Tree Mortality Across an Environmental Stress Gradient.” *Global Change Biology* 21 (10): 3685–95. <https://doi.org/10.1111/gcb.12976>.
- Reineke, L. H. 1933. “PERFECTING A STAND-DENSITY INDEX FOR EVEN-AGED FORESTS’,” 12.
- Reyer, Christopher, Petra Lasch-Born, Felicitas Suckow, Martin Gutsch, Aline Murawski, and Tobias Pilz. 2014. “Projections of Regional Changes in Forest Net Primary Productivity for



Different Tree Species in Europe Driven by Climate Change and Carbon Dioxide.”

Ribbens, Eric, John A. Silander, and Stephen W. Pacala. 1994. “Seedling Recruitment in Forests: Calibrating Models to Predict Patterns of Tree Seedling Dispersion.” *Ecology* 75 (6): 1794–1806. <https://doi.org/10.2307/1939638>.

Scheiter, Simon, and S. I. Higgins. 2009. “Impacts of Climate Change on the Vegetation of Africa: An Adaptive Dynamic Vegetation Modelling Approach.” *Global Change Biology*.

Scheiter, Simon, Liam Langan, and Steven I. Higgins. 2013. “Next-Generation Dynamic Global Vegetation Models: Learning from Community Ecology.” *New Phytologist* 198 (3): 957–69. <https://doi.org/10.1111/nph.12210>.

Scheller, Robert M., James B. Domingo, Brian R. Sturtevant, Jeremy S. Williams, Arnold Rudy, Eric J. Gustafson, and David J. Mladenoff. 2007. “Design, Development, and Application of LANDIS-II, a Spatial Landscape Simulation Model with Flexible Temporal and Spatial Resolution.” *Ecological Modelling* 201 (3-4): 409–19. <https://doi.org/10.1016/j.ecolmodel.2006.10.009>.

Schmid, Ueli, Christof Bigler, Monika Frehner, and Harald Bugmann. 2021. “Abiotic and Biotic Determinants of Height Growth of *Picea Abies* Regeneration in Small Forest Gaps in the Swiss Alps.” *Forest Ecology and Management* 490 (June): 119076. <https://doi.org/10.1016/j.foreco.2021.119076>.

Schumacher, Sabine, Björn Reineking, Jason Sibold, and Harald Bugmann. 2006. “Modeling the Impact of Climate and Vegetation on Fire Regimes in Mountain Landscapes.” *Landscape Ecology* 21 (4): 539–54. <https://doi.org/10.1007/s10980-005-2165-7>.

Seidl, Rupert, Werner Rammer, Robert M. Scheller, and Thomas A. Spies. 2012. “An Individual-Based Process Model to Simulate Landscape-Scale Forest Ecosystem Dynamics.” *Ecological*

- 985     *Modelling* 231 (April): 87–100. <https://doi.org/10.1016/j.ecolmodel.2012.02.015>.
- 986     Seidl, Rupert, and Monica G. Turner. 2022. “Post-Disturbance Reorganization of Forest Ecosys-
- 987     tems in a Changing World.” *Proceedings of the National Academy of Sciences* 119 (28):
- 988     e2202190119. <https://doi.org/10.1073/pnas.2202190119>.
- 989     Shugart, Herman Henry. 1984. *A Theory of Forest Dynamics. The Ecological Implications of*
- 990     *Forest Succession Models*. NY, USA: Springer-Verlag.
- 991     Smith, Benjamin, I. Colin Prentice, and Martin T. Sykes. 2001a. “Representation of Vegetation
- 992     Dynamics in the Modelling of Terrestrial Ecosystems: Comparing Two Contrasting Approaches
- 993     Within European Climate Space: *Vegetation Dynamics in Ecosystem Models*.” *Global Ecology*
- 994     *and Biogeography* 10 (6): 621–37. <https://doi.org/10.1046/j.1466-822X.2001.t01-1-00256.x>.
- 995     ———. 2001b. “Representation of Vegetation Dynamics in the Modelling of Terrestrial Ecosys-
- 996     tems: Comparing Two Contrasting Approaches Within European Climate Space: *Vegetation*
- 997     *Dynamics in Ecosystem Models*.” *Global Ecology and Biogeography* 10 (6): 621–37. <https://doi.org/10.1046/j.1466-822X.2001.t01-1-00256.x>.
- 998
- 999     Snell, Rebecca S., Ché Elkin, Sven Kotlarski, and Harald Bugmann. 2018. “Importance of Climate
- 1000     Uncertainty for Projections of Forest Ecosystem Services.” *Regional Environmental Change*
- 1001     18 (7): 2145–59. <https://doi.org/10.1007/s10113-018-1337-3>.
- 1002     Speich, Mjr. 2019. “Quantifying and Modeling Water Availability in Temperate Forests: A Review
- 1003     of Drought and Aridity Indices.” *iForest - Biogeosciences and Forestry* 12 (1): 1–16. <https://doi.org/10.3832/ifor2934-011>.
- 1004
- 1005     Thrippleton, Timothy, Clemens Blattert, Leo Gallus Bont, Reinhard Mey, Jürgen Zell, Esther
- 1006     Thürig, and Janine Schweier. 2021. “A Multi-Criteria Decision Support System for Strategic
- 1007     Planning at the Swiss Forest Enterprise Level: Coping With Climate Change and Shifting

Demands in Ecosystem Service Provisioning.” *Frontiers in Forests and Global Change* 4 (August): 693020. <https://doi.org/10.3389/ffgc.2021.693020>.

Trugman, Anna T. 2022. “Integrating Plant Physiology and Community Ecology Across Scales Through Trait-Based Models to Predict Drought Mortality.” *New Phytologist* 234 (1): 21–27. <https://doi.org/10.1111/nph.17821>.

Vacchiano, Giorgio, Davide Ascoli, Fabio Berzaghi, Manuel Esteban Lucas-Borja, Thomas Caig-nard, Alessio Collalti, Paola Mairota, et al. 2018. “Reproducing Reproduction: How to Sim-ulate Mast Seeding in Forest Models.” *Ecological Modelling* 376 (May): 40–53. <https://doi.org/10.1016/j.ecolmodel.2018.03.004>.

Vanclay, J. K., and J. P. Skovsgaard. 1997. “Evaluating Forest Growth Models.” *Ecological Mod-elling* 98 (1): 1–12. [https://doi.org/10.1016/S0304-3800\(96\)01932-1](https://doi.org/10.1016/S0304-3800(96)01932-1).

Vanclay, Jerome K. 1994. *Modelling Forest Growth and Yield: Applications to Mixed Tropical Forests*. Wallingford, U.K: CAB International.

Walck, Jeffrey L., Siti N. Hidayati, Kingsley W. Dixon, Ken Thompson, and Peter Poschlod. 2011. “Climate Change and Plant Regeneration from Seed.” *Global Change Biology* 17 (6): 2145–61. <https://doi.org/10.1111/j.1365-2486.2010.02368.x>.

Wehrli, A., P. J. Weisberg, W. Schönenberger, P. Brang, and H. Bugmann. 2006. “Improving the Establishment Submodel of a Forest Patch Model to Assess the Long-Term Protective Effect of Mountain Forests.” *European Journal of Forest Research* 126 (1): 131–45. <https://doi.org/10.1007/s10342-006-0142-6>.

Woltjer, M., W. Rammer, M. Brauner, R. Seidl, G. M. J. Mohren, and M. J. Lexer. 2008. “Cou-pling a 3D Patch Model and a Rockfall Module to Assess Rockfall Protection in Mountain Forests.” *Journal of Environmental Management* 87 (3): 373–88. <https://doi.org/10.1016/j>.

1031 [jenvman.2007.01.031](#).

1032 Wood, S N. 2011. “Fast Stable Restricted Maximum Likelihood and Marginal Likelihood Estima-  
1033 tion of Semiparametric Generalized Linear Models.” *Journal of the Royal Statistical Society*  
1034 73 (1): 3–36. <https://doi.org/doi.org/10.1111/j.1467-9868.2010.00749.x>.

1035 Zell, Jürgen, Brigitte Rohner, Esther Thürig, and Golo Stadelmann. 2019. “Modeling Ingrowth  
1036 for Empirical Forest Prediction Systems.” *Forest Ecology and Management* 433 (February):  
1037 771–79. <https://doi.org/10.1016/j.foreco.2018.11.052>.

For Review Only

1038 **10 Table**

For Review Only

A useful table. I'd encourage the authors to write a lengthier table heading, which briefly summarises the methods section, so that readers can know what "start from", "runtime for sampling" mean without having to delve into the text. Also I'd like to see an explanation of "formulation complexity" in the text and here. The supplementary information gives more details about model assumptions, and I do wonder whether those could be included here; in particular, seed production and dispersal is clearly important for regeneration, so could columns be introduced to compare assumptions of model with respect to these. Also deer browsing, herb-layers and nurse logs all have an influence of regeneration, but not incorporated into these models; I suggest the table heading makes that clear.

Table 1: Models included and their characteristics.

Model	Scale(a)	Type(b)	Population structure(c)	Feedback	Start from(d)	Mean regeneration formulation complexity (Bugmann & Seidl 2022)	Species simulated	Runtime for sampling (spin up) [years]	Climate data type (use of years)	Reference(e)
4C	S	PB	C	N	saplings	-0.04	F. sylvatica, P. sylvestris, P. abies, Betula spp., Quercus spp.	2000 (500)	D (loop)	Lasch-Born et al. (2020)
ForClim	S	PB	C	N	ingrowth	0.28 (ForClim 4.0.1)	All	200 (1000)	M (weather generator)	Bugmann (1996)
ForCEEPS	S	PB	I	N / Y (f)	saplings	0.43	All	2000 (2000)	M (random)	Morin et al. (2021)
FORMIND	S	PB	I	N	ingrowth	-0.57	All	12000 (1000)	D (random)	Bohn et al. (2014) and Fischer et al. (2016)
PICUS	S	PB	I	Y	seeds	0.81	All	2000 (600)	M (random)	Lexer & Hönninger (2001)
SIBYLA	S	EM	I	Y	seeds	NA	All	2500 (500)	M (weather generator)	Fabrika (2005)
xComp	S	EM	I	Y	seedlings	NA	All (-F. excelsior, -A. glutinosa)	2000 (750)	M (random)	Mette (2014)
iLand	L	PB	I	Y	seeds	1.08	All	510 (1500)	D (random)	Seidl et al. (2012)
LandClim	L	PB	C	Y	ingrowth	0.5	All	2000 (2000)	M (random)	Schumacher et al. (2006)
Landis-II	L	PB	C	Y	saplings	-0.1	All	1280 (700)	M (random)	Scheller et al. (2007)
TreeMig	L	PB	C	Y	seedbank	0.12	All	100 (900)	M (random)	Lischke et al. (2006)
LPJ-GUESS	G	PB	C	Y	saplings	0.35	All (-A. pseudo-platanus, -A. glutinosa)	37 (500)	D (loop)	Smith et al. (2001) and Hickler et al. (2012)
aDGVM2	G	PB	I	Y	seedbank	-0.08	Ecological strategies	37 (600)	D (loop)	Langan et al. (2017) and Scheiter et al. (2013)

<sup>a</sup> S-Stand, L-Landscape, G-Global  
<sup>b</sup> PB-Process based, EM-Empirical  
<sup>c</sup> C-Cohort, I-Individual  
<sup>d</sup> Y-Yes, N-No  
<sup>e</sup> D-Daily, M-Monthly

52

## 11 Figure captions

**Figure 1.** The 200 sites of the EuFoRIa network (EuFoRIa, 2019) used in the present study, the colors show the dominant tree species per site in the observed regeneration at the 10 cm threshold.

**Figure 2.** Mean regeneration levels across all samples per site, plotted for the 200 sites and for each model. The red dashed lines shows the 25th and 75th percentiles for the 7 cm diameter threshold in the observed data. There are two boxplots for each model where the left lighter boxplot corresponds to 7 cm and the right darker boxplot to 10 cm

**Figure 3.** Shannon index of tree regeneration, calculated by basal area, as the mean value across the 200 samples per site for the diameter thresholds of 7 and 10 cm, respectively. The red dashed lines shows the 25th and 75th percentiles for the 7 cm diameter threshold in the observed data.

**Figure 4.** Mean Shannon index across all samples per site for observed and simulated data. Each plot shows one pattern represented by one exemplary model of each category (overpredicted, intermediate and underpredicted). The full data with the grouping of the models are shown in Figures S3 and S4. n indicates the number of models falling in each group. A) Examples for the three trends across models for species diversity at the stand level. B) Examples for the three trends across models for regeneration at the 7 cm threshold.

**Figure 5.** Ratio of tree regeneration rates between the 7 and 10 cm thresholds. Dashed blue lines mark a ratio equal to 1, indicating no decrease in tree regeneration between 7 and 10 cm, and a ratio equal to 1.77, corresponding to the Reineke self-thinning ratio under even-aged conditions.

**Figure 6.** Ratio of tree regeneration between the 7 and 10 cm thresholds (regeneration 7 cm / regeneration 10 cm) and the overestimation proportion at 7 cm ( $[\text{simulated} - \text{observed}] / \text{observed}$ )

for the mean regeneration per model across sites and samples. The horizontal dashed lines show a ratio equal to 1, indicating no decrease of regeneration between 7 and 10 cm, and a ratio equal to 1.77 corresponding to the Reineke self-thinning line under even-aged conditions. The vertical line indicates zero overestimation.

**Figure 7.** Mean regeneration values across the 200 samples per site with the y-axis scaled differently by model, for the 200 sites against gradients of (a) total basal area; (b) climatic water balance; (c) seasonal degree-day sum. The values were split into ten bins; the red lines represent a GAM model showing the trend in the observed data. For comparing the magnitude of recruitment across models the same graphs with equally scaled y-axis can be found in Figure S7.

**Figure 8.** Regeneration levels of the five main species in terms of their basal area share in the observations (top row) and the performance of each model across the environmental gradients (other rows) for the 7 cm regeneration threshold. The values shown are the mean of the 200 samples per site and across the sites in each bin (tile), with ten bins per gradient. The sizes of the circles represent the ratio between the regeneration basal area of the species and the total regeneration basal area for all species. The absence of a circle indicates a zero basal area share in the regeneration, or the absence of regeneration altogether. The color gradient (for the models only) shows the difference between the simulated and observed ratio of regeneration basal area of the species and the total regeneration basal area for all the species.

[Explain the fitted curves](#)



12 Figures

1078

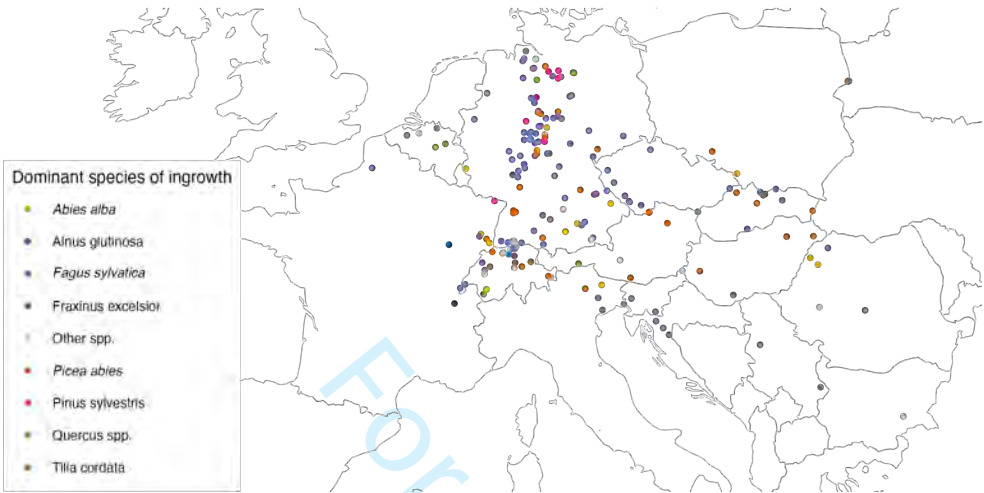


Figure 1: .

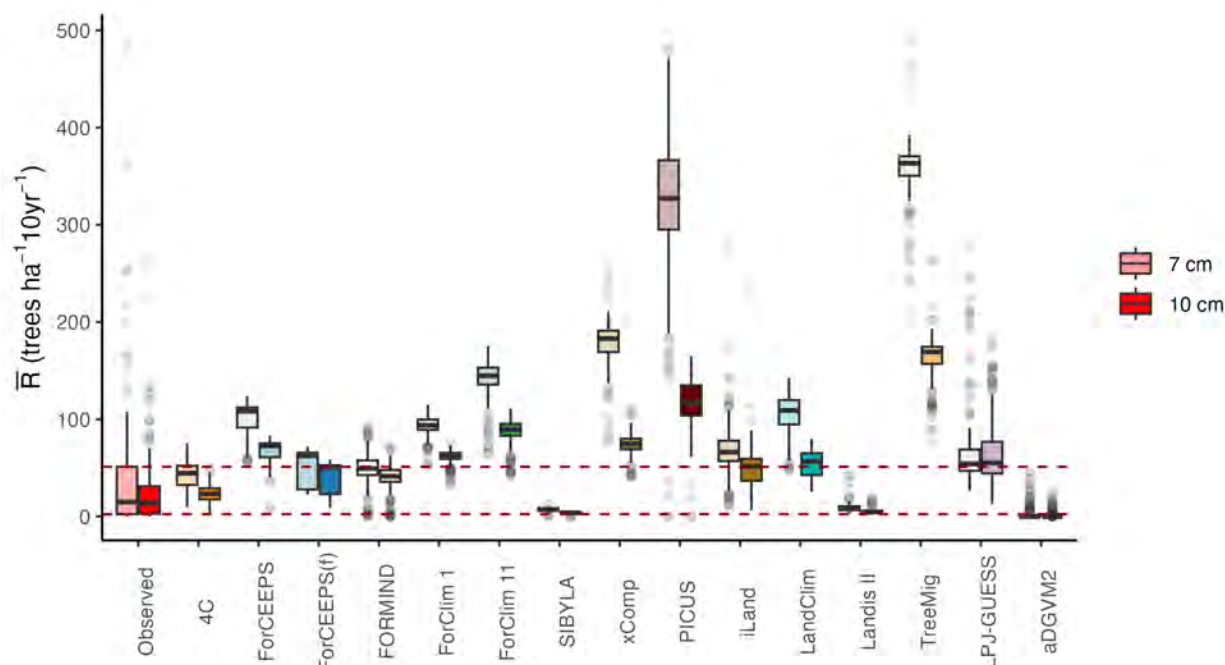


Figure 2: .

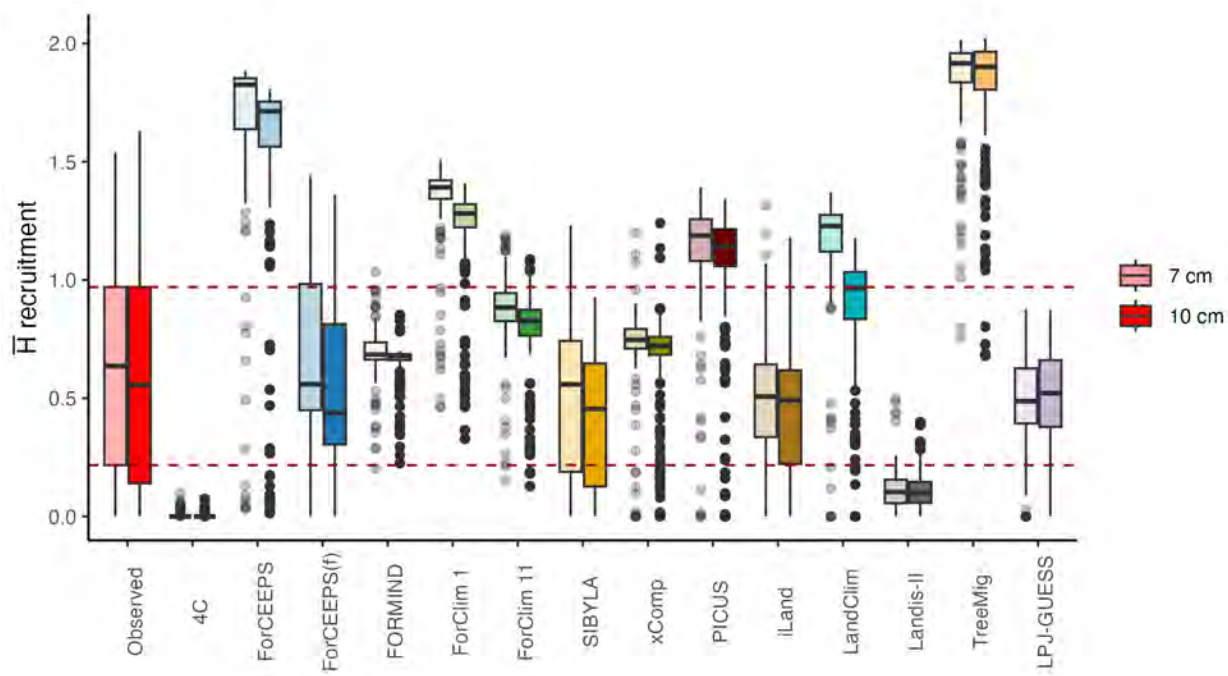


Figure 3: .

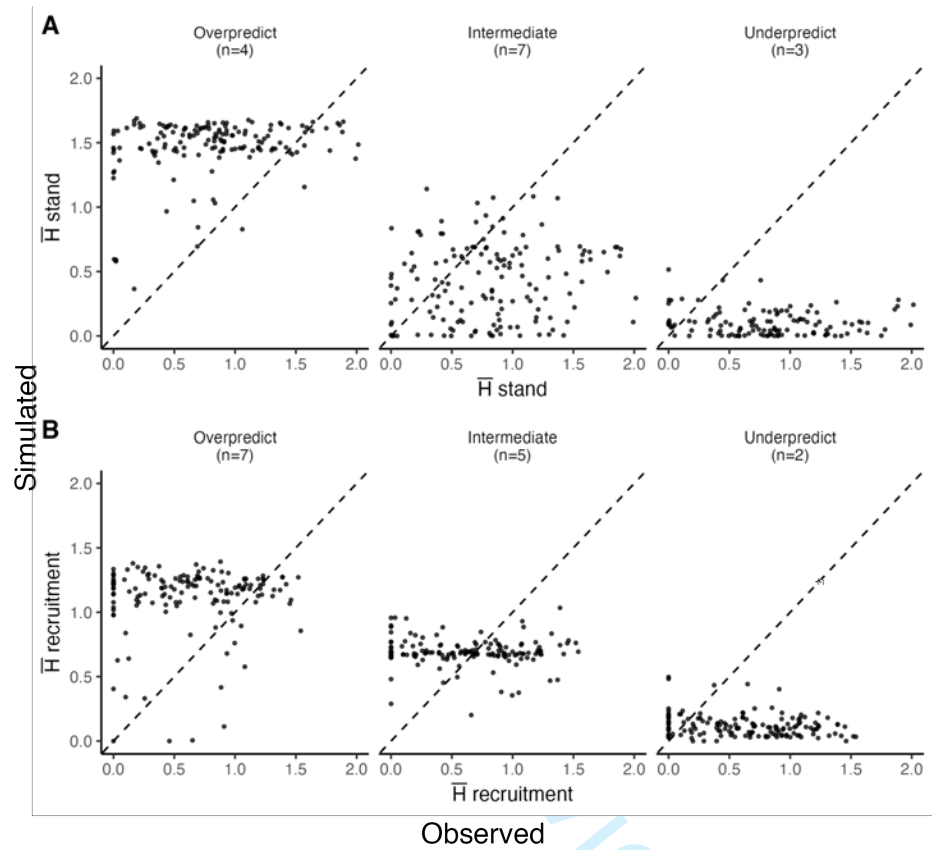


Figure 4:

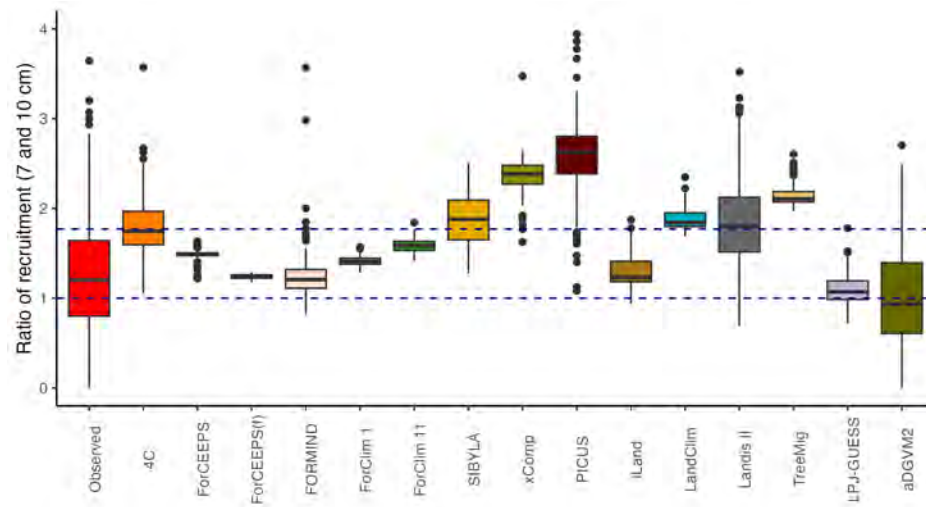


Figure 5: .

good to see  
"recruitment"  
here

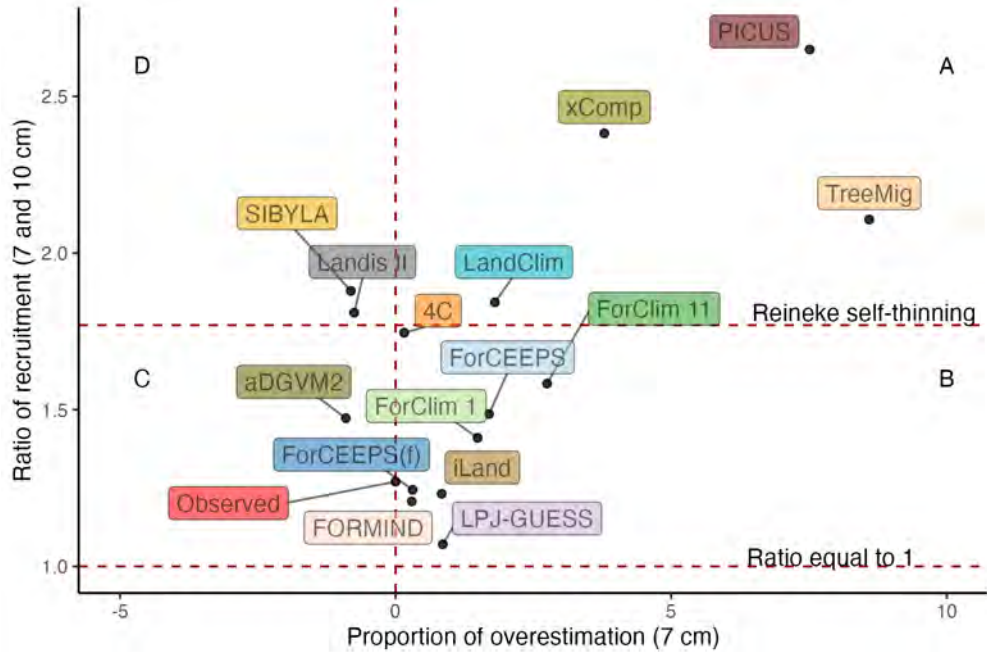


Figure 6: .

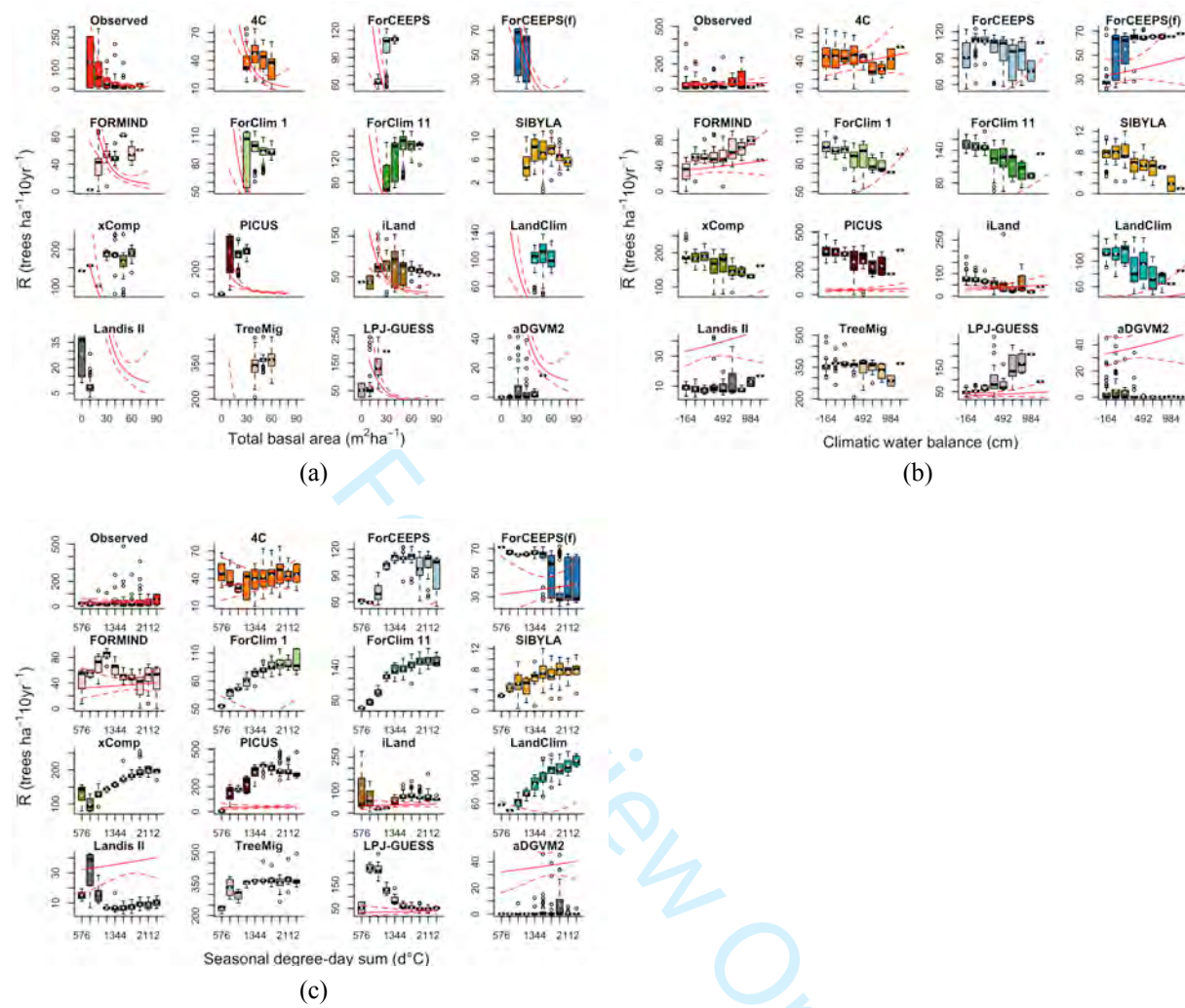


Figure 7: .



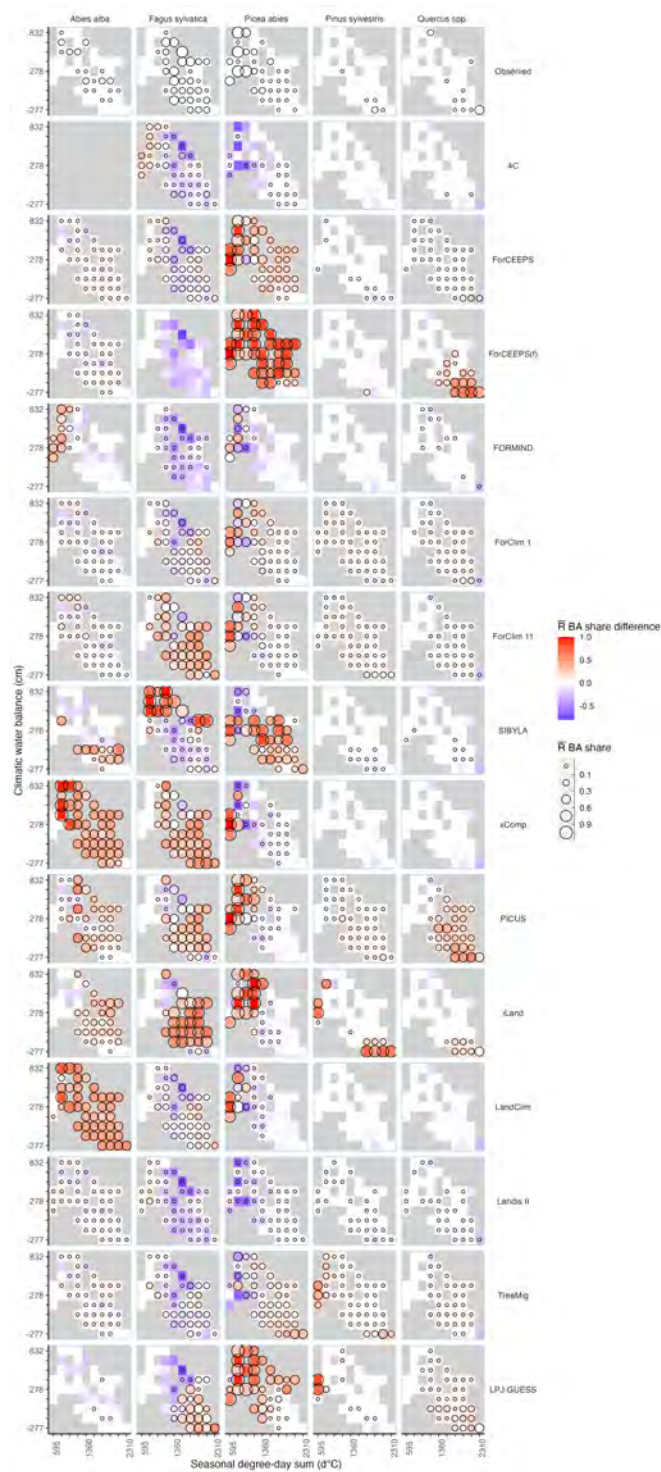


Figure 8: .



# Appendix

## Tree regeneration in models of forest dynamics: a key priority for further research

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 Kristin H. Braziunas, Josef Brůna, Rico Fischer,  
 Samuel M. Fischer, Jessica Hetzer, Thomas Hickler,  
 Christian Hochauer, Manfred J. Lexer, Heike Lischke,  
 Mats Mahnken, Paola Mairota, Ján Merganič,  
 Katarina Merganičová, Tobias Mette, Marco Mina, Xavier Morin,  
 Werner Rammer, Christopher P.O. Reyer, Simon Scheiter,  
 Daniel Scherrer, Harald Bugmann

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30 **1 Appendix 1: Model reports**

31 **1.1 4C**

32 **1.1.1 Authors**

33 Mahnken M., Gutsch M., Reyer C.P.O., Lasch-Born P.

34 **1.1.2 Model**

35 The most complete reference resource for the 4C (v2.2) model and regeneration module is:

- 36 • Lasch-Bonn et al. 2020. Description and evaluation of the process-based forest model 4C
- 37 v2.2 at four European forest sites. DOI: <https://doi.org/10.5194/gmd-13-5311-2020>)

38 **1.1.3 Climate**

39 We used the provided daily ERA5-CHELSA climate data set and complemented the CHELSA time

40 series data regarding relative humidity with the model after [Eccel et al. \(2012\)](#) based on minimum

41 and mean daily temperature to accomodate data needs of 4C. The missing data for January 2nd

42 and 3rd 2013 were filled with data from January 1st and 4th 2013 respectively. For construction

of longer climate time series we looped through the provided time series from 1981 to 2018 up to the maximum simulation length of 2500 years. We amended situations where leap year inconsistencies arised by removing February 29 or duplicating data from February 28. Otherwise, the unaltered daily data were used to run 4C on a daily basis. We applied a constant atmopsheric CO<sub>2</sub> concentration of 380 ppm.

#### 1.1.4 Soil

We used parametrized soils readily available for 4C from the EU soil data base. The link from parametrized soil to soil quality was done by extracting the plant available water storage capacity as the model bucket size of the rooted soil horizons. We excluded bucket size values of lower than 10 cm and larger than 35 cm. The bucket size was reprojected to the range from 0 to 1. In addition we tested the sensitivity of dominant tree height at age 100 years for monospecific stands of all five species simulated to the available soils using model simulations with 4C. The dominant tree height at age 100 years was then also reprojected to the range from 0 to 1 in order to derive a model specific soil quality indicator for all paramterized soils. Then we multiplied this relative model specific soil quality with the relative soil quality derived from the bucket size to the range from 1 to 5. The match between paramterized soil and plot was then done by finding the pair of soil quality with the minimum difference between simuation protocol prescribed soil quality and the soil quality of the paramterized soils as described above.

#### 1.1.5 Topography

Topographical information was not considered in the simulations.

**1.1.6 Tree species**

We initialized stands with five out of the eleven proposed species/genera: *Fagus sylvatica* (fasy), *Picea abies* (piab), *Betula* spp. (betu; 4C parameters for *Betula pendula*), *Quercus* spp. (quer; 4C parameters for *Quercus robur*) and *Pinus sylvestris* (pisy) since only these are fully parameterized for an application as proposed in the simulation protocol. Each plot was initialized with all five tree species with similar distributions of height classes and number of individuals: 2000 individuals/ha with height around 0.25 m, 1000 individuals/ha with height around 0.75 m and 500 individuals/ha with height around 1.75 m. In total 17500 individuals/ha. *Carpinus betulus*, *Tilia cordata*, *Acer pseudoplatanus*, *Fraxinus excelsior*, *Alnus glutinosa* and *Abies alba* are not fully parameterized in 4C.

**1.1.7 Simulations**

**1.1.7.1 Dispersal and seed input** There is no explicitly modelled seed dispersal in a stand and between stands. We applied a constant sapling establishment rate every five years of 2000 individuals/ha for all five species; 10000 individuals/ha in total every five years. The constant sapling establishment provides constant regeneration potential if favorable conditions for sapling growth (especially light and water regime) are present. This approach enables regeneration of other species than only those present in the stand to establish if competition allows. The resulting recruitment patterns are an outcome of the dynamical processes from the sapling stage onward. Seed production and germination were not explicitly simulated.

### 1.1.7.2 Simulation length and equilibrium criteria

To reach equilibrium and obtain dynamics in the equilibrium period, we simulated a maximum of 2500 years. 4C is usually applied for much shorter simulation periods and different technical as well as model-theory related issues arise when simulating longer than 100-150 years. Therefore 2500 years can be seen as the upper limit of continuous simulation in the defined simulation setup. The first 500 years were not sampled for recruitment as we assume the model needs this time to reach equilibrium. In this long simulation period 4C partially projects unrealistically large tree heights resulting in premature termination of the simulation (36 plots) so that not all plots were simulated for the full 2500 years. We started sampling the recruits after the first 500 simulation years from non-overlapping 10 year periods to obtain 200 samples. For shorter simulation periods we produced 200 samples from overlapping 10 year periods. In addition, we excluded those plots in which 4C simulated unrealistically high basal area values of over 150 m<sup>2</sup> (19 plots). We used this large threshold to give the model maximum flexibility to explore the solution space in these long simulation runs although we acknowledge that this is an unrealistic overestimation that is probably originating from misrepresented density dependent mortality processes in long simulation runs and misrepresented single tree dimensions due to wrong assumptions of tree geometry and biomass share of such old-aged individuals. Furthermore those plots with less than 1000 simulation years (16 plots) before termination were excluded because the sample space after the first 500 years was too small. Additionally we included another subset criterion removing all samples that have a  $ba > 90$  to exclude unrealistically high samples without the need to exclude the full site. This resulted in discarding 0.8 % of the samples.

### 1.1.8 Outputs

We provide 200 samples each for 48 plots and at least 190 samples each for 117 plots while not simulating 35 plots (see reason for excluded plots in “Simulation length and equilibrium criteria”). These stem from 10 year periods that overlap partially (for < 2500 simulation years) or do not overlap (for 2500 simulation years). The number of recruits ( $r.trees$ ) is the sum of individuals that cross the threshold diameter (7/10 cm) in the 10 year sample period per hectare that have not already died until the sample year. The recruit’s basal area ( $r.ba$ ) is the sum of the basal area per hectare of the trees that cross the diameter threshold that have not already died until the sample year. The total stand basal area ( $ba$ ) is the basal area per hectare of all trees in the stand > 0 cm diameter at breast height (no lower boundary) at the sample time per species. We provide the data for both diameter thresholds, 7 and 10 cm. In over 90 % of the decades no recruitment takes place.

4C (v2.2) is usually not used for simulations of forest equilibrium dynamics, potential natural vegetation assessment and long simulation periods but rather shorter-term simulations (up to 100-150 years). In addition, only five species out of the pool of eleven potentially relevant species here are parameterized in 4C so that projections of the potential natural vegetation done with 4C need to be considered in the light of model uncertainty. For example, the spatial homogeneity in the model leads to cyclic recruitment patterns. When the adult stands dies of, young individuals are recruited into the larger diameter classes because more light reaches lower canopy layer since larger (adult) trees do not anymore prevent the light reaching lower canopy layers. This results in increased growth of the regeneration layer during those times. In most stands *Fagus sylvatica* dominates the stand after some time but occasionally individuals of other species, like *Picea abies* or *Quercus* spp. cross the recruitment diameter threshold.

## 1.2 ForCEEPS & ForCEEPS(f)

### 1.2.1 Author

Xavier Morin & François de Coligny

### 1.2.2 Model

The most complete reference resource for the ForCEEPS & ForCEEPS(f) model and regeneration module are:

- Morin X., de Coligny F., Bugmann H., Limousin J.-M., Ourcival J.-M., Martin-StPaul N., Simioni G., Cailleret M., Prevosto B., Toïgo M., Vennetier M., Cateau E., Guillemot J. 2021. Beyond forest succession: a gap model to study ecosystem functioning and tree community composition under climate change. *Functional Ecology*. 35, 955-975.
- Jourdan M., Dreyfus, P., Riond C., Cordonnier T., Cornet B., de Coligny F., Morin X. 2021. Managing mixed stands can mitigate severe climate change impacts on French alpine forests. *Regional Environmental Change*. 21, 78.
- Morin X., Damestoy T., Toïgo M., Jactel H., Castagneyrol B. Meredieu C. 2020. Using forest gap models and experimental data to explore long-term effects of tree diversity on the productivity of mixed planted forests. *Annals of Forest Science*. 77 <https://doi.org/10.1007/s13595-020-00954-0>.

**1.2.3 Climate**

ForCEEPS requires monthly data. A 4000-yr long time-series was obtained for each site by randomizing available years from the CHELSA database, with mean monthly temperature and monthly sum of precipitations (see 1.2.2).

**1.2.4 Soil**

Soil quality is represented by a continuous value between 1 and 5, as provided (see 1.2.3) Soil Field Capacity (SFC) was assessed as follows:  $SFC = 8 + (X - 1) * (25 - 8) / (5 - 1)$ , in which X is the 'soil\_qual' value in the provided 'soil\_quality\_200.csv' file.

**1.2.5 Topography**

Not considered.

**1.2.6 Simulations**

In each site, the simulation consists of 4000 yr-long simulation of 1ha of forest (ie. 10 patches of 1000 m<sup>2</sup>), starting from bare-ground. There was no dispersal between patches. Two kinds of simulations have been carried out in each of the 200 sites. In a first set of simulations, regeneration dynamics was simulated with a seed rain from a potential species list, thus independent from the actual forest composition, as classically done in gap models. Under this design, a number of seedling is randomly chosen for each patch, and a species identity is randomly sorted from a potential species list (defined at the start of simulation) assigned to each seedling. Then each seedling



tries to colonize the site depending on whether the suitability between species requirements and site conditions (climate, light, soil quality, browsing index). In a second set of simulations, regeneration dynamics was simulated with a seed rain whose composition depended on the actual forest composition. Under this design, a number of seedling is randomly chosen for each patch, but the species identity is assigned according to species relative abundance (calculated across all 10 patches according to species biomass). For instance, if at year  $i$  the adult trees of species  $j$  represent 60% of the total biomass across the 10 patches, then 60% of the seedlings that try to colonize the patches at year  $i$  will belong to species  $j$ . Then, similarly to the first design, each seedling tries to colonize the site depending on whether the suitability between species requirements and site conditions. In the two sets of simulations, simulations have been run for both thresholds for regeneration (7 and 10 cm).

### 1.2.7 Outputs

Outputs consisted in species specific regeneration rates per decade and per ha, by considering the last 2000 years of simulations to ensure that pseudo-equilibrium state is reached. Results were aggregated for every 10 years for the last 2000 years at the 1ha-level. Variables: - Site: numbers corresponding to the climate data file - Sample: one per decade, for a total of 2000 years = identified from 1 to 200 - Species: name specified as requested (eg. 'fasy') - r.trees: number of trees outcrossing the threshold (7 or 10 cm) during the decade, for the 10 patches simulated (= 1ha), per species - r.ba: summed basal area of the r.trees, per species - ba: summed basal area of all trees per species at the end of the decade - dbh: threshold used

179 **1.3 FORMIND**

180 **1.3.1 Authors**

181 Samuel M. Fischer, Friedrich Bohn, Rico Fischer

182 **1.3.2 Model**

183 A full description of the model can be found in Fischer et al (2016) . The basis for the parameteri-  
184 zation we applied is described in Bohn et al (2014):

- 185 • Bohn, F. J., Frank, K., & Huth, A. (2014). Of climate and its resulting tree growth: Simulat-  
186 ing the productivity of temperate forests. Ecological Modelling, 278, 9–17. [https://doi.org/](https://doi.org/10.1016/j.ecolmodel.2014.06.011)  
187 [10.1016/j.ecolmodel.](https://doi.org/10.1016/j.ecolmodel.2014.06.011)
- 188 • Fischer, R., Bohn, F., Dantas de Paula, M., Dislich, C., Groeneveld, J., Gutiérrez, A. G.,  
189 Kazmierczak, M., Knapp, N., Lehmann, S., Paulick, S., Pütz, S., Rödig, E., Taubert, F.,  
190 Köhler, P., & Huth, A. (2016).Lessons learned from applying a forest gap model to under-  
191 stand ecosystem and carbon dynamics of complex tropical forests. Ecological Modelling,  
192 326, 124–133. [https://doi.org/10.1016/j.ecolmodel.2015.](https://doi.org/10.1016/j.ecolmodel.2015.11.011)

193 **1.3.3 Climate**

194 To incorporate climate, we used the data set ‘daily\_era5\_chelsa\_200.csv’, which contains climate  
195 data on a daily resolution. We considered the covariates precipitation, temperature, and irradiance,  
196 the latter of which we converted to units used in Formind. Adding on to these data, we used a

constant and site-independent potential evapotranspiration (PET) value of  $4 \frac{\text{mm}}{\text{d}}$  and assumed that the mean day length was 12h at all sites.

Since we simulated longer time periods than the 38 years for which we had climate data, we used the provided data in a randomized fashion. For each simulation year, we applied the climate data of a randomly selected year. We neglected the existence of leap years, which led to a minor time shift in climate data of later years.

#### **1.3.4 Soil**

We modelled soil conditions by using the provided soil quality values as proxy for soil depth. To that end, we scaled the provided values to the typical range of soil depth values used in Formind for temperate forests. Specifically, we multiplied the soil quality values by factor 0.5 to obtain the modelled soil depth in meters.

#### **1.3.5 Topography**

We did not use any topography data.

#### **1.3.6 Tree species**

We considered each of the 11 species in the protocol explicitly. We chose the model parameters for the individual species based on the work by Bohn et al (2014). For species that were not covered by Bohn et al (2014), we used parameter values of similar species with known parameters. The species composition was not predefined and evolved solely from the seed input and the model dynamics.

215 **1.3.7 Simulations**

216 **1.3.7.1 Simulation area** We simulated a forest area of 1ha, which was divided into 25 patches  
 217 of size 20m  $\times$  20m. No interactions between trees from different patches were considered in the  
 218 model. That is, the 25 patches were independent replicates of one another.

219 **1.3.7.2 Seed generation and dispersal** We modelled seed generation as global external seed  
 220 rain. Specifically, we assumed that for each species, there is a constant seed inflow of 250  $\frac{\text{seeds}}{\text{ha}\cdot\text{yr}}$ ,  
 221 which is distributed evenly among the 25 individual patches. We supposed that all seeds promptly  
 222 establish to seedlings with initial stem diameters at breast height (DBH) of 5cm.

223 **1.3.7.3 Simulation length and sampling approach** We started the simulation at each site with  
 224 a burn-in phase of 1000 years and collected samples of the output variables in subsequent years. The  
 225 length of the burn-in phase was chosen based on earlier experiences with the model. To confirm that  
 226 the model reached its limiting behaviour, we plotted the evolution of the output variables (e.g. the  
 227 basal area) at selected sites over time and verified that no trends were visible after the burn-in phase.  
 228 We computed the output variables in equidistant time intervals of 60 years. Before taking a sample,  
 229 we saved parts of the model's state. Then, we simulated the forest for 10 years and computed the  
 230 output variables, comparing the model's current state with the state saved earlier (see below). After  
 231 taking the sample, we simulated the forest for another 50 years to reduce correlations between  
 232 samples. Then, we repeated the procedure until the desired number of 200 samples was collected.

### 1.3.8 Outputs

To determine the number and basal area of recruits, we compared the set of large trees before and after the regeneration time period of 10 years. Prior to simulating the forest for the regeneration time period, we saved the internal IDs of all trees with DBHs above the thresholds of 0.07m or 0.1m, respectively. We stored these IDs in set data structures  $S_{0.07}^{\text{prior}}$  and  $S_{0.1}^{\text{prior}}$ , corresponding to one threshold value each. After the regeneration time, we repeated the procedure, obtaining tree ID sets  $S_{0.07}^{\text{posterior}}$  and  $S_{0.1}^{\text{posterior}}$ . We then computed the set differences  $S_{0.07}^{\text{recruits}} = S_{0.07}^{\text{posterior}} \setminus S_{0.07}^{\text{prior}}$  and  $S_{0.1}^{\text{recruits}} = S_{0.1}^{\text{posterior}} \setminus S_{0.1}^{\text{prior}}$  and determined both the number and cumulative basal area of the trees in  $S_{0.07}^{\text{recruits}}$  and  $S_{0.1}^{\text{recruits}}$  by considered species, respectively.

Finally, we computed the total basal area for each considered species by adding up the basal areas of all corresponding individuals. Note that the initial DBH of seedlings in our model was 0.05m. Consequently, smaller trees were not included in the basal area computation.

## 1.4 ForClim 1 & ForClim 11

### 1.4.1 Authors

Yannek Käber, Harald Bugmann

### 1.4.2 Model

The most complete reference resource for the ForClim 1 & ForClim 11 model and regeneration module is:

- Bugmann, H. (1994). On the ecology of mountainous forests in a changing climate: A simulation study.
- Huber, N., Bugmann, H., & Lafond, V. (2020). Capturing ecological processes in dynamic forest models: Why there is no silver bullet to cope with complexity. Ecosphere, 11(5). <https://doi.org/10.1002/ecs2.3109>

### 1.4.3 Climate

Temperature and precipitation were aggregated to monthly means and sums, respectively, including their standard deviation. These values served as input for the weather generator within the model. The weather generator simulates wheather conditions in an annual time step based on the monthly average temperatures and precipitations sums.

### 1.4.4 Soil

Soil data were translated to bucket sizes values based on the assumption that the lowest soil quality value of 1 refers to a bucket size of 10 cm and the highest soil quality of 5 refers to a bucket size of 35 cm. Specifically we used the following formula to calculate the bucket size  $\text{bucket\_size} = 10 + (\text{soil\_quality}-1) / 4 * 25$ .

### 1.4.5 Topography

Topographic information was included by specifying the kSlAsp parameter. This parameter defines a value between -2 and 2 which affects the calculated Potential Evapotranspiration within the model. For details on the calculation of this value see Käber et. al. 2021.

#### 1.4.6 Tree species

All species required were simulated: *Fagus sylvatica*, *Picea abies*, *Abies alba*, *Carpinus betulus*, *Tilia cordata*, *Acer pseudoplatanus*, *Betula* spp., *Fraxinus excelsior*, *Quercus* spp., *Alnus glutinosa*, *Pinus sylvestris*

In addition the following species were simulated: *Acer campestre*, *Acer platanoides*, *Alnus incana*, *Alnus viridis*, *Castanea sativa*, *Corylus avellana*, *Larix decidua*, *Pinus montana*, *Populus nigra*, *Populus tremula*, *Salix alba*, *Sorbus aria*, *Sorbus aucuparia*, *Taxus baccata*, *Tilia platyphyllos*, *Ulmus glabra*, *Pinus cembra*

#### 1.4.7 Simulations

All simulations were run according to the protocol. For each site we simulated on 16 ha (i.e., 100 patches of 0.08 ha). We defined a spin up phase of 1000 years. After the spin up we simulated 200 years of forest dynamics.

#### 1.4.8 Outputs

We sampled in 10 year intervals between the simulation years 1010 to 1200, which resulted in 16 times 20 intervals each with one ha.

### 1.5 SIBYLA

#### 1.5.1 Authors

Ján Merganič, Katarína Merganičová, Marek Fabrika, Peter Valent

### 1.5.2 Model

SIBYLA is the simulator of forest biodynamics. It belongs to the category of semi-empirical tree growth simulators. It consists of the set of mathematical models and algorithms that are transformed into an integrated software package SIBYLA Suite. The model has been developed at the Department of Forest Management and Geodesy, Technical University in Zvolen, Slovakia. The basis of the model was the modelling principle and algorithms implemented in SILVA 2.2 (Pretzsch 1992, Kahn 1994). The model is sensitive to climatic factors (length of growing season, mean temperature during growing season, annual temperature amplitude, and total precipitation during growing season). The climatic factors modify height and diameter growth potential, and consequently tree increment. The climatic factors also influence tree regeneration model.

The most complete reference resource for the SIBYLA model and regeneration module are:

- Fabrika (2005) “Simulátor biodynamiky lesa SIBYLA.” *Koncepcia, konštrukcia a programové riešenie. Habilitačná práca, Technická univerzita vo Zvolene*
- Materials available in <http://etools.tuzvo.sk/sibyla/english/model.htm>.

### 1.5.3 Climate

We used CHELSEA monthly and daily time series from 1981 to 2018 to derive climate variables necessary for simulations with SIBYLA as follows: Monthly average temperature (tas) values were used to derive the SIBYLA site-specific characteristic called the „annual temperature amplitude” (labelled as TAMPL or s5 in the model) that was calculated as a difference between the maximum and minimum monthly average temperatures. Monthly average temperature (tas) values for months



April to September were used to derive the SIBYLA site-specific characteristic called the „average temperature during the growing season” (labelled as TEMP or s6 in the model). Monthly precipitation sums (pr) for months April to September were summed up to derive the SIBYLA site-specific characteristic called the „precipitation total during the growing season” (labelled as PRECIP or s8 in the model). Daily average temperature (tas) values were used to derive the SIBYLA site-specific characteristic called the „length of the growing season” (labelled as DAYS or s4 in the model).

#### **1.5.4 Soil**

The information on site-specific soil quality (file name: soil\_quality\_200.csv) was used to define two SIBYLA site-specific characteristic called the „soil moisture” (labelled as MOIST or s7 in the model) and the „soil nutrient supply” (labelled as NUTR or s3). Since these two characteristics can obtain values in the range from 0 to 1, the provided values on soil quality were converted to this range by dividing each value with 5 (the maximum). We used the long-term average of CO<sub>2</sub> concentrations in air that represented the period 1981 – 2018. The long-term average of CO<sub>2</sub> was calculated from the annual CO<sub>2</sub> data obtained from Mauna Loa observations (Keeling et al. 1976). Similarly, we used the long-term NO<sub>x</sub> concentration representing the time period 1981-2018. This was obtained by averaging annual values of NO<sub>x</sub> concentration in air calculated using the equation by Kahn (1994), where the year is the driving variable.

#### **1.5.5 Topography**

The growth simulator SIBYLA uses the model of ecological classification applied in the growth simulator SILVA 2.2, which was derived by Kahn (1994). Site is specified using ecological site

328 characteristics describing climate, air, and soil, also called site variables:

329 • s1 (N2O) ... NO<sub>x</sub> concentration in air (ppb)

330 • s2 (CO<sub>2</sub>) ... CO<sub>2</sub> concentration in air (ppm)

331 • s3 (NUTR) ... soil nutrient supply (relative value in the range from 0 to 1)

332 • s4 (DAYS) ... number of days in the vegetation period (days with daily mean temperature above  
333 10°C)

334 • s5 (TAMPL) ... annual temperature amplitude (the difference between minimum and maximum  
335 monthly temperature in °C)

336 • s6 (TEMP) ... daily mean temperature in the vegetation period in °C (from April to September)

337 • s7 (MOIST) ... soil moisture (relative value in the range from 0 to 1)

338 • s8 (PRECIP) ... precipitation amount in the vegetation period in mm (from April to September)

339 • s9 (ARID)... aridity index according to de Martone in mm.°C<sup>-1</sup> They directly influence the pro-  
340 duction capacity of a stand (tree height and diameter increment).

### 341 1.5.6 Tree species

342 At the beginning of the simulations we determined balanced tree species composition of all 12 tree  
343 species pre-defined in the „Regeneration workshop protocol”. It means that at the beginning each  
344 species was represented by the same volume, mean tree diameter, mean tree height, and age.

### 1.5.7 Simulations

The simulations were performed following the “Regeneration workshop protocol”. Hence, we simulated the pre-defined 200 sites with the model SIBYLA under current climate. The simulations were performed with the help of two software tools for automatised handling of multiple sites to speed up the process called DBCreator and Automat (Valent et al. 2018).

**1.5.7.1 Simulation area and site** We set the simulation area to 1ha, i.e. each site was represented by an area of 1 ha, to enable a sufficiently large area for species interactions. Larger areas were not possible due to the restrictions in the number of trees per plot (the maximum number of trees per plot is 6,000). Due to the restriction in the maximum number of trees per plot we established a 40-year-old forest stand at each site with the balanced tree species composition as defined above. We used site-specific elevation and aspect obtained from the information on topography and elevation (file name: topo\_data\_200.csv).

**1.5.7.2 Simulation length** Each site was simulated for 3,000 years. Based on the analysis of the temporal development of multiple stand variables including number of trees, mean tree and stand characteristics, the simulation time until the equilibrium was set to 500 years. Hence, the first 500 simulated years were excluded from the results. The submitted output includes the required information per decade during the 2,500 years.

**1.5.7.3 Dispersal** Relevant aspects of the dispersal (if any) and seed input parameters in your model The regeneration model operates if there are mature trees able to produce seeds. Hence, the initial forest stand had to be established to allow the reproduction and regeneration module. The

seed yield of individual trees is predicted in relation to species-specific characteristics including tree age interval of seed production and fertility (age of start, optimum and end), seed production per adult tree, transmission distance, seed purity, seed quality, germination capacity, absolute weight of seeds. Seed tree production is further modified with the regulators and reduction factors, which describe other conditions necessary for the germination, survival, and the establishment of the next generation, e.g. stand canopy closure (Fabrika 2005, Merganič and Fabrika 2009, Fabrika et al. 2009, 2011).

### 1.5.8 Outputs

To derive the required information, we worked with the model output for individual trees per decade. First, we calculated basal area of individual trees from the simulated diameter at breast height using the equation for the area of a circle. Total basal area (ba) was obtained by summing tree basal areas per species and decade. The number of recruits (r.trees) per species was derived by counting the trees that exceeded the diameter threshold (7 or 10 cm) in the specific time. The basal area of recruits (r.ba) per species was calculated by summing tree basal areas of recruits per species. NA was assigned if no trees of a specific species occurred in the period.

### 1.5.9 References

Fabrika M., Merganič J., Merganičová K., 2009: Natural regeneration density model developed for the purposes of the individual-tree growth simulator. *Acta Facultatis Forestalis Zvolen*, 51(3), p. 125-137, ISSN: 0231-5785 Fabrika, M., (2005): *Simulátor biodynamiky lesa SIBYLA, koncepcia, konštrukcia a programové riešenie*. Habilitačná práca. Technická univerzita vo

Zvolene, 238 p. Kahn, M., (1994): Modellierung der Höhenentwicklung ausgewählter Baumarten in Abhängigkeit vom Standort. Forstliche Forschungsber. München, Vol. 141, 221 p. Keeling C. D., R. B. Bacastow, A. E. Bainbridge, C. A. Ekdahl Jr., P. R. Guenther, L. S. Waterman, J. F. S. Chin 1976: Atmospheric carbon dioxide variations at Mauna Loa Observatory, Hawaii. Tellus. XXVIII, 6: 538-551, <https://doi.org/10.1111/j.2153-3490.1976.tb00701.x>

Merganič J., Fabrika M., 2009: Determination of climatic-site strata based on rectified climatic rasters for the purposes of natural regeneration density model. Acta Facultatis Forestalis Zvolen, 51(3), p. 113-124, ISSN: 0231-5785

Merganič, J., Fabrika, M., Merganičová, K., 2011: Submodel of height-diameter function for climatic-site strata of the model of natural regeneration in the growth simulator SIBYLA. Acta Facultatis Forestalis Zvolen, 53(1), p.155-168, ISSN: 0231-5785

Pretzsch, H., (1992): Konzeption und Konstruktion von Wachstumsmodellen für Rein- und Mischbestände. Forstliche Forschungsberichte München, Nr.115, 358 p. Valent, P., Merganič J., Výbošťok J. 2018: Optimus – Software for Multi-criteria analysis. TU Zvolen.

## **1.6 xComp**

### **1.6.1 Authors**

Tobias Mette, LWF.

## 1.6.2 Model

The forest growth model xcomp was developed to simulate gap dynamics of monospecific stands with a strong emphasis on position-dependent individual tree competition. The model consists of three units: (1) the main growth phase which determines the growth and mortality of each individual tree above 5 cm dbh, (2) the old-growth phase where individual trees exceeding a certain dbh-limit decline in vitality and eventually die, and (3) the regeneration phase where seedling growth and mortality is modelled depending on light availability. The primary focus of the model was to establish a set of robust algorithms that can be flexibly calibrated for different species attributes. The model was used to simulate single-species stand development cycles for *Nothofagus pumilio* in Patagonia (Mette 2014), for European beech in NE-Bavaria (Mette et al. 2016) and a Norway spruce stand with different mortality algorithms (Bugmann et al. 2019). For the current article the model was (4) connected to a climate sensitive species distribution model to modify growth and mortality in dependence of the site conditions, and (5) extended from single to multi-species simulations (c.f. Section 1.6.7).

The most complete reference resource for the xComp model and regeneration module are:

- Mette, T. (2014). xcomp Tutorial (v2014\_08). Technical Report, TUM. DOI: 10.13140/RG.2.2.32524.59529
- Mette, T. (2014) Using Reineke to self-calibrate mortality in individual tree based forest growth modelling. Beiträge zur Forstwissenschaftlichen Tagung, Dresden, 17.-20.09.2014. 10.13140/RG.2.2.11553.07527

### 1.6.3 Climate

The species parameterisation in xcomp is sensitive to long-term climate, i.e. 30-year averages of summer temperature, summer precipitation and winter temperature. Reactions to daily, monthly or periodic extremes are not implemented as deterministic but as stochastically processes functionally dependent on the long-term climate. The climate sensitivity of growth, mortality and regeneration is described in Section 1.6.7.

### 1.6.4 Soil

Soil moisture class MOIST was used to modify the climate sensitivity via summer precipitation PJJA by  $PJJA(mod) = PJJA + 15 * MOIST - 45$  (in mm).

### 1.6.5 Topography

Topography is no input parameter in xcomp. It may only effect the simulation results indirectly through climate or soil parameters.

### 1.6.6 Tree species

From the suggested species spectrum *Alnus glutinosa* and *Fraxinus excelsior* were not included in the species mix. *Quercus spec* was split into *Q. petraea* and *Q. pubescens*, but united in the validation to meet the protocol.

### 1.6.7 Simulations

The simulation was carried out according to the protocol by Bugmann et al. (2022). I.e. the simulation is initiated for mixed species stands of 1 ha size at 200 sites of with given climate and soil conditions. The initial species mix consists of up to 10 species of equal shares with an initial root mean square diameter  $dq$  of 8 cm. Xcomp simulates forest growth in 5 year intervals. Data are validated after having reached a climate dependent equilibrium – which is typically the case after 750 years (= 150 simulation periods). Starting with year 760, data are read out for 200 10 year intervals (until year 2750, simulation period 550). Further simulation relevant model details:

(1) The main growth phase is determined by the processes growth and mortality. Mortality is determined by the Reineke exponent  $rke$  and the stand density  $sdi$  and calibrated over a range of 8 cm to 50 cm  $dq$  (= root mean square diameter) so that stem number  $N$  equals:  $N = sdi * (dq/25)^{rke}$ . A tree's resource acquisition area  $res$  (m<sup>2</sup>) is approximated as  $res = 1e4 / (sdi * (dbh/25)^{rke})$ . As the Reineke exponent is fixed to  $\approx 1.6$ , species with higher/ lower  $sdi$  have a lower/ higher resource acquisition area for a given  $dbh$ . Potential  $dbh$  growth  $dd$  is calculated by multiplying a reference  $dbh$  growth with a site specific temperature dependent modifier. The individual  $dbh$  growth in the stand is further modified by the neighbourhood competition.

(2) The old growth phase sets in when a tree passes a certain old growth  $dbh$  ( $ogDbh$ ) which depends on the site conditions. Having passed this threshold  $dbh$  a tree is assigned a mortality period that assumes a value not greater than a site independent maximum  $ogPer$ . The maximum old growth time span ranges from 100 years (birch) to 350 years (fir). During the old growth phase  $dbh$  growth declines and more light becomes available for regeneration.

(3) The regeneration phase allows seedling development on a 1x1 m grid over the entire stand.



First, a light availability matrix (1x1 m) is calculated from a cumulative crown shadow which decreases with increasing distance to the tree center. Next, regeneration matrices (1x1 m) are created for each of the stand's species. In the initial period, the regeneration matrix of each species is empty, but at the end of each period, a light dependent dbh growth and mortality is calculated for each 1m raster cell. The dbh growth is scaled so that under full light 5 cm dbh is reached in a defined regeneration period (regnPer) that depends on the site conditions. The default value is set to 15 years and equal for all species. Dbh growth is modified by the light availability and the species' regeneration light demand. This is a decisive difference between the species and favours shadow-tolerant trees like fir and beech in the absence of large gaps. However, each raster cell is afflicted with a species bonus or malus that provides local variation to the global regeneration parameters. Mortality in the regeneration raster occurs as a random process, the likelihood of which depends on the climate.

(4) The climate sensitivity was calculated by methods of species distribution modelling. Effectively species abundance in European NFI-plots (Mauri et al. 2017) was related to climate of the plots (Karger et al. 2017) using generalized additive models as in Thurm et al. (2018). Input variables were summer temperature mean (Jun-Aug), winter temperature mean (Dec-Feb) and summer precipitation sum (Jun-Aug). Abundance was transformed into prevalence () so that the values for each species can assume a range from 0 to 1. The prevalence values modify dbh growth  $dd$ , old growth dbh  $ogDbh$ , the regeneration period  $regnPer$ , and the regeneration mortality  $regnMort$ .

(5) The extension from single to multiple species simulation introduced no technical changes to the single-species growth and mortality behaviour. Competition as the main interaction between trees depends on the crown size and density of the neighbouring trees and can turn out an dis/advantage for one or the other species. But species calibration parameters were not changed due to mixture-

specific interaction.

### 1.6.8 Outputs

Since the simulation output tables contain all biometric variables on an individual tree basis, all required outputs can be derived directly from the output tables. Being a very deterministic model what typically happens in xcomp is that the equilibria consist of one or two species. Shade tolerance favours fir and beech in the absence of large gaps creating disturbances. The second most important parameter is the site suitability which is estimated by the modelled species prevalence and affects growth and thereby competitiveness. As it is the first time that xcomp is used in a multiple species application there is room for improvements. The automation of a robust calibration of the main growth phase is a precondition to investigate how for instance larger disturbances, a weighted regeneration potential oriented at the main stand, higher or selective mortality of the regeneration affect the species composition and turnover.

### 1.6.9 References

1. Bugmann, H., Seidl, R., Hartig, F., Bohn, F., Bruna, J., Cailleret, M., ... & Reyer, C. P. (2019). Tree mortality submodels drive simulated long-term forest dynamics: Assessing 15 models from the stand to global scale. *Ecosphere*, 10(2), e02616.
2. Karger, D. N., Conrad, O., Böhner, J., Kawohl, T., Kreft, H., Soria-Auza, R. W., ... & Kessler, M. (2017). Climatologies at high resolution for the earth's land surface areas. *Scientific data*, 4(1), 1-20.
3. Mauri, A., Strona, G., & San-Miguel-Ayanz, J. (2017). EU-Forest, a high-resolution tree

occurrence dataset for Europe. Scientific data, 4(1), 1-8.

4. Mette, T., Falk, W., Blaschke, M., Förster, B., Walentowski, H. (2016). Modelling natural forest dynamics in individual tree based forest growth simulators. Beiträge zur Forstwissenschaftlichen Tagung, Freiburg, 26.-29.09.2016. 10.13140/RG.2.2.29169.15201
5. Thurm, E. A., Hernandez, L., Baltensweiler, A., Ayan, S., Rasztovits, E., Bielak, K., ... & Falk, W. (2018). Alternative tree species under climate warming in managed European forests. Forest Ecology and Management, 430, 485-497.

## 1.7 PICUS

### 1.7.1 Authors

Christian Hochauer, Manfred J. Lexer

### 1.7.2 Model

The core elements of PICUS are described in Lexer and Hönninger (2001) and Seidl et al. (2005).

Specific details regarding the regeneration module can be found in Woltjer et al. (2008).

The most complete reference resource for the SIBYLA model and regeneration module are:

- Lexer MJ, Hönninger K (2001) A modified 3D-patch model for spatially explicit simulation of vegetation composition in heterogeneous landscapes. For Ecol Manag 144:43–65. doi:10.1016/S0378-1127(00)00386-8
- Seidl R, Lexer MJ, Jäger D, Hönninger K (2005) Evaluating the accuracy and generality of a hybrid patch model. Tree Physiol 25:939–951. doi:10.1093/treephys/25.7.939

- Woltjer M, Rammer W, Brauner M, Seidl R, Mohren GMJ, Lexer MJ (2008) Coupling a 3D patch model and a rockfall module to assess rockfall protection in mountain forests. J Environ Manag 87:373–388. [doi:10.1016/j.jenvman.2007.01.031](https://doi.org/10.1016/j.jenvman.2007.01.031)

### 1.7.3 Climate

We used the provided monthly climate data (monthly\_era5\_chelsa\_200.csv). The provided solar radiation rds was converted to MJ per m<sup>2</sup>. Additionally, vpd was calculated.

### 1.7.4 Soil

Based on the provided continuous value for soil quality between 1 and 5 minimum (soil quality = 1) and maximum (soil quality = 5) values for soil water holding capacity (80mm, 200mm), plant available Nitrogen (40 kg ha<sup>-1</sup> yr<sup>-1</sup>, 100 kg ha<sup>-1</sup> yr<sup>-1</sup>) and soil pH (4.2, 5.6) were defined. Linear interpolation was used to scale between the minimum and maximum values.

### 1.7.5 Topography

Not considered.

### 1.7.6 Tree species

The species composition was defined by the given species from the protocol: *Fagus sylvatica*, *Picea abies*, *Abies alba*, *Carpinus betulus*, *Tilia cordata*, *Acer pseudoplatanus*, *Betula* spp., *Fraxinus excelsior*, *Quercus* spp., *Alnus glutinosa* and *Pinus sylvestris*. For *Betula* spp. *Betula pendula* was simulated, for *Quercus* spp. the species *Quercus petraea* and *Quercus robur* were used. The

establishment from bare ground was achieved via external seed input (see also in section seed dispersal), so depending on the environment and random components all the given species had a chance to grow into the respective simulation. In addition, on site production of seed is considered depending on age and size of potential parent trees.

### 1.7.7 Simulations

**1.7.7.1 Simulation Area** In PICUS the area is defined via the number of 10 m by 10 m patches. For this simulation we used an area of 12 by 12 patches resulting in an area of 1.44 ha. This size of the simulated forest provides relatively stable species composition & structure and reasonable simulation time.

**1.7.7.2 Seed dispersal** For the experiment seed input to the simulated forest happens via 2 pathways: (1) external seed input to every patch in any simulated year (fixed number of seed per patch per species). (2) locally produced seed by parent trees growing in the simulated forest. Seed production depends on species, and tree size and a random component accounting for mast years. Seed dispersal depends on whether a species is anemochorous or zoochorous. If anemochorous tree height and seed characteristics determine the maximum dispersal range and the shape of the dispersal function. Based on germination rate, the environmental factors (temperature, soil moisture, Nitrogen, light) and the amount of seeds in combination with a random component seedling establishment is calculated per patch in any given year. Seedling cohorts grow through 4 height classes and are then eventually recruited into the tree population.

**1.7.7.3 Simulation length** We decided to use the temporal sampling. We first run the model into a quasi equilibrium and continue afterwards with another 2000 years. The simulation time until equilibrium was chosen with 600 years from experience in other projects and a few simulations with test sites where 600 years was a sufficiently long simulation time to reach an equilibrium state.

**1.7.8 Output**

Output consisted of species-specific regeneration rates per decade and per ha. Oak species were aggregated. A sample was taken for every 10 years for a total period of 2000 years once the model had reached equilibrium (see 1.7.7.3). Ingrowth was determined by counting the trees passing the 7cm and 10cm DBH thresholds every 10 years. Basal area of the ingrowth was determined at the end of each decade.

**1.8 iLand**

**1.8.1 Authors**

Werner Rammer, Kristin Braziunas

**1.8.2 Model**

The most complete reference resource for the iLand regeneration module is:

- Seidl, R., Spies, T. a. T. A. T. a., Rammer, W., Steel, E. A. A., Pabst, R. J. R. J. R. J., & Olsen, K. (2012). Multi-scale Drivers of Spatial Variation in Old-Growth Forest Carbon

Density Disentangled with Lidar and an Individual-Based Landscape Model. *Ecosystems*,  
15(8), 1321-1335. <https://doi.org/10.1007/s10021-012-9587-2>

### 1.8.3 Climate

Climate inputs for iLand are at daily temporal resolution. We used daily climate from the CHELSA dataset for maximum and minimum temperature, precipitation, and surface shortwave radiation. We calculated daily vapor pressure deficit (VPD) from these inputs assuming daily minimum temperature is dewpoint temperature, a reasonable assumption except under very arid conditions (Campbell and Norman 2000). We calculated vapor pressure from temperature using the Tetens formula with different coefficients for temperatures above or below 0° C (Murray 1967). We then followed methods outlined by the Food and Agriculture Organization of the United Nations (Allen et al. 1998) to calculate vapor pressure deficit as the difference between average daily saturation vapor pressure (derived from minimum and maximum temperature) and ambient vapor pressure derived from dewpoint temperature. Some daily VPD values were negative because there were days in the CHELSA dataset where minimum temperature exceeded maximum temperature; negative VPD values were set to 0.

As recommended by workshop organizers, we filled in daily values for two missing days in 2013 (Jan 2 and Jan 3) with daily values for Jan 1 and 4, respectively.

Atmospheric CO<sub>2</sub> concentration was set to 380 ppm and latitude was set to 50° N for all sites. Annual climate year was drawn randomly with replacement from the full dataset (1981-2018) for each site for the duration of the simulation.

**1.8.4 Soil**

Inputs for soil depth, texture, and fertility (plant available nitrogen) were extracted from a previously compiled Europe-wide dataset (unpublished dataset). We averaged values in a 1 km buffer around blurred site coordinates provided by workshop organizers. Relationships between ranked site quality provided by workshop organizers and soils data from our Europe-wide dataset were weak (Pearson's  $|r|$  ranged from 0.04 to 0.34), but followed expected trends with lower sand content, higher water holding capacity, and higher fertility associated with higher site quality. Albeit the weak correlation, we chose to use our available data set because we could avoid additional assumptions as it included all site variables needed for the model.

**1.8.5 Topography**

Topographic information was not used.

**1.8.6 Tree species**

Tree composition is defined at the species level. All individually requested species (*Fagus sylvatica*, *Picea abies*, *Abies alba*, *Carpinus betulus*, *Tilia cordata*, *Acer pseudoplatanus*, *Fraxinus excelsior*, *Alnus glutinosa*, *Pinus sylvestris*) were included. For the two taxa where species was not defined, we identified a representative species (*Betula pendula* for *Betula* spp. and *Quercus robur* for *Quercus* spp.). No other species were included in model simulations.



## 1.8.7 Simulations

**1.8.7.1 Simulation area** The simulation extent for each site was 1000 m x 1000 m (total area = 100 ha). Environmental conditions were homogeneous for each site.

**1.8.7.2 Dispersal** Dispersal parameters are species-specific and include maturity age, fecundity (seedling potential per m<sup>2</sup> crown area), masting (lower seed production in non-mast years), and dispersal distance (probabilistic dispersal kernel). A small fraction of seeds are dispersed over longer distances (long distance dispersal algorithm). Dispersal is calculated at 20 m spatial resolution. Seedling establishment is further modified by other environmental constraints and is stochastically spatially distributed at finer (2 m) resolution. The simulation extent is treated as a spatially explicit landscape, so neighboring cells can serve as seed sources for each other.

We initialized our simulation experiments from bare ground with uniform probability of seed availability set to a low level (0.001) for all species. Once trees reached maturity, they also contributed to seed availability and dispersal.

**1.8.7.3 Simulation length** Simulations were run for 2010 years, and equilibrium was reached at year 1500. We assessed temporal patterns of species composition and basal area and defined equilibrium as when forest composition and structure stabilized across all sites (“potential natural vegetation”). Some sites had high interannual variation, especially in basal area, after equilibrium; this variation did not represent directional change and appeared instead to be related to sites with extreme growth conditions and variation in randomly selected annual climate.

**1.8.7.4 Simulation approaches** Only one simulation was run per site.

**1.8.8 Output**

For each site, we generated decadal outputs for the full simulation extent every 100 years after equilibrium was reached (i.e., 1500-1509, 1600-1609, ..., 2000-2009). This resulted in outputs for a total of 600 ha (100 ha simulation extent x 6 decades). From this list, we randomly sampled 200 ha without replacement.

We derived recruit density and basal area annually by species. Trees > 4 m in height are represented as individuals in iLand, so we were able to identify individual trees that crossed the DBH threshold of either 7 or 10 cm each year. We summed the number of annual recruits and their basal area in the year they crossed the recruitment threshold for each 10-year output period.

We averaged total density and basal area by species for each decade. We further included 0 values (complete cases) for species that were missing from a given sample and site.

**1.8.9 References**

Allen, R. G., L. S. Pereira, D. Raes, and M. Smith. 1998. Crop evapotranspiration - Guidelines for computing crop water requirements. FAO - Food and Agriculture Organization of the United Nations, Irrigation and drainage paper 56. Campbell, G. S., and J. M. Norman. 2000. An Introduction to Environmental Biophysics. Springer Science & Business Media. Murray, F. W. 1967. On the computation of saturation vapor pressure. Journal of Applied Meteorology 6:203–204.

## 1.9 LandClim

### 1.9.1 Authors

Olalla Díaz-Yáñez, Harald Bugmann

### 1.9.2 Model

We used LandClim version 2.0, which calculates forest dynamics at a decadal time step. The complete reference resources for the LandClim model and its regeneration module are:

- SCHUMACHER, S., H. BUGMANN, AND D. J. MLADENOFF. (2004). “Improving the formulation of tree growth and succession in a spatially explicit landscape model” *Ecological Modelling* 180: 175-194.
- SCHUMACHER, S. AND H. BUGMANN. (2006). “The relative importance of climatic effects, wildfires and management for future forest landscape dynamics in the Swiss Alps” *Global Change Biology* 12: 1435-1450.
- SCHUMACHER, S., B. REINEKING, J. SIBOLD, AND H. BUGMANN. (2006). “Modeling the impact of climate and vegetation on fire regimes in mountain landscapes” *Landscape Ecology* 21: 539-554.
- Manual available on the model web page: <https://ites-fe.ethz.ch/openaccess/products/landclim>

### 1.9.3 Climate

Climate inputs for LandClim are at monthly temporal resolution. We used monthly climate from the CHELSA dataset provided in the protocol, using temperature and precipitation variables. During the simulations, we randomly sampled the annual climate data from the CHELSA time series.

### 1.9.4 Soil

We used the soil quality provided in the protocol to infer the Available Water Holding Capacity (WHC) needed in LandClim. We assigned WHC = 8 cm for soil quality one and WHC = 25 cm for soil quality five, and interpolated the values for the other categories linearly between these two extremes.

### 1.9.5 Topography

We used the altitude and soil information provided in the protocol to create 200 landscapes, one per site. However, each landscape created per site had no slope, altitude, or aspect variation.

### 1.9.6 Tree species

We simulated forest dynamics considering only the 11 species proposed in the protocol: *Fagus sylvatica*, *Picea abies*, *Abies alba*, *Carpinus betulus*, *Tilia cordata*, *Acer pseudoplatanus*, *Betula* spp., *Fraxinus excelsior*, *Quercus* spp., *Alnus glutinosa*, and *Pinus sylvestris*.

### 1.9.7 Simulations

We simulated forest dynamics from bare ground for each site, using patches (pixels) with a size of 20x20 cm<sup>2</sup>. We prepared landscapes of 250x250 m without topographical variation for each site. The simulations we run from bare ground to 2000 years, and the samples were taken starting in the year 2000. In the regeneration module, we used (1) a base seeding probability of 0.001, which defines if seeds are available due to background seed rain; (2) a dispersal mode based on the formulation ‘random asymmetric’; and (3) the same establishment probability of 0.9 for all species included in the simulation of, which sets the same probability for all the species to regenerate successfully, provided that the abiotic and light conditions are suitable for establishment.

### 1.9.8 Outputs

We estimated the outputs based on a sample of 25 random cells every ten years from the simulation years 2010 to 4000 for one simulation per site, thus providing the required 200 samples per site.

## 1.10 Landis II

### 1.10.1 Authors

Josef Bruna, Paola Mairota, Marco Mina, Giorgio Vacchiano

### 1.10.2 Model

Landscape scale forest simulation model LANDIS-II (Scheller et al. 2007) with PnET-Succession extension (version 4.1). PnET-Succession is based on the Biomass Succession extension of Scheller

and Mladenoff (2004), embedding elements of the PnET-II ecophysiology model of Aber et al. (1995) to mechanistically simulate growth as a competition for available light and water (De Bruijn et al. 2014). PnET-Succession simulates the competition among cohorts for water and light at a monthly time-step as a function of photosynthetic processes and maintenance respiration that are explicitly linked to environmental drivers such as temperature, precipitation, photosynthetic active radiation (PAR), and CO<sub>2</sub> concentration. Regeneration depends on distance from a seed source, soil water, and subcanopy light, while competition is modeled by partitioning incoming light through multiple canopy layers. Growth of specific cohort biomass components is allocated in the following order: non structural carbon, first, then foliage then root and stem. Biomass growth decreases as cohorts approach their longevity age but mortality can occur at any time when carbon reserves production is insufficient to support growth due to shading, water competition, and/or drought (Gustafson et al. 2015), or by any disturbance or management extension used. For output, we selected Biomass Community Output Extension version 2.0.1, which generates output in the format: species age biomass (g / m<sup>2</sup>) at specified time steps.

The most complete reference resources for the LANDIS-II model and regeneration module are:

- Scheller R.M. & Mladenoff D.J. (2004) A forest growth and biomass module for a landscape simulation model, LANDIS: design, validation, and application. *Ecological Modelling* 180: 211–229. <https://doi.org/10.1016/j.ecolmodel.2004.01.022>
- Scheller, R. M., Domingo J. B. , Sturtevant B. R. , Williams J. S. , Rudy A. , Gustafson E. J. & Mladenoff D. J. (2007) Design, development, and application of LANDIS-II, a spatial landscape simulation model with flexible temporal and spatial resolution. *Ecological Modelling* 201(3-4): 409–419. <https://doi.org/10.1016/j.ecolmodel.2006.10.009>

- de Bruijn A., Gustafson E.J., Sturtevant B.R., Foster J.R., Miranda B.R., Lichti N.I. & Jacobs D.F. (2014) Toward more robust projections of forest landscape dynamics under novel environmental conditions: Embedding PnET within LANDIS-II. *Ecological Modelling* (287): 44–57 <https://doi.org/10.1016/j.ecolmodel.2014.05.004>
- Petter G., Mairota P., Albrich K., Bebi P., Bruna J., Bugmann H., Haffenden A., Scheller R.M., Schmatz D.R., Seidl R., Speich M., Vacchiano G. & Lischke H. (2020) How robust are future projections of forest landscape dynamics? Insights from a systematic comparison of four forest landscape models. *Environmental Modelling & Software* 134: 104844. <https://doi.org/10.1016/j.envsoft.2020.104844> (supplementary material)
- Gustafson E.J., De Bruijn A.M.G., Pangle R.E., Limousin J.M., McDowell N.G., Pockman W.T., Sturtevant B.R., Muss J.D. & Kubiske M.E. (2015) Integrating ecophysiology and forest landscape models to improve projections of drought effects under climate change. *Global Change Biology* 21: 843–856. <https://doi.org/10.1111/gcb.12713>

### 1.10.3 Climate

Climate input was generated by randomly selecting entire years from the monthly data from the CHELSA dataset and collating them one after the other to create a 2000 years series. The sampling was repeated 10 times with different random order of years to create the 10 climate replicates. Selecting a year at a time eliminates inconsistent seasons (especially summer). We used monthly mean, minimum and maximum temperatures and precipitation as input for PnET succession extension. PnET-Succession also requires mean monthly values of PAR during daylight hours, which

we calculated by dividing the monthly rsds data by the number of daylight seconds in each month for latitude 47 to get W/m<sup>2</sup>. We then multiplied this by 4.6 to get  $\mu\text{mol/m}^2/\text{s}$  and multiplied by 0.5 to get PAR part of the spectrum, based on the approximation by Tsubo et al. (2005). Leap years were not considered. The PAR distribution across all sites and years is in range with values that are typical for temperate regions.

CO<sub>2</sub> concentration with yearly timestep was added from the concentrations table available from EEA (2019). For years 0-1750 CO<sub>2</sub> concentration was maintained fixed to 278 ppm. As for the period 1750-1975 there was only one value each 5 years, we used a constant value for each 5-year period. CO<sub>2</sub> concentration was added to the climate input file after randomization of temperature, precipitation and PAR (see above), so it reflects realistic values for the simulated years. Simulations were run from year 0 to 1990 but sampled outputs did not exceed year 1910. Thus, the drastic increase in CO<sub>2</sub> concentration during the second half of the 1900s did not affect the delivered results.

#### 1.10.4 Soil

Soil type was set to LOAM at all sites. Rooting depth was calculated from soil quality codes (1-5, original values ranged from 1.13 to 4.87) multiplied by 205. This produces a soil depth in the range 231 - 998 mm, that are within the typical range for PnET-Succession (maximum 1000 mm). A clear trend emerged - deeper soils resulted in higher biomass, although with some exceptions.



### 1.10.5 Topography

The ecoregion-specific parameter Precipitation Loss Fraction denotes the water lost to runoff induced by topographic slope. We estimated this parameter for each site from topo\_data\_200 dataset as slope \* 0.01 (e.g., 12% slope = 0.12 PrecLossFrac). We acknowledge that this is a simplification and that better parameterization would be possible if soil types were available for each site. Tests showed that sites with extreme slope tended to have lower biomass, but the signal was not that clear. The correlation between slope and elevation was 0.6 which could obscure the results.

Some sites at very high elevation had, correspondingly, very low temperature. At these sites, the model showed a visible trend in producing lower biomass (down to zero at a few sites). Yet this was probably not apparent in the regeneration results, as extremely low biomass could still support regeneration, even if cohorts do not live long, due to our modification of sexual maturity age.

### 1.10.6 Tree species

As LANDIS-II cannot start from bare ground, initial communities were set to include all species defined in the protocol at all sites starting with 10-years old cohorts of the following species: fasy (*Fagus sylvatica*), pabi (*Picea abies*), abal (*Abies alba*), cabe (*Carpinus betulus*), tico (*Tilia cordata*), acps (*Acer pseudoplatanus*), betu (*Betula spp.*), frex (*Fraxinus excelsior*), quer (*Quercus spp.*), algl (*Alnus glutinosa*), pisy (*Pinus sylvestris*). The species-specific parameter denoting sexual maturity was set to 10 years equally for all species, so that seed source of all species is available from the onset of the simulations at all sites and to maintain seed in the landscape pool. Vegetative regeneration (resprouting) was prevented, since this would have an effect on allometry and regeneration.

Some species may be under or overrepresented because their occurrence in LANDIS-II simulations is typically due to small-scale disturbances or management which were not included in the simulations.

The model requires two sets of parameters representing species-specific life traits. The first set is used by the LANDIS-II core module. The species-specific parameter denoting “longevity” and “sexual maturity” were the only parameters of this set considered in the current exercise. The “sexual maturity” was set to 10 years equally for all species, so that seed source of all species is available from the onset of the simulations at all sites and to maintain seed in the landscape pool. Vegetative regeneration (resprouting) was prevented since this would influence allometry and regeneration.

The second set is used by the PnET-Succession extension and includes several ecophysiological parameters. For this second set we started with the values already applied in Petter et al. (2020) with a previous version of PnET. The values of some of the parameters to which PnET is most sensitive and/or for which the range of variation had been modified for PnET4.1 were then iteratively adjusted (individually and then in combination) to meet the requirements of PnET version 4.1 used in this exercise. The changes were implemented one by one in simulations with the exercise data and those leading to an output deemed realistic and to a relative stabilization of the biomass trend through the simulation were retained for the implementation of the full set of replicates. The retained changes include: 1) decreased percentage of foliar nitrogen for *algl* (*Alnus glutinosa*); 2) rescaling to the new ranges for all species of the values of the Halfsat and the FracBelowG. The first of these parameters represents shade tolerance and its value affects the probability of establishment of a species (Half saturation light level for photosynthesis.); the latter regulates allocation between

above and below ground pool (Fraction of non-foliar biomass that is belowground (root pool)) ; 3)  
a slight decrease of the value of the parameter (Fracfol) affecting the yearly allocation to foliage  
of the active total woody biomass for the three conifers abal (*Abies alba*), piab (*Picea abies*), pisy  
(*Pinus sylvestris*).

### 1.10.7 Simulation

Simulation area was defined as a rectangle of 10×20 dimension with sites (i.e., cells) of 1-ha. Each  
site is an individual ecoregion (i.e., one cell - as in our case - or group of cells sharing similar  
climate and soil conditions, as a way in LANDIS-II to define differences in biophysical conditions  
across landscapes) with specific values for soil quality, topography and climate, based on the data  
provided. The model runs with a yearly timestep using monthly climate. We started each model  
run with initial communities of all species at age 10 at all sites. Each run was simulated for 1980  
years.

**1.10.7.1 Dispersal** We have used the non-spatial seeding algorithm “universal dispersal” for all  
the model runs. This way, every species can seed any forest site in the landscape (across all the  
200 sites). This mode does not take into account the spatial arrangement and contiguity of cells  
(i.e., no active seed dispersal), which is proper for the sake of the model comparison exercise. Yet  
in real landscape seed limitation can also play a role in species composition. The seed number  
is affected by species-specific age of maturity, which we have modified. This setting ensures an  
influx of seeds from outside consistent with the original settings.

### 1.10.7.2 Sampling design

We have sampled each site 20 times along the simulation run in two time windows starting 50 years after the first cycle following typical species longevity. After the year 700, biomass of most species was relatively stable and we sampled every 50 years, starting at 750 until the year 1200. The next sampling period started from 1450 and continued until 1900, i.e., after the next longevity peak, again every 50 years. At each selected sampling time, we extracted cohorts of each species according to the age related to the two DBH thresholds (7cm/10cm). Additionally, we extracted cohorts that were up to 9 years older than these thresholds, to get the expected results for a 10-year interval. For example, *Fagus sylvatica* reaches DBH 7cm at 17 years, therefore we have selected all cohorts with age 17-26.

To deliver more than one simulation per site, we created 10 replicates with different climate replicate and random number generator seed number to account for stochastic processes in PnET-Succession. This resulted in the expected 200 samples for each site.

### 1.10.8 Outputs

#### Sample number code

Number (1-200) was defined as sample in time + (replicate-1)\*20, with sample in time (1-20) according to the sample order. Replicate (1-10) combines random number and climate sequence. For example sample number 25 was taken from the climate replicate 2 and the fifth sample in time (year 950).

#### r.trees

As LANDIS-II outputs are expressed in terms of cohort age and mean biomass per site, we have calculated the mean DBH and biomass of each species based on age. We estimated the age when

each species reaches 7 cm and 10 cm DBH and the number of individuals using allometric models from the Italian forest inventory collected in R package ForIT (Puletti et al. 2014), and unpublished data from the study by Mina et al. (2021). Please note that the equations used predict DBH >0 already for a tree with age 1, this is because it is based on forestry data and tree cores. The real age when reaching 1.3 m height is species specific and we did not implement this offset. For each cohort, we divided the cohort biomass reported by LANDIS-II, recalculated to kg/ha by the mean biomass of a tree of the same species and age to obtain the number of trees of each species per site. We rounded all results up to the nearest integer to avoid any fraction of trees. The number of individuals was aggregated for all the cohorts of the age of reaching 7 cm or 10 cm DBH and all cohorts of the same species that were up to 9 years older. This approach does not reflect influence of site conditions or stand densities on Age-DBH and Age-Biomass. Relationships between age and DBH were derived by fitting asymptotic regressions using individual tree measurements from an ensemble of forest inventory plots distributed across south-eastern Canada (see Supporting information of Mina et al. 2021). This was the only public dataset for which we could relate tree age, derived from stem coring and tree ring analysis, to measured DBH. Although tree age measurements were obtained with a robust methodology, these functions do not disentangle the influence of site conditions or stand densities. Additionally, they reflect growing conditions of tree genera in Eastern North America.

r.ba basal area of regeneration Calculated as a sum of r.ba of all the cohorts selected in r.trees using the following formula:  $DBH^2 * \pi/4 * r.tree$ .

ba: total basal area We have not calculated this since our allometric equations do not cover older ages. Therefore, we produced the following two biomass variables as a surrogate. The basal area

was later calculated as a sum of  $r.ba$  and estimated  $ba$  based on biomass. The estimation includes transformation of  $kg$  into tonnes / ha and expansion factor 12.5 to transform  $ba\ m^2/ha$ .

$(( (landis\$sum.bio - landis\$r.bio.sum) * 0.001) / 12.5)$ . This includes

$sum.bio$

Biomass of all cohorts of the species on site including the regeneration and even younger regeneration (units  $kg/ha$ ).

$r.bio.sum$  Biomass of the regeneration cohorts corresponding to the  $r.ba$  and  $r.trees$  on site (units  $kg/ha$ ).

Please notice that we included 0 values for species missing in a given sample and for samples in sites where Landis did not simulate any tree.

#### 1.10.9 References

Aber J. D. & Federer C. A. (1992). A generalized, lumped-parameter model of photosynthesis, evapotranspiration and net primary production in temperate and boreal forest ecosystems. *Oecologia* 92(4): 463-474.

Aber J.D., Ollinger S.V., Federer C.A., Reich P.B., Goulden M.L., Kicklighter D.W., Melillo J.M. & Lathrop R.G. Jr. (1995) Predicting the effects of climate change on water yield and forest production in the northeastern United States. *Climate Research* 5(3): 207–22.

de Bruijn A., Gustafson E.J. , Sturtevant B.R., Foster J.R., Miranda B.R., Lichti N.I. & Jacobs D.F. (2014) Toward more robust projections of forest landscape dynamics under novel environmental conditions: Embedding PnET within LANDIS-II. *Ecological Modelling* (287): 44–57

- EEA (2019) Trends in atmospheric concentrations of CO<sub>2</sub> (ppm), CH<sub>4</sub> (ppb) and N<sub>2</sub>O (ppb), between 1800 and 2017 available at [https://www.eea.europa.eu/ds\\_resolveuid/217c026ca03649398aadf39d87623e5](https://www.eea.europa.eu/ds_resolveuid/217c026ca03649398aadf39d87623e5)
- Gustafson, E. J., A. M. G. De Bruijn, R. E. Pangle, J.-M. Limousin, N. G. McDowell, W. T. Pockman, B. R. Sturtevant, J. D. Muss, and M. E. Kubiske. 2015. Integrating ecophysiology and forest landscape models to improve projections of drought effects under climate change. *Global Change Biology* 21:843-856.
- Mina, M., Messier, C., Duveneck, M., Fortin, M. J., & Aquilué, N. 2021. Network analysis can guide resilience-based management in forest landscapes under global change. *Ecological Applications*, 31(1), 1–18.
- Petter G., Mairota P., Albrich K., Bebi P., Bruna J., Bugmann H., Haffenden A., Scheller R.M., Schmatz D.R., Seidl R., Speich M., Vacchiano G. & Lischke H. (2020) How robust are future projections of forest landscape dynamics? Insights from a systematic comparison of four forest landscape models. *Environmental Modelling & Software* 134: 104844. <https://doi.org/10.1016/j.envsoft.2020.104844>
- Puletti N., Mura M., Castaldi C., Marchi N., Chiavetta U. and Scotti R. (2014). ForIT: Functions from the 2nd Italian Forest Inventory (INFC). R package version 1.0. <https://CRAN.R-project.org/package=ForIT>
- Scheller, R. M., Domingo J. B. , Sturtevant B. R. , Williams J. S. , Rudy A. , Gustafson E. J. & Mladenoff D. J. (2007) Design, development, and application of LANDIS-II, a spatial landscape simulation model with flexible temporal and spatial resolution. *Ecological Modelling* 201(3-4): 409–419. <https://doi.org/10.1016/j.ecolmodel.2006.10.009>

Tsubo M. & Walker S. (2005) Relationships between photosynthetically active radiation and clear-  
ness index at Bloemfontein, South Africa. Theoretical and Applied Climatology 80: 17–25. <https://doi.org/10.1007/s00704-004-0080-5>

## 1.11 TreeMig

### 1.11.1 Authors

Heike Lischke

### 1.11.2 Model

The model TreeMig (see [treemig.wsl.ch](http://treemig.wsl.ch)) was originally based on the ForClim model, then aggregated by a distribution based approach (Lischke et al. 1998), and extended to a forest landscape model by including seed production, seed dispersal, seed bank dynamics and seedling establishment (Lischke and Löffler 2006, Lischke et al. 2006).

The most complete reference resource for the TreeMig model and regeneration module are:

- Lischke, H., T. J. Löffler, and A. Fischlin. 1998. Aggregation of individual trees and patches in forest succession models: Capturing variability with height structured, random, spatial distributions. Theor Popul Biol 54:213-226.
- Lischke, H., N. E. Zimmermann, J. Bolliger, S. Rickebusch, and T. J. Löffler. 2006. TreeMig: A forest-landscape model for simulating spatio-temporal patterns from stand to landscape scale. Ecological Modelling 199:409-420.



- Lischke, H., and T. J. Löffler. 2006. Intra-specific density dependence is required to maintain species diversity in spatio-temporal forest simulations with reproduction. *Ecological Modelling* 198:341-361.
- The online resources available at [treemig.wsl.ch](http://treemig.wsl.ch)

### 1.11.3 Climate

As climatic input, the monthly time series of mean temperature and precipitation sum were used. With these climatic variables and additional data about slope, aspect and soil field capacity, yearly time series of the following bioclimatic variables were calculated: (1) DDSum, the yearly day degree sum above 5.5°C, (2) MinWiT, the lowest mean monthly temperature, (3) DrStr, drought stress according to a bucket model that estimates a monthly PET following (Thornthwaite and Mather 1957), using temperature, latitude, slope and aspect as input, and calculates the monthly soil water content based on soil water content in the previous month, precipitation, interception, and field capacity (“bucketsize”) (Bugmann 1994, Fischlin et al. 1995). Drought stress is then given by 1 - the ratio between demand (PET-interception) and the supply, a function of the soil water content. To get climate data also for the spin-up, bioclimate was calculated from the monthly data as given, and then extended by sampling from the given data from the end of the climate data to get 1000 years. The same sequence of sampling years was used in all simulations and sites.

### 1.11.4 Soil

The soil bucketsize (available water capacity of the upmost 1m soil layer) required for the drought stress calculation, was derived from the soil quality data set, by  $\text{Bucketsize} = 10 + (\text{soil\_quality} - 1)$

945  $/4 * 25$  , to covert the range from 10 cm to 35cm

#### 946 **1.11.5 Topography**

947 Slope and aspect were taken from the topographic data set and converted to a common variable  
948 entering the PET calculation, by  $slasp = 2\cos(aspect \pi/180) * \min(1, slope/60)$

#### 949 **1.11.6 Tree species**

950 Thirty Central European tree species were simulated, including the standard species of the project  
951 . Only *Betula pubescens* was not simulated, because we did not have a parametrization for this  
952 species at hand. Species: *Abies alba*, *Larix decidua*, *Picea abies*, *Pinus cembra*, *Pinus montana*,  
953 *Pinus sylvestris*, *Taxus baccata*, *Acer campestre*, *Acer platanoides*, *Acer pseudoplatanus*, *Alnus*  
954 *glutinosa*, *Alnus incana*, *Alnus viridis*, *Betula pendula*, *Carpinus betulus*, *Castanea sativa*, *Corylus*  
955 *avellana*, *Fagus sylvatica*, *Fraxinus excelsior*, *Populus nigra*, *Populus tremula*, *Quercus petraea*,  
956 *Quercus pubescens*, *Quercus robur*, *Salix alba*, *Sorbus aria*, *Sorbus aucuparia*, *Tilia cordata*, *Tilia*  
957 *platyphyllos*, *Ulmus glabra*

#### 958 **1.11.7 Simulation**

959 The simulations were carried out on a grid of 15 x 15 cells, each with 200 m side length.

960 **1.11.7.1 Dispersal** The seeds produced by the mother trees are transported from the source cell  
961 according to a double negative exponential, species specific that determines the share of the seeds  
962 in the source cell landing in a sink cell in a given distance to the source cell. In the sink cells,

the seeds enter the seed bank . At the start of the simulation for 10 years seeds of all species are available in all grid cells, from then on, the normal seed dispersal starts.

**1.11.7.2 Regeneration processes** TreeMig simulates the full feedback from seed production to ingrowth. Some of the involved processes depend on environment. (1) Overall seed production in TreeMig is described by multiplying a species specific seed production per tree that depends on tree size and thus indirectly on the growth, which depends on DDsum, drought stress, nutrients and light and the adult tree number that depends on survival that depends on DDsum, drought stress, nutrients and light. (2) Seed dispersal is independent of environment. (3) Seed bank dynamics – also environment independent - is given by seed input, seed mortality, and germination. Additionally, the number of seeds  $S$  of a species in the seed bank of this species ( $SB$ ) is limited to a carrying capacity  $C$  of 1000, by

$$SB = C + (SB - C) * \text{Exp}(-S/C).$$

(4) Germination and seedling survival depend on browsing, drought, winter temperature, DDsum and light. (5) The saplings up to 1.37 die and grow like adult trees, depending on DDsum, drought stress and light. Only the parameter value of the light dependence differs from that of the adult trees.

The regeneration processes were simulated annually in the order 1. germination, 2. germinated seeds leave the seed bank, 3. mortality of seeds in the seed bank, 4. seed entry by seed dispersal. The ingrowth numbers were very sensitive to this order. Simulations with another sequence, in which the seeds in the seed bank died first and then the remaining ones germinated, resulted in about half the ingrowth.

**1.11.7.3 Simulation length** The simulations were started on bare ground and run for 1000 years, when at all sites the equilibrium was reached.

**1.11.7.4 More simulations per site** TreeMig simulates directly the mean dynamics of entire stands, but based on the variability of light conditions within the stand [distribution based approach, Lischke, 1998, aggregation. To come up with the required 200 random patches of 1 ha, temporal and spatial variability intrinsic to TreeMig were combined. Temporal variability was given by sampling from each decade of the last 100 years of the simulation, i.e. years 900-1000. For each of these 10 decades, 20 grid cells were sampled from the simulated grid, reflecting spatial variability, results from demographic stochasticity and short-range spatial interactions

### **1.11.8 Outputs**

In contrast to gap models, TreeMig is based on the concept of frequency distributions of tree densities classes in different tree heights on ca. 1/12 ha (833m<sup>2</sup>) patches, and the resulting frequency distributions in discrete light. During the simulation, in each height class the frequencies of the different light classes were recorded, as well as the ingrowth of each species in the height-light class. By sampling 12 times from the height-light class ingrowths according to the height-light class frequency distribution and summing up, the stochastic ingrowths into all TreeMig height classes for one ha were calculated for each grid cell. Then the height class boundaries were translated into DBH and the ingrowths into the height classes linearly interpolated to 7cm and 10cm. The ingrowth basal areas into the height classes were obtained by multiplying the interpolated ingrowth numbers with the basal areas at 7cm and 10cm, i.e.  $r.trees * \pi * (0.07/2)^2$  and  $r.trees * \pi * (0.1/2)^2$ . The species specific basal area (at 1.37m) sums are a standard output of TreeMig, given by multi-

plying the state variables (number of trees per grid cell, height class, and species) with the species specific basal area of each height class. To account for the ingrown trees dying within a decade, as an approximation the survival in each year to the power of 5 was used. Thereby, it was assumed that the trees have to survive in average 5 years in each decade, and that the current mortality is valid for these 5 years.

### 1.11.9 References

- Bugmann, H. 1994. On the ecology of mountainous forests in a changing climate: A simulation study. Dissertation. Swiss Federal Institute of Technology, Zurich.
- Fischlin, A., H. Bugmann, and D. Gyalistras. 1995. Sensitivity of a forest ecosystem model to climate parametrization schemes. *Env. Poll.* 87:267-282.
- Lischke, H., and T. J. Loffler. 2006. Intra-specific density dependence is required to maintain species diversity in spatio-temporal forest simulations with reproduction. *Ecological Modelling* 198:341-361.
- Lischke, H., T. J. Loffler, and A. Fischlin. 1998. Aggregation of individual trees and patches in forest succession models: Capturing variability with height structured, random, spatial distributions. *Theor Popul Biol* 54:213-226.
- Lischke, H., N. E. Zimmermann, J. Bolliger, S. Rickebusch, and T. J. Loffler. 2006. TreeMig: A forest-landscape model for simulating spatio-temporal patterns from stand to landscape scale. *Ecological Modelling* 199:409-420.
- Thornthwaite, C. W., and J. R. Mather. 1957. The water balance. *Publications in Climatology*

1025 VIII:1-69.

## 1026 **1.12 LPJ-GUESS**

### 1027 **1.12.1 Authors**

1028 Tim Anders, Jessica Hetzer, Thomas Hickler

### 1029 **1.12.2 Model**

1030 The model was originally developed by Ben Smith of Lund University in a collaboration also in-  
1031 volving the Potsdam Institute for Climate Impact Research and the Max-Planck Institute for Bio-  
1032 geochemistry. Over the years, many people from institutes around the world have contributed to  
1033 the refinement and further development of the model.

1034 We used the process-based mechanistic model LPJ-GUESS to simulate vegetation dynamics con-  
1035 sidering tree species, age cohorts, gap dynamics and biogeochemical cycles. Parameters of the  
1036 model reflect an updated version of the most common European tree species as well as typical  
1037 shrub PFTs as described by Hickler et al. (2012).

1038 The most complete reference resource for the LPJ-GUESS model and regeneration module is:

- 1039 • Smith, B. (2001). LPJ-GUESS-an ecosystem modelling framework. Department of Physical  
1040 Geography and Ecosystems Analysis, INES, Sölvegatan, 12, 22362.
- 1041 • Smith, B., Wårlind, D., Arneth, A., Hickler, T., Leadley, P., Siltberg, J., & Zaehle, S.  
1042 (2014). Implications of incorporating N cycling and N limitations on primary production

in an individual-based dynamic vegetation model. *Biogeosciences*, 11(7), 2027-2054.

- Source code is available on demand (see <https://web.nateko.lu.se/lpj-guess/>).

### 1.12.3 Climate

We used the provided daily time series of climatic variables from 1981 to 2018. The climatic variables base on the CHELSA data set with a spatial resolution of  $0.008^{\circ} \times 0.008^{\circ}$  (~ 1 km) (Karger et al., 2021). Daily average temperature (tas) [°C], daily average maximum temperature (tasmax) [°C], daily average minimum temperature (tasmin) [°C], precipitation sum (pr) [mm] and surface solar (shortwave) radiation (rsds) were taken to set up the LPJ-GUESS simulation. Used climatic variables were converted to netCDF files. As LPJ-GUESS requires the climatic variables in specific units, temperature variables (tas, tasmax, tasmin) [°C] were converted to Kelvin and surface solar radiation (rsds) [Jm<sup>-2</sup>] was converted to W/m<sup>2</sup> by dividing rsds by 86400 s (3600 s/h \* 24 h). Nitrogen deposition was considered to be constant at a level of 10 kgN/ha/year. Atmospheric carbon dioxide concentration data from 1900 to 2018 was taken from the global carbon project (Quéré et al. 2018).

### 1.12.4 Soil

All sites were simulated with default values for a medium textured soil type (sand: 0.35, clay: 0.15, silt: 0.5) in LPJ-GUESS.

### 1.12.5 Topography

Topography was not considered.

### 1.12.6 Tree species

LPJ-GUESS can be run in different modes, with different levels of abstraction of the population and community processes. For this study, the more detailed ‘cohort’ mode was used, in which individuals, patches and vertical canopy structure are represented explicitly, but living individuals within a cohort (age class) of a given tree species in a given patch are assumed to be identical (in terms of all state variables, such as height and stem diameter). Simulations consider the main tree species as well as other PFTs yielding an appropriate representation of European vegetation, including only tree and shrub species that are widely distributed across Europe and can become dominant in some areas (Hickler et al., 2012). Mediterranean rain-green small shrubs with shallow roots (e.g. *Lavendula* spp., *Rosmarinus* spp.) and alpine/arctic shrubs (e.g. *Vaccinium* spp.) were represented as PFTs in the model. As in earlier applications of LPJ-GUESS, herbaceous vegetation was represented by two ‘generic herb’ PFTs, with C3 and C4 photosynthesis, respectively. The final set included 16 tree species, one Mediterranean shrub PFT, one boreal/alpine shrub PFT, and the two herbaceous PFTs described earlier (Table 2). To increase the chances of shade-intolerant species becoming established, patch-destroying disturbances were allowed as described in Hickler et al. 2012. *Acer pseudoplatanus* and *Alnus glutinosa* are not parameterized in LPJ-GUESS and therefore not considered.

### 1.12.7 Simulation

In this study, vegetation is simulated in so called patches that represent forest areas of fixed size. Patches can be regarded as sample stands in a grid cell, each of which represents an 0.1 ha (comparable to figure 1 of the tree regeneration workshop protocol). In this study, vegetation dynamics



were simulated by 2000 replicate patches each 0.1 ha in size. To match the required sample size, we processed the data so that ten 0.1 ha patches were merged to one 1 ha sample.

**1.12.7.1 Dispersal** Model formulations of establishment are based on those employed within the ‘forest gap’ model FORSKA (Leemans & Prentice, 1989; Prentice et al., 1993). The number of new saplings of each woody PFT/species and in each patch each year is drawn at random from the Poisson distribution, with an expectation influenced by a PFT/species-specific maximum establishment rate and by the ‘propagule pool’, i.e. the amount of carbon allocated to reproduction by all individuals of the PFT/species at all patches in the previous year. No saplings are established in a given patch if the minimum PAR level at the forest floor is below a PFT/species-specific threshold, which is higher for more light-demanding PFTs/species.

**1.12.7.2 Simulation length** What is the simulation length, and how have you determined the simulation time until the equilibrium?

The simulations were initialized from bare ground (no biomass) and the model was spun up for 500 years until the modelled vegetation was in approximate equilibrium with the climate and CO<sub>2</sub> around the year 1900 (Smith et al., 2001; Hickler et al., 2012).

If you have run more than one simulation per site, please describe the differences of the approaches used. We performed one simulation per site.

## **1.12.8 Output**

The generated output file is called Output\_SGN\_LPJGUESS.txt. Each row of the output dataset contains variables regarding the decade 2008-2018. The first two columns describe the study site

(column “site”, values reflect site ID) and the 1 ha samples of that specific site (column “sample”, values range from 1 to 200). Output variables are species-specific. Although we simulated a total of 20 European tree species and PFTs, our output file considers only the species required by the protocol (column “species”, values are the abbreviations for the species name (“abal” for *Abies alba*, “cabe” for *Carpinus betulus*, “fasy” for *Fagus sylvatica*, “frex” for *Fraxinus excelsior*, “pabi” for *Picea abies*, “pisy” for *Pinus sylvestris*, “tico” for *Tilia cordata*, “betu\_pen” for *Betula pendula*, “betu\_pub” for *Betula pubescens*, “quer\_il” for *Quercus ilex*, “quer\_pub” for *Quercus pubescens*, and “quer\_rob” for *Quercus robur*). Since *Acer pseudoplatanus* (“acps”) and *Alnus glutinosa* (“algl”) are not parameterized for LPJ-GUESS so far, we have not included these species in the output. Further we excluded shrubs (alpine/arctic shrubs and *Quercus coccifera*) and herbaceous vegetation from the final output as this study focusses on tree regeneration only. The first variable is the number of 7 cm recruits “r\_7cm.trees” calculated as the sum of all trees of the same species that cross the threshold of 7 cm DBH between 2008 and 2018 in that specific sample of that specific site. The variable “r\_10cm.trees” refers to 10 cm threshold respectively. The 7 cm recruits’ basal area „r\_7cm.ba” is calculated as a weighted sum of r\_7cm.trees multiplied by recruits basal area at that time (with  $ba = (dbh/2) \cdot \pi$ ). Similarly, r\_10cm.ba was calculated for 10 cm recruits. The last two columns describes the mean annual basal area and the mean number of trees per site, sample, and species overall years between 2008 and 2018 (column “ba”).

Table 1: Species/PFT characteristics and parameter of Hickler et al. 2012. r base respiration rate, kallm1 constant in allometry equations, Tc,min minimum winter temperature for establishment, Tc,max maximum coldest-month temperature for establishment, GDD5 minimum degree-day sum above 5 °C for establishment, fAWC minimum growing-season fraction of available soil

water holding capacity in the first soil layer, rfire fraction of individuals surviving fire, kla:sa leaf longevity, CAm<sub>max</sub> maximum woody crown area. Parameter that are associated with establishment processes are marked in bold. Species/PFT

Species/PFT	Short name	Geographic range	$P^{*1}$ (gCgN/day <sup>1</sup> )	Growth form	$K_{0.001}^{*2}$	$T_{2.001}^{*3}$ (°C)	$T_{0.001}^{*4}$ (°C)	$GDD^{*5}$ (°Cd)	IAWC	Chilling requirement <sup>6</sup>	Shade tolerance class	$f_{\text{fire}}$	$K_{0.12}^{*7}$	$Z_{1+}^{*8}$	$R_{\text{low}}^{*9}$ (yr)	$R_{\text{high}}^{*10}$ (yr)	$CA_{\text{max}}^{*11}$ (m <sup>2</sup> )
<i>Abies alba</i>	abal	temperate	0,055	tree	150	-4,5	-2	1450	0,35	-	tolerant	0,1	4000	0,8	4	350	40
<i>Betula pendula</i>	betu_pen	temperate	0,055	tree	250	-30	-	700	0,42	intermediate	intolerant	0,1	5000	0,8	0,5	200	40
<i>Betula pubescens</i>	betu_pub	boreal	0,11	tree	250	-	-	350	0,5	intermediate	intolerant	0,1	5000	0,8	0,5	200	40
<i>Carpinus betulus</i>	cabe	temperate	0,055	tree	250	-8	-	1200	0,33	high <sup>12</sup>	intermediate	0,1	5000	0,7	0,5	350	40
<i>Corylus avellana</i>	cor_ave	temperate	0,055	tree	250	-8	-	800	0,3	intermediate	intolerant	0,1	4000	0,7	0,5	300	15
<i>Fagus sylvatica</i>	fasy	temperate	0,055	tree	250	-9,5	-	1500	0,3	high <sup>12</sup>	tolerant	0,1	5000	0,8	0,5	500	40
<i>Fraxinus excelsior</i>	frex	temperate	0,055	tree	250	-16	-	1100	0,4	low	intermediate	0,1	5000	0,8	0,5	350	40
<i>Juniperus oxycedrus</i>	jun_oxy	Mediterranean	0,055	shrub	150	0	-	2200	0,01	-	intolerant	0,4	1500	0,5	1,5	200	10
<i>Picea abies</i>	pabi	boreal	0,11	tree	150	-30	-1,5	600	0,43	-	tolerant	0,1	4000	0,8	4	500	40
<i>Pinus halepensis</i>	pin_hal	Mediterranean	0,055	tree	150	3	-	3000	0,05	-	intolerant	0,4	2000	0,6	2	350	40
<i>Pinus sylvestris</i>	pisyl	boreal	0,11	tree	150	-30	-1	500	0,25	-	intermediate	0,4	2000	0,6	2	500	40
<i>Quercus coccifera</i>	quer_coc	Mediterranean	0,055	shrub	250	0	-	2200	0,1	-	intermediate	0,3	2500	0,5	1,5	350	10
<i>Quercus ilex</i>	quer_il	Mediterranean	0,055	tree	250	-2	-	1800	0,1	-	intermediate	0,3	3000	0,5	2	350	40
<i>Quercus pubescens</i>	quer_pub	supra-Mediterranean	0,055	tree	250	-5	-	1900	0,2	low	intermediate	0,2	4000	0,6	0,5	500	40
<i>Quercus robur</i>	quer_rob	temperate	0,055	tree	250	-16	-	1100	0,25	low	intermediate	0,2	4000	0,6	0,5	500	40
<i>Tilia cordata</i>	tico	temperate	0,055	tree	250	-18	-	1000	0,33	high <sup>12</sup>	intermediate	0,1	5000	0,8	0,5	350	40
Boreal evergreen shrub <sup>*</sup>	BES	boreal	0,11	shrub	250	-	-1	300	0,25	-	intolerant	0,1	500	0,8	2	50	3
Mediterranean raingreen shrub <sup>*</sup>	MRS	Mediterranean	0,055	shrub	250	0	-	2200	0,01	low	intolerant	0,3	1500	0,8	1	100	10
C <sub>3</sub> herbaceous		temperate-boreal	0,055	herbaceous	-	-	-	-	0,01	-	-	0,5	-	0,9	1	-	-
C <sub>4</sub> herbaceous		tropical	0,011	herbaceous	-	15,5	-	-	0,01	-	-	0,5	-	0,9	1	-	-

## 1.12.9 References

- Hickler, T., Vohland, K., Feehan, J., Miller, P. A., Smith, B., Costa, L., ... & Sykes, M. T. (2012). Projecting the future distribution of European potential natural vegetation zones with a generalized, tree species-based dynamic vegetation model. *Global Ecology and Biogeography*, 21(1), 50-63.
- Karger, D. N., Lange, S., Hari, C., Reyer, C. P., & Zimmermann, N. E. (2021). CHELSA-W5E5 v1. 1: W5E5 v1. 0 downscaled with CHELSA v2. 0.
- Leemans, R., & Prentice, I. C. (1989). FORSKA-a general forest succession model. *Meddelanden*

Från Växtbiologiska Institutionen. Prentice et al., 1993

Quéré, C., Andrew, R. M., Friedlingstein, P., Sitch, S., Hauck, J., Pongratz, J., ... & Zheng, B. (2018). Global carbon budget 2018. *Earth System Science Data*.

Smith, B. (2001). LPJ-GUESS-an ecosystem modelling framework. Department of Physical Geography and Ecosystems Analysis, INES, Sölvegatan, 12, 22362.

Smith, B., Wårlind, D., Arneth, A., Hickler, T., Leadley, P., Siltberg, J., & Zaehle, S. (2014). Implications of incorporating N cycling and N limitations on primary production in an individual-based dynamic vegetation model. *Biogeosciences*, 11(7), 2027-2054.

## **1.13 aDGVM2**

### **1.13.1 Authors**

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### **1.13.2 Model**

We used aDGVM2, an individual-based dynamic vegetation model that is based on concepts from community assembly theory and uses a functional trait approach (Langan et al., 2017; Scheiter et al., 2013). The model simulates growth, reproduction, and mortality of individual plants while keeping track of state variables, such as biomass, height, and leaf area. Each plant in aDGVM2 is characterized by a plant-specific set of trait values. Traits describe growth form, leaf characteristics, hydraulic characteristics, resource allocation, architecture, reproduction, mortality, and

response to disturbance. Most plant traits are linked by trade-offs to constrain possible trait combinations. Selection and trait inheritance assemble plant communities that are adapted to biotic and abiotic conditions. Plants with trait combinations that allow sufficient growth and reproduction rates, and that allow plants to cope with competition and disturbances can contribute their trait values to the community trait pool. Trait mutation and recombination may alter trait values in the community trait pool. Randomly drawn seeds from the trait pool are added to the plant population and new plants start growing from seeds. Plants that are not adapted to the prevailing disturbance regimes, biotic and abiotic conditions, or that do not allocate enough carbon to reproduction disappear from the population. Therefore, successful ecological strategies emerge dynamically from these community assembly and reproduction process. Due to the trait-based approach, species or plant functional types (PFTs) are not pre-defined and hard-coded in aDGVM2. Rather, different PFTs or ecological strategies that are adjusted to the prevailing biotic and abiotic conditions emerge from community assembly processes (Scheiter et al., 2013), and plants can be classified into PFTs or ecological strategies based on their trait values in a post-processing step. The aDGVM2 has primarily been developed for tropical and sub-tropical ecosystems and it has not been tested and benchmarked for Europe. We applied the model in the original version. Data-model comparisons with model results were not done and the model was not changed to improve agreement with any data for Europe.

The most complete reference resource for the aDGVM2 model and regeneration module is:

- Scheiter S, Langan L, Higgins SI (2013) Next generation dynamic global vegetation models: learning from community ecology. *NEW PHYTOLOGIST*, 198, 957-969.

### 1.13.3 Climate

The aDGVM2 simulates vegetation at daily temporal resolution. We therefore used daily climate input data for the period 1981-2018 according to the modeling protocol.

### 1.13.4 Soil

Soil quality data was converted to maximum rooting depth. Specifically, the soil quality value multiplied by 2 and the result was used as maximum rooting depth. We used the multiplication, as we typically use maximum soil depth and maximum rooting depth of 10m. Previous model simulations showed that rooting depth and soil dept have strong impacts on vegetation dynamics by influencing water availability to plants (Langan et al., 2017). We therefore considered it as adequate representation of soil quality. Other soil characteristics including volumetric water-holding capacity, soil hydraulic conductivity, soil bulk density, soil depth, soil texture, soil carbon content, soil wilting point and field capacity were taken from the FAO (<http://www.fao.org>, Nachtergaele et al., 2009).

### 1.13.5 Topography

We used elevation according to the modeling protocol. In aDGVM2, elevation is used to calculate atmospheric pressure which in turn influences ecophysiological processes related to water and carbon fluxes at leaf and canopy level. Information on slope and aspect was not used, as related processes (e.g., impacts on runoff or radiation balance) are not implemented in aDGVM2.

### 1.13.6 Tree species

The aDGVM2 does not simulate pre-defined species or PFTs. The 11 tree species included in the modeling protocol cannot be implemented and parametrized with reasonable effort. We therefore classified simulated trees into different ecological strategies as a post-processing step. We used all combinations of evergreen/deciduous, light/water triggered phenology, low/high SLA. Evergreen/deciduous phenology and light/water triggered phenology are traits implemented in aDGVM2. The threshold to distinguish high and low SLA was defined as 20 m<sup>2</sup>/kg. We used these traits as previous simulation experiments showed that patterns of these traits emerge along environmental gradients while patterns of other traits implemented in aDGVM2 are often less clear. Ecological strategies considered are: low SLA, deciduous, rain-triggered; low SLA, deciduous, light-triggered; low SLA, evergreen, rain-triggered; low SLA, evergreen, light-triggered; high SLA, deciduous, rain-triggered; high SLA, deciduous, light-triggered; high SLA, evergreen, rain-triggered; high SLA, evergreen, light-triggered.

### 1.13.7 Simulations

Simulations followed the modeling protocol. Simulations were conducted for all sites using the provided daily climate and soil data. By default, aDGVM2 simulates 1ha stands. To implement the modeling protocol, adjustments to scale model results to 1 ha level were therefore not required. The model was initialized by default initialization routines, i.e., traits of individual plants were drawn randomly from a pre-defined range of values for each trait. Ranges of trait values are provided in Langan et al. (2017). The model was initialized with bare ground and 2880 tree seedlings with 100g each. The aDGVM2 simulates both trees and grasses. As the simulation experiment aims at

tree/forest regeneration, simulations were conducted only with trees while grasses were removed.

We conducted 5 replicates for each of the 200 sites to account for stochastic processes in aDGVM2.

Stochastic processes include random initialization of trait values of initial plant populations, demo-

graphic processes such as plant mortality or selection of seeds from seed bank, or the community

assembly processes including mutation and cross-over. Climate time series used for different repli-

cates were identical such that variation between replicates can be attributed by stochastic processes

in aDGVM2.

Although aDGVM2 includes routines to simulate fire, simulations were conducted in the absence

of fire. Management was not simulated.

### **1.13.8 Dispersal**

The aDGVM2 does not simulate seed dispersal.

### **1.13.9 Simulation length**

We first conducted a 600-year spin-up with a randomized order of years 1981-2018 provided in the

CHELSA daily climate data. Spin-up is required to ensure that both state variables such as biomass

and tree cover and community trait composition have stabilized and are in a dynamic equilibrium

with climate. Previous model simulations showed that a 600-year spin-up is sufficient to reach such

an equilibrium state (Langan et al., 2017). Following the spin-up, we simulated transient vegetation

dynamics with daily CHELSA climate data for the period 1981-2018.



### 1.13.10 Outputs

To create output variables, we randomly selected 10-year periods within the transient phase (i.e., period 1981-2018 after spin-up phase) and calculated averages of all required output variables following the modeling protocol. The selected 10-year periods differed between sites and replicates.

The aDGVM2 does not simulate pre-defined species or PFTs and trees were classified into different ecological strategies (see section Tree species). Codes for the ecological strategies in the species column of the output files are: 1 - low SLA, deciduous, rain-triggered 2 - low SLA, deciduous, light-triggered 3 - low SLA, evergreen, rain-triggered 4 - low SLA, evergreen, light-triggered 5 - high SLA, deciduous, rain-triggered 6 - high SLA, deciduous, light-triggered 7 - high SLA, evergreen, rain-triggered 8 - high SLA, evergreen, light-triggered

Simulations were conducted for all 200 sites. We conducted 5 replicates per site to account for stochastic processes in aDGVM. In the output files, replicates are given as follows: Replicate 1 – sample 1:200 Replicate 2 – sample 201:400 Replicate 3 – sample 401:600 Replicate 4 – sample 601:800 Replicate 5 – sample 801:1000

### 1.13.11 References

Langan L; Higgins SI; Scheiter S (2017) Climate-biomes, pedo-biomes or pyro-biomes: which world view explains the tropical forest - savanna boundary in South America? JOURNAL OF BIOGEOGRAPHY, 44, 2319-2330.

Nachtergaele, F., van Velthuisen, H., Verelst, L., Batjes, N., Dijkshoorn, K., Van Engelen, V., Fischer, G., Jones, A., Montanarella, L., and Petri, M.: Harmonized world soil database (version

1253 1.1), FAO, Rome, Italy, IIASA, Laxenburg, Austria, 2009.

1254 Scheiter S, Langan L, Higgins SI (2013) Next generation dynamic global vegetation models: learn-

1255 ing from community ecology. NEW PHYTOLOGIST, 198, 957-969.

For Review Only

## 2 Appendix 2: Supplementary figures and tables

### 2.1 Ingrowth levels, tree diversity and mortality in tree establishment

Table S1: Number of total samples, samples with zero recruitment and the proportion of zero recruitment per model and observed data.

Model	Total (7 cm)	Total (10cm)	No recruitment (7 cm)	No recruitment (10cm)	Percentage of no recruitment (7 cm)	Percentage of no recruitment (10 cm)
Observed	5676	6564	203	238	3.63	3.58
4C	133000	165000	23898	30177	18.29	17.97
ForCEEPS	363000	440000	1	137	0.03	0.00
ForCEEPS(f)	363000	440000	42	202	0.05	0.01
FORMIND	363000	440000	8663	10082	2.29	2.39
ForClim 1	396000	480000	7	28	0.01	0.00
ForClim 11	396000	480000	77	192	0.04	0.02
SIBYLA	363000	440000	1565	5539	1.26	0.43
xComp	297000	360000	0	0	0.00	0.00
PICUS	363000	440000	400	400	0.09	0.11
iLand	363000	440000	26	143	0.03	0.01
LandClim	363000	440000	378	1347	0.31	0.10
Landis II	363000	440000	28621	34844	7.92	7.88
TreeMig	396000	480000	0	0	0.00	0.00
LPJ-GUESS	328000	398000	6742	7140	1.79	2.06
aDGVM2	6600	8000	603	824	10.30	9.14

Table S2: Test of the significance of the differences of Shannon index in each model for 7 and 10 cm threshold.

model	.y.	group1	group2	p	p.adj	p.format	p.signif	method
Observed	ShannonIndexRecruit	7	10	0.5752324	1.0e+00	0.5752300	ns	T-test
4C	ShannonIndexRecruit	7	10	0.0112379	7.9e-02	0.0112400	*	T-test
ForCEEPS	ShannonIndexRecruit	7	10	0.0022439	2.0e-02	0.0022400	**	T-test
ForCEEPS(f)	ShannonIndexRecruit	7	10	0.0001502	1.8e-03	0.0001500	***	T-test
FORMIND	ShannonIndexRecruit	7	10	0.0018175	1.9e-02	0.0018200	**	T-test
ForClim 1	ShannonIndexRecruit	7	10	0.0000000	2.0e-07	0.0000000	****	T-test
ForClim 11	ShannonIndexRecruit	7	10	0.0000078	1.0e-04	0.0000078	****	T-test
SIBYLA	ShannonIndexRecruit	7	10	0.0017112	1.9e-02	0.0017100	**	T-test
xComp	ShannonIndexRecruit	7	10	0.0089858	7.2e-02	0.0089900	**	T-test
PICUS	ShannonIndexRecruit	7	10	0.0343325	2.1e-01	0.0343300	*	T-test
iLand	ShannonIndexRecruit	7	10	0.0539118	2.7e-01	0.0539100	ns	T-test
LandClim	ShannonIndexRecruit	7	10	0.0000000	0.0e+00	0.0000000	****	T-test
Landis II	ShannonIndexRecruit	7	10	0.3486993	1.0e+00	0.3487000	ns	T-test
TreeMig	ShannonIndexRecruit	7	10	0.4182782	1.0e+00	0.4182800	ns	T-test
LPJ-GUESS	ShannonIndexRecruit	7	10	0.8213248	1.0e+00	0.8213200	ns	T-test

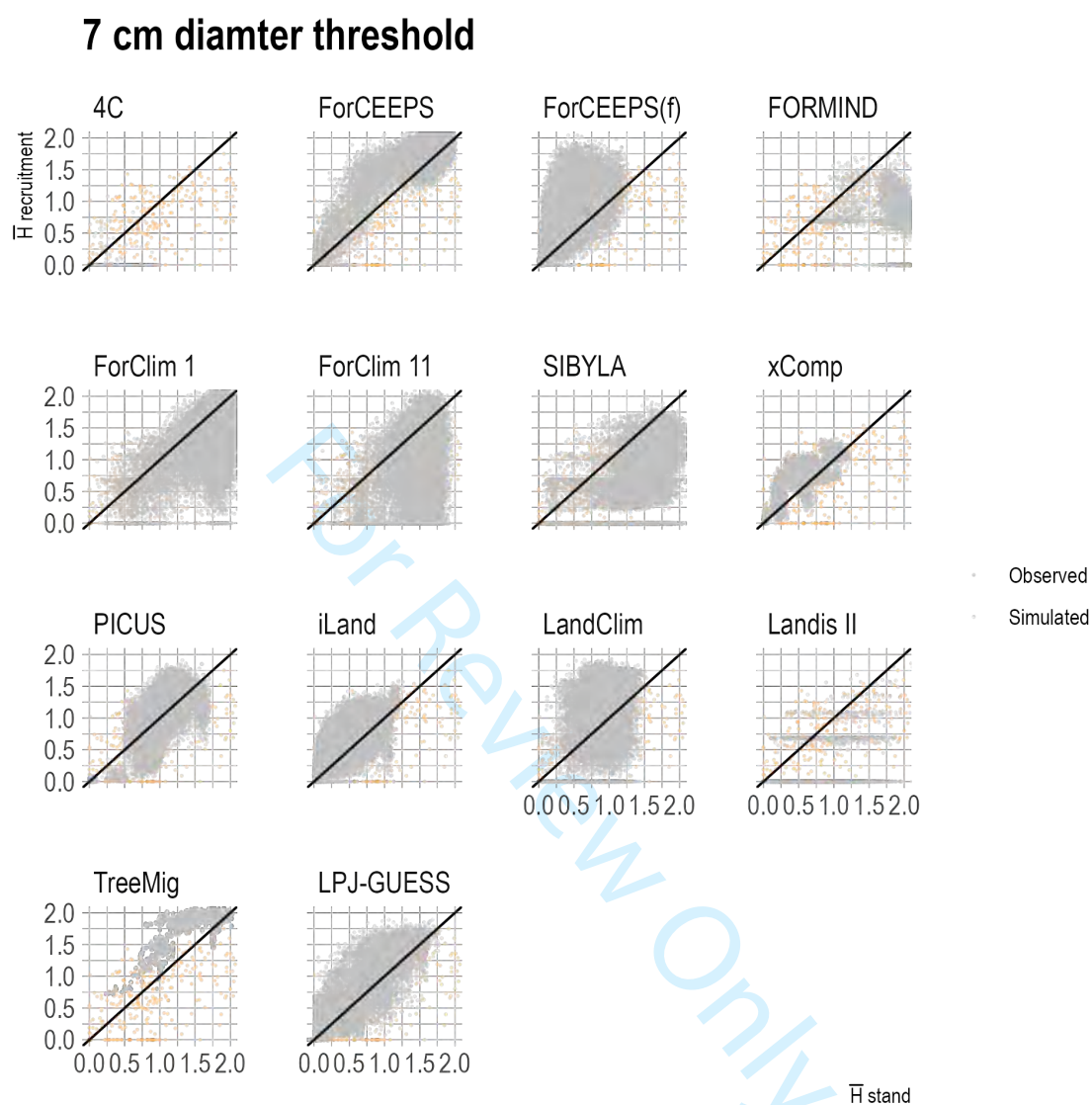


Figure S1: Mean Shannon index per site at recruitment and at the stand level both for observed and simulated values for the diameter threshold of 7cm

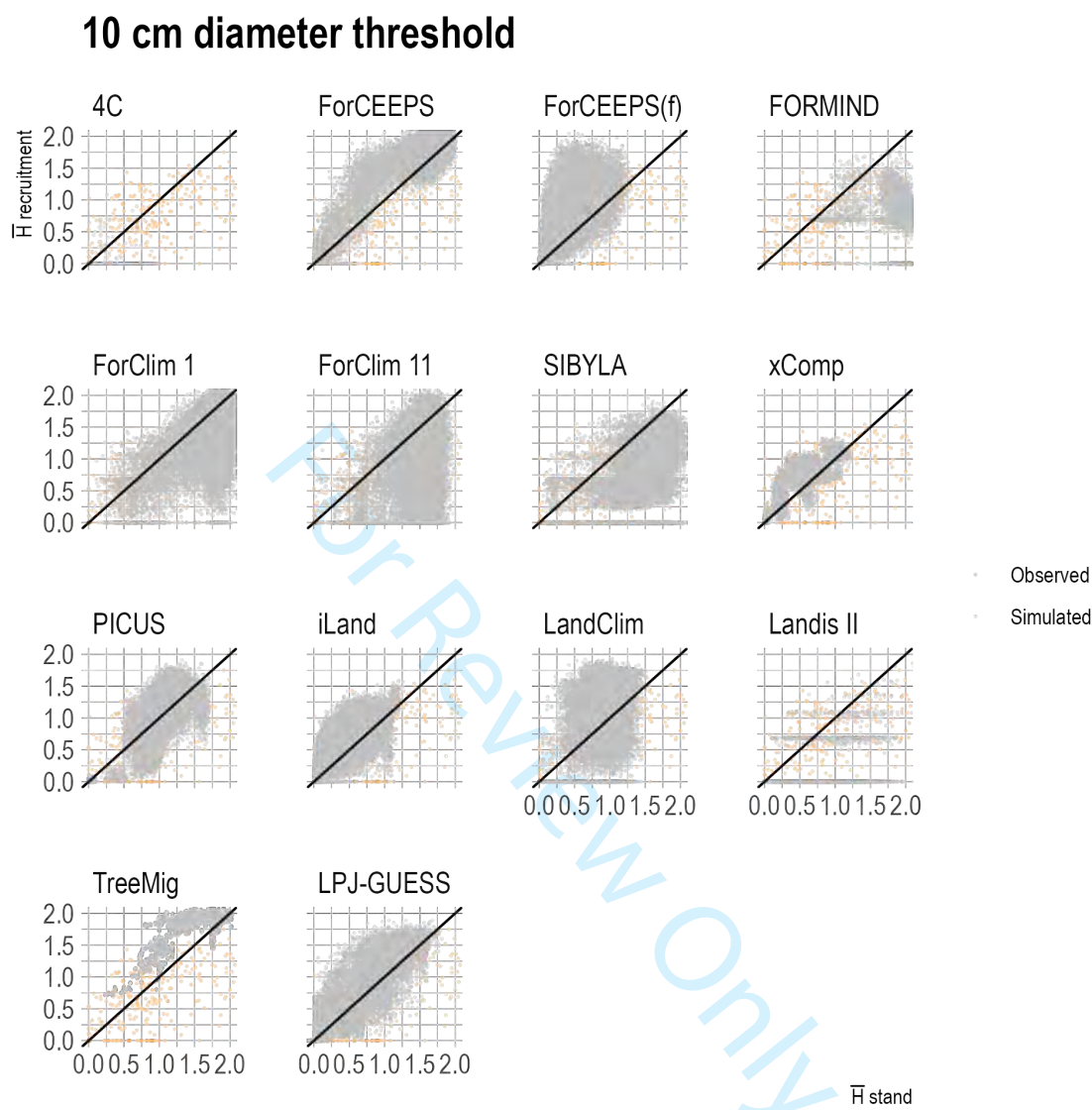


Figure S2: Mean Shannon index per site at recruitment and at the stand level both for observed and simulated values for the diameter threshold of 10cm

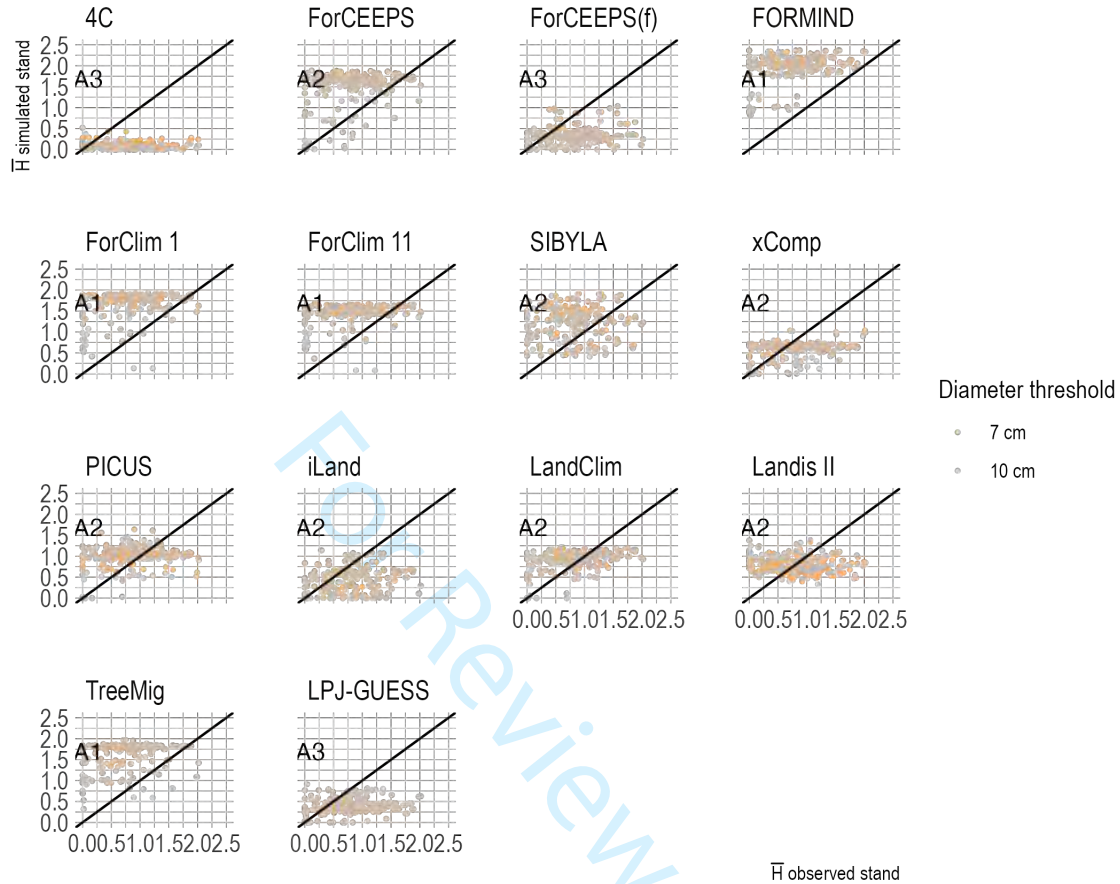


Figure S3: Mean species richness at the stand level per site in the simulated versus observed species richness. The species richness is estimated using the Shannon index calculated by basal area. A1) groups models where the simulated species composition in adults is higher than the observed, A2) groups models where the simulated species composition in adults is similar to the observed, A3) groups models where the simulated species composition in adults is lower than the observed. NOTE: The recruitment threshold for threshold 7 cm in the empirical data has several sites with no recruitment or no data and the Shannon index for those sites is NA

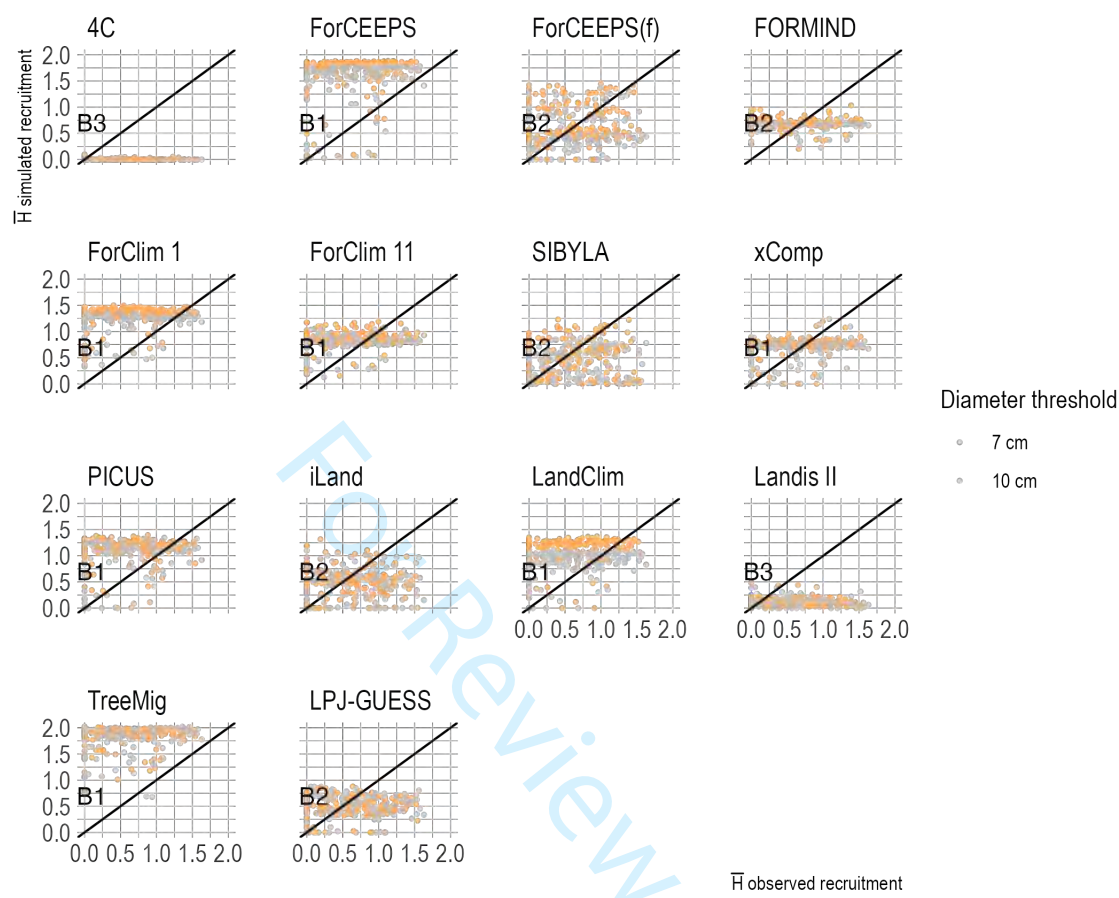


Figure S4: Mean species richness per site in the simulated recruitment versus observed species richness in the recruitment. The species richness is estimated using the Shannon index using the basal area. B1) groups models where the simulated species composition in recruitment is higher than the observed, A2) groups models where the simulated species composition in recruitment is similar to the observed, A3) groups models where the simulated species composition in recruitment is lower than the observed. NOTE: The recruitment threshold recruitment for threshold 7 cm in the empirical data has several sites with no recruitment or no data and the Shannon index for those sites is NA



Table S3: Test of the significance of the differences of rate of recruitment at 7 cm threshold over 10 cm threshold between the observed values and the simulated values per model.

.y.	group1	group2	p	p.adj	p.format	p.signif	method
nn710	Observed	4C	0.0029101	0.02300	0.00291	**	T-test
nn710	Observed	ForCEEPS	0.8983518	1.00000	0.89835	ns	T-test
nn710	Observed	ForCEEPS(f)	0.0253484	0.18000	0.02535	*	T-test
nn710	Observed	FORMIND	0.0599409	0.36000	0.05994	ns	T-test
nn710	Observed	ForClim 1	0.5961405	1.00000	0.59614	ns	T-test
nn710	Observed	ForClim 11	0.2516446	0.75000	0.25164	ns	T-test
nn710	Observed	SIBYLA	0.0001381	0.00150	0.00014	***	T-test
nn710	Observed	xComp	0.0000000	0.00000	1.7e-15	****	T-test
nn710	Observed	PICUS	0.0000000	0.00000	< 2e-16	****	T-test
nn710	Observed	iLand	0.0763056	0.38000	0.07631	ns	T-test
nn710	Observed	LandClim	0.0000770	0.00092	7.7e-05	****	T-test
nn710	Observed	Landis II	0.0002095	0.00210	0.00021	***	T-test
nn710	Observed	TreeMig	0.0000000	0.00000	5.7e-10	****	T-test
nn710	Observed	LPJ-GUESS	0.0013718	0.01200	0.00137	**	T-test
nn710	Observed	aDGVM2	0.1399178	0.56000	0.13992	ns	T-test

Table S4: Models trends in mortality between 7 and 10cm, and the ingrowth at 7cm, based in the mean oer site .

model	Slope	Significance
Observed	0.0037753	0.0279745
4C	0.0054194	0.0144707
ForCEEPS	0.0010021	0.0008576
ForCEEPS(f)	0.0009907	0.0000000
FORMIND	0.0014378	0.4006453
ForClim 1	0.0007425	0.2244471
ForClim 11	-0.0015530	0.0000009
SIBYLA	0.0537439	0.0000001
xComp	0.0034694	0.0000000
PICUS	0.0066061	0.0000000
iLand	0.0026891	0.0000000
LandClim	-0.0028046	0.0000000
Landis II	0.0340037	0.0001270
TreeMig	0.0005776	0.0090166
LPJ-GUESS	0.0021195	0.0017540
aDGVM2	1.6129755	0.3680442

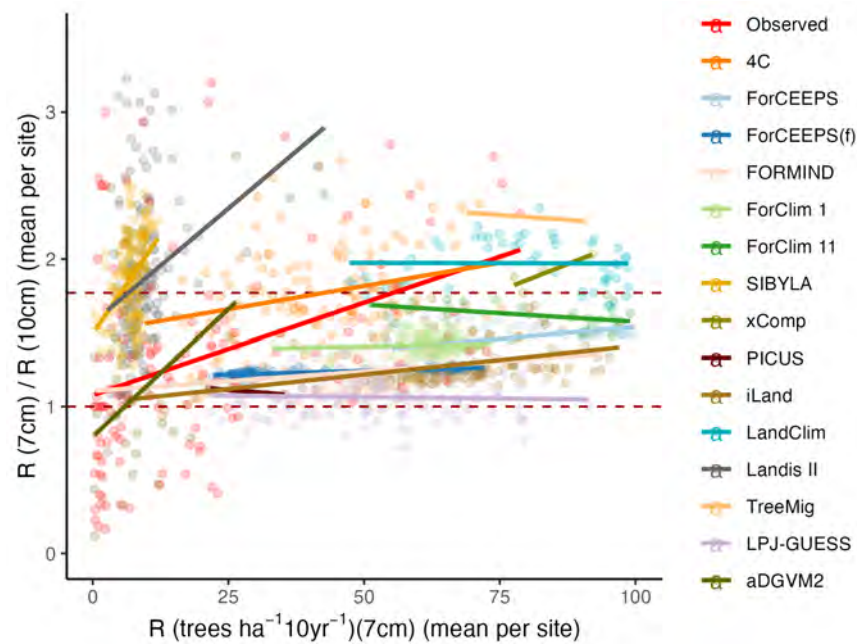


Figure S5: Recruitment ratio between 7 and 10cm and the initial recruitment tree number at 7cm. Dashed red lines mark a ratio equal to 1 indicating no decrease between 7 and 10cm tree recruitment and ratio equal to 1.77 corresponding with the Reineke self-thinning ratio under evenaged conditions

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2.2 Model traits and model performance

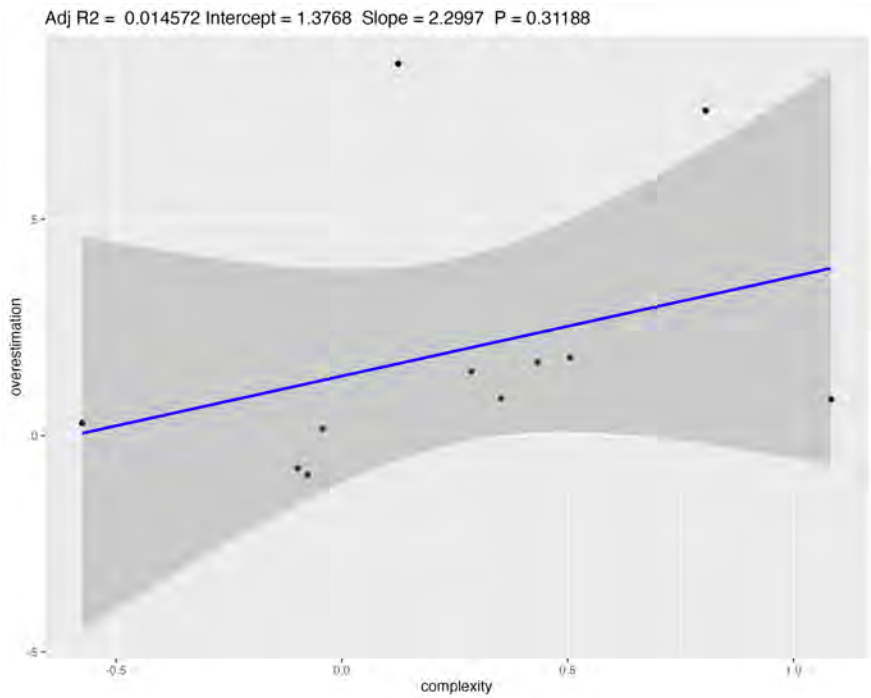


Figure S6: Plot and summary statistics of the linear model between the overestimation proportion in ingrowth levels and the mean complexity value of the establishment modules

Table S5: Test of the significance of the differences of rate of recruitment at 7 cm threshold of the observed values and the simulated values per model.

.y.	group1	group2	p	p.adj	p.format	p.signif	method
r.trees	Observed	4C	0.4154356	4.2e-01	0.42	ns	T-test
r.trees	Observed	ForCEEPS	0.0000000	0.0e+00	< 2e-16	****	T-test
r.trees	Observed	ForCEEPS(f)	0.0000007	2.0e-06	6.8e-07	****	T-test
r.trees	Observed	FORMIND	0.0000021	4.3e-06	2.1e-06	****	T-test
r.trees	Observed	ForClim 1	0.0000000	0.0e+00	< 2e-16	****	T-test
r.trees	Observed	ForClim 11	0.0000000	0.0e+00	< 2e-16	****	T-test
r.trees	Observed	SIBYLA	0.0000000	0.0e+00	< 2e-16	****	T-test
r.trees	Observed	xComp	0.0000000	0.0e+00	< 2e-16	****	T-test
r.trees	Observed	PICUS	0.0000000	0.0e+00	< 2e-16	****	T-test
r.trees	Observed	iLand	0.0000000	0.0e+00	< 2e-16	****	T-test
r.trees	Observed	LandClim	0.0000000	0.0e+00	< 2e-16	****	T-test
r.trees	Observed	Landis II	0.0000000	0.0e+00	< 2e-16	****	T-test
r.trees	Observed	TreeMig	0.0000000	0.0e+00	< 2e-16	****	T-test
r.trees	Observed	LPJ-GUESS	0.0000000	0.0e+00	< 2e-16	****	T-test
r.trees	Observed	aDGVM2	0.0000000	0.0e+00	< 2e-16	****	T-test

Table S6: Test of the significance of the differences of rate of recruitment at 7 cm threshold of the observed values and the simulated values per model.

.y.	group1	group2	p	p.adj	p.format	p.signif	method
ShannonIndexRecruit	Observed	4C	0.0000000	0.0000	< 2e-16	****	T-test
ShannonIndexRecruit	Observed	ForCEEPS	0.0000000	0.0000	< 2e-16	****	T-test
ShannonIndexRecruit	Observed	ForCEEPS(f)	0.1785631	0.1800	0.17856	ns	T-test
ShannonIndexRecruit	Observed	FORMIND	0.0737762	0.1500	0.07378	ns	T-test
ShannonIndexRecruit	Observed	ForClim 1	0.0000000	0.0000	< 2e-16	****	T-test
ShannonIndexRecruit	Observed	ForClim 11	0.0000000	0.0000	4.5e-10	****	T-test
ShannonIndexRecruit	Observed	SIBYLA	0.0161000	0.0640	0.01610	*	T-test
ShannonIndexRecruit	Observed	xComp	0.0270897	0.0810	0.02709	*	T-test
ShannonIndexRecruit	Observed	PICUS	0.0000000	0.0000	< 2e-16	****	T-test
ShannonIndexRecruit	Observed	iLand	0.0046237	0.0230	0.00462	**	T-test
ShannonIndexRecruit	Observed	LandClim	0.0000000	0.0000	< 2e-16	****	T-test
ShannonIndexRecruit	Observed	Landis II	0.0000000	0.0000	< 2e-16	****	T-test
ShannonIndexRecruit	Observed	TreeMig	0.0000000	0.0000	< 2e-16	****	T-test
ShannonIndexRecruit	Observed	LPJ-GUESS	0.0006268	0.0038	0.00063	***	T-test

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## 2.3 Total ingrowth and individual species regeneration niches

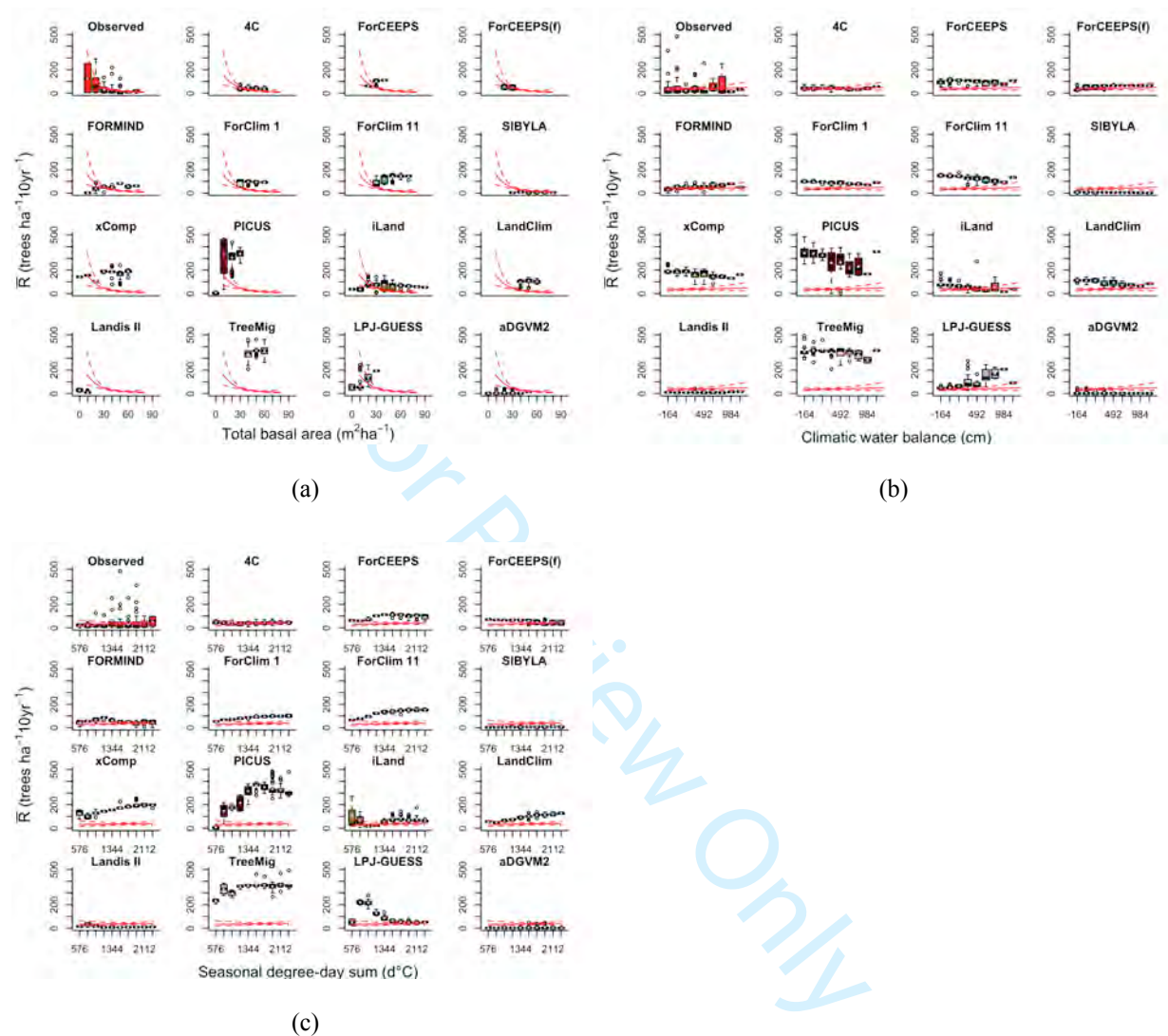


Figure S7: Mean ingrowth values across the 200 samples per site, for the 200 sites against gradients of (a) total basal area; (b) climatic water balance; (c) seasonal degree sum. The values were split into ten bins; the red lines represent a GAM model showing the trend in the observed data.



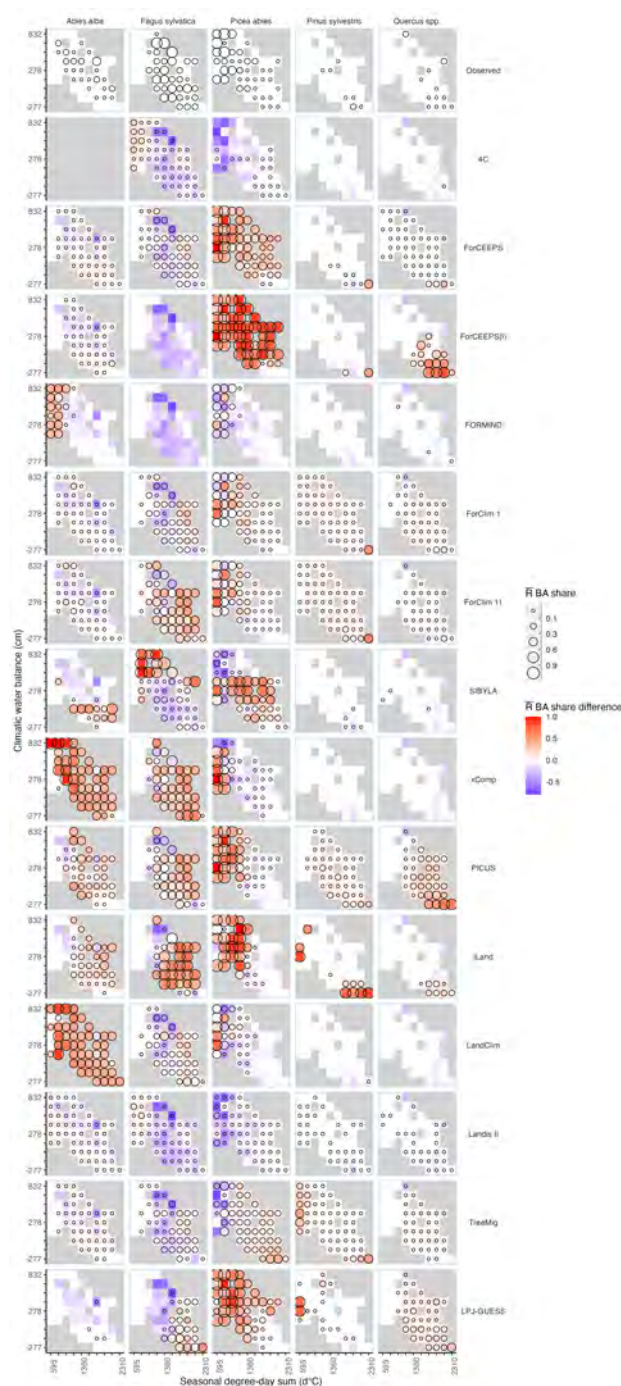


Figure S8: Departure of each model in the representation of the main species recruitment relative abundance from the observations across the environmental gradients for a 10cm threshold. The values shown are the mean of samples per site and across sites in bins, where the range of the climatic water balance (cm) and seasonal degree-day sum (d°C) was divided in 10 bins. The point sizes represent ratio between recruited basal area of the species and the total recruited basal area for all the species. The color gradient shows the difference between the simulated and observed ratio between recruited basal area of the species and the total recruited basal area: grey cell represent areas of the environmental gradient in which the model had R BA share and the empirical data did not because both recruitment and stand level recruitments were equal to zero.