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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](#ref-díaz-yáñez2022)) ([with link: https://osf.io/czdxp/](https://osf.io/czdxp/)). We will make publicly available the code and data if the manuscript is accepted.

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# 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 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.

# Introduction

Forests provide a wide range of products and services of vital importance to humankind ([FOREST EUROPE 2020](#ref-foresteurope2020)). Under the pressure of climate change, increasing disturbance impacts and changing societal demands on forest ecosystem services, it is becoming ever more important to understand 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](#ref-lindner2010); [Seidl and Turner 2022](#ref-seidl2022)). A wide range of models of forest dynamics were developed over the past decades considering the impacts of climate ([Bugmann and Seidl 2022](#ref-bugmann2022)). From these studies, it is evident that we have a reasonably good understanding how to model tree growth ([J. K. Vanclay and Skovsgaard 1997](#ref-vanclay1997); [Bugmann et al. 1996](#ref-bugmann1996)), and substantial efforts have been dedicated to improving the representation of tree mortality ([Bugmann et al. 2019](#ref-bugmann2019); [Cailleret et al. 2017](#ref-cailleret2017)). In contrast, tree regeneration is a much less studied process that is often represented rather coarsely in models ([Walck et al. 2011](#ref-walck2011); [Leishman et al. 1992](#ref-leishman1992); [Price et al. 2001](#ref-price2001)). Which is a clear research gap in the context of climate-induced forest disturbances and forest resilience.

Tree regeneration arises from multiple processes such as pollination, fruit maturation, seed production, dispersal, germination, juvenile growth and survival ([Price et al. 2001](#ref-price2001); [Vacchiano et al. 2018](#ref-vacchiano2018)). All these processes are difficult to assess, and some of them are scarcely understood and thus appear highly stochastic ([Bogdziewicz et al. 2021](#ref-bogdziewicz2021)). 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](#ref-konig_tree_2022); [Bugmann and Seidl 2022](#ref-bugmann2022)): from 1) entirely ignoring it (as done in classical forest growth models, e.g., Pretzsch et al. [2002](#ref-pretzsch2002)), across 2) the use of a few simple environmental filters, as done in most forest “gap” models ([Shugart 1984](#ref-shugart1984)) and Dynamic Global Vegetation Models (e.g., [Hickler et al. 2012](#ref-hickler2012); [Smith, Prentice, and Sykes 2001a](#ref-smith2001)), 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](#ref-seidl2012); [Wehrli et al. 2006](#ref-wehrli2006)), or 4) field-based statistical parameterizations, which however are not easy to extrapolate in space and time (e.g., [Ribbens, Silander, and Pacala 1994](#ref-ribbens1994)).

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](#ref-gutiérrez2016)), 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](#ref-lischke2006)). 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](#ref-schumacher2006)) or by restricting the number of seeds per species in the seedbank ([Lischke and Löffler 2006](#ref-lischke2006)). 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](#ref-wehrli2006)).

Thus, a focus on the modeling of tree regeneration processes is sorely needed and overdue ([Price et al. 2001](#ref-price2001); [Walck et al. 2011](#ref-walck2011)) 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](#ref-hanbury-brown2022)), although many sub-processes have been studied in detail ([Miina, Eerikäinen, and Hasenauer 2006](#ref-miina2006)). 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](#ref-clark1999)). On the one hand, monitoring on permanent plots (such as National Forest Inventories) often measures tree regeneration ([Zell et al. 2019](#ref-zell2019)), however with a design that captures the rate after the stand initiation phase ([Hallsby et al. 2015](#ref-hallsby2015)). Data from permanent plots, although available across regions, are highly heterogeneous, rendering their use difficult in a modeling context ([Käber et al. 2021](#ref-käber2021)). 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](#ref-berdanier2016); [Collet and Chenost 2006](#ref-collet2006)).

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](#ref-käber2023)). 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](#ref-bugmann1996); [M. Fabrika and Ďurský 2012](#ref-fabrika2012); [Lexer and Hönninger 2001](#ref-lexer2001); [Reyer et al. 2014](#ref-reyer2014)). 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](#ref-grubb1977)).

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?

# Material and methods

## 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 @ref(tab:tableModels)). 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](#ref-vanclay1994); [König et al. 2022](#ref-konig_tree_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](#ref-bugmann2022)), 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 @ref(tab:tableModels)). Two models, ForClim and ForCEEPS, were used here with two alternative variants of regeneration. ForClim variant 1 ([Bugmann et al. 1996](#ref-bugmann1996)) is based on a recruitment module that adheres closely to the concept introduced by Botkin, Janak, and Wallis ([1972](#ref-botkin1972)), 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](#ref-huber2020)). 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.

## Observed data

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. 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](#ref-euforia2019)) (Figure @ref(fig:map)). 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.

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., slope and aspect). Each of these sites featured at least two consecutive measurements. Regeneration thresholds for these sites differed between diameters of 0 and 10 cm. For our study, we defined two datasets where one included 165 sites with a diameter threshold of 7 cm or lower, and the other 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](#ref-käber2023)) to provide regeneration rates per ha and per decade. The observations 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 unique dataset and the detailed regeneration information, cf. Käber et al. ([2023](#ref-käber2023)).

## Simulation protocol

The overarching goal of the 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 tree regeneration as the passing of a breast height diameter threshold of 7 or 10 cm, respectively (synonym: ingrowth). To this end, each modeling group was provided with a detailed protocol ([Díaz-Yáñez, Käber, and Bugmann 2022](#ref-díaz-yáñez2022)) with instructions how to perform the simulations, providing input variables on climate and soil conditions, and the list of expected output variables. 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](#ref-muñozsabater2019)), daily and monthly resolution (CHELSA data, Karger et al. [2021](#ref-karger2021)). 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 @ref(tab:tableModels)). Soil quality data were provided as continuous values between 1 and 5 (Soilgrids dataset, Hengl et al. [2017](#ref-hengl2017)). The protocol also provided the elevation, slope and aspect for each of the 200 sites ([ASTER Science Team 2019](#ref-asterscienceteam2019)), 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 @ref(tab:tableModels)). Further details on how each modeling team prepared the simulations and the outputs are available in Supplementary Material 1.

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

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

Two models did not provide results from all the simulated samples or sites to avoid unrealistic results, as follows. In the model 4C, a threshold of a maximum basal area of 90 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.

## 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 based on the relative proportion of the species in terms of basal area. It was calculated for the regeneration () (Equation ) and at the stand level () (Equation ). The higher the value of the index, the higher the species diversity at a particular site and sample.

where is the total number of species present and that have a basal area larger than zero in sample ; is the proportion of species in sample calculated as the regeneration basal area () for that species relative to total recruited basal area () of the sample ; is the proportion of species calculated as the basal area of all trees () of that species relative to total basal area () of the sample . Species diversity was not assessed for aDGVM2 as this model does not simulate individual species.

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](#ref-reineke1933); [Hans Pretzsch and Biber 2003](#ref-pretzsch2005)) 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 .

We assessed model performance in relation to model traits focusing on (1) model complexity as defined by Bugmann and Seidl ([2022](#ref-bugmann2022)), (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](#ref-allen1976); [Fischlin, Bugmann, and Gyalistras 1995](#ref-fischlin1995)) as a proxy for growing season warmth, and the climatic water balance as a proxy for soil moisture ([Speich 2019](#ref-speich2019)). 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](#ref-wood2011)) 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:

where is the total number of species simulated, and is the mean basal area in the regeneration (subsequently referred to as “regeneration basal area”) of species per site across the available samples at that site. Furthermore, regarding the share in the regeneration basal area per species (), we categorized this as zero when the regeneration basal area of that species () was zero, but also when both the regeneration basal area of that species () and the total regeneration basal area ( ) equaled zero.

# Results

## 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 @ref(fig:over)). 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 @ref(fig:over)). 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 @ref(fig:over)) 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.

## Tree species diversity of regeneration

Most models matched the level of diversity of the observed data quite well (Figure @ref(fig:H710)). 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 @ref(fig:combinedRichness)A, 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 @ref(fig:combinedRichness)A, left). Several models underpredicted species diversity, i.e., LPJ-GUESS, ForCEEPS(f) and 4C (Figure @ref(fig:combinedRichness)A, right).

The majority of the models overpredicted regeneration diversity; as already observed in Figure @ref(fig:H710), only two of them underestimated it (4C and Landis-II) (Figure @ref(fig:combinedRichness)B 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.

## Mortality in tree regeneration

There were strong differences among the models regarding the mortality rate between 7 and 10 cm (Figure @ref(fig:mortality11)). 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 @ref(fig:over) 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 @ref(fig:over)). Interestingly, two models that underestimated overall regeneration levels (SIBYLA and Landis-II; cf. Figure @ref(fig:over)) featured mortality rates that were close to but still above the self-thinning line (Figure @ref(fig:mortality11)).

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 @ref(fig:mortality13)A). The other models that overestimated regeneration had mortalities lower than the expected self-thinning ratio, with the exception of LandClim (Figure @ref(fig:mortality13)B). 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 @ref(fig:mortality11)). aDGVM2 was the only model that underestimated regeneration at the 7 cm threshold while featuring a low mortality between the two thresholds (Figure @ref(fig:mortality13)C), 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 @ref(fig:mortality13)D; 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.

## Model performance and model traits

There was no significant relationship between the mean complexity of the regeneration module (Table @ref(tab:tableModels)) 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)).

## 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 @ref(fig:nvTrend710BAlightTemp) 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 @ref(fig:nvTrend710BAlightTemp)a). 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 @ref(fig:nvTrend710BAlightTemp)b,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 @ref(fig:diff), 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 @ref(fig:diff), 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 @ref(fig:diff)). 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 @ref(fig:diff)). 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).

# 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](#ref-seidl2022)). 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.

The EuFoRIa data ([Käber et al. 2023](#ref-käber2023)) 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](#ref-trugman2022)).

## 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](#ref-pugh2019); [Pan et al. 2011](#ref-pan2011)). 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](#ref-huber2021)) or in a decision support context (e.g., [Thrippleton et al. 2021](#ref-thrippleton2021)).

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](#ref-rammer2021)). There are multiple constraints to the regeneration niche of tree species ([Price et al. 2001](#ref-price2001)), and therefore the absence of regeneration is likely to be common ([Fortin and DeBlois 2007](#ref-fortin2007)), 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](#ref-heiri2009)), leading to less regeneration than in an equilibrium situation.

## 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](#ref-redmond2015); [Seidl and Turner 2022](#ref-seidl2022)). 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](#ref-konig_tree_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](#ref-hanbury-brown2022)), 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](#ref-grubb1977)).

## Regeneration mortality

There are several factors that lead to mortality during the regeneration phase, such as competition ([Casper and Jackson 1997](#ref-casper1997)) and multiple abiotic factors ([Schmid et al. 2021](#ref-schmid2021); [Cunningham et al. 2006](#ref-cunningham2006)). 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](#ref-klopcic2015)), 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](#ref-pugh2019)). 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.

## 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](#ref-konig_tree_2022)) could have implied that model performance would be much worse than what we found.

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](#ref-bugmann2022)). 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](#ref-franklin2020)). Thus, the question of what level of detail is appropriate and parsimonious for modeling tree regeneration processes remains open ([König et al. 2022](#ref-konig_tree_2022); [Bugmann and Seidl 2022](#ref-bugmann2022)).

## Regeneration gradients on regeneration niches

Competition for light as a strong filter for tree regeneration has been widely documented ([Messier et al. 1999](#ref-messier1999); [Collet and Chenost 2006](#ref-collet2006); [Berdanier and Clark 2016](#ref-berdanier2016)), 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](#ref-schmid2021)). 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](#ref-woltjer2008)). 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](#ref-seidl2022); [Grubb 1977](#ref-grubb1977)). 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 Boncina 2012](#ref-klopcic2012); [Zell et al. 2019](#ref-zell2019)). 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](#ref-klopcic2015)). 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

## 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](#ref-brzeziecki2021)) 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](#ref-price2001)). In reality, many environmental constraints are acting on young trees ([Käber et al. 2021](#ref-käber2021)) 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](#ref-portier2022)). 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](#ref-snell2018); or Lehsten et al. [2019](#ref-lehsten2019)), as they are usually lacking dispersal between cells and are based on a strong abstraction of horizontal space ([Hanbury-Brown, Ward, and Kueppers 2022](#ref-hanbury-brown2022)). 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).

## 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](#ref-albrich2020)). If it should be necessary to include more detail in the regeneration models, this will come with higher parameterisation efforts. This will most likely lead to lower generalization because the required data will have to be collected from specific locations, as currently there is no general, comprehensive regeneration dataset available.

Therefore, we further recommend that more effort should be invested into collecting harmonized datasets on tree regeneration. We emphasize that datasets such as EuFoRIa are invaluable and should be expanded in both their spatial extent (e.g., towards boreal and Mediterranean conditions) as well as in time (e.g., continuing the monitoring into the future). Such data will allow for a better evaluation of forest models and help to reduce the uncertainty in their projections, which is crucial when they are used as tools for predicting e.g. the impacts of anthropogenic climate change.

In the present study, we have considered tree regeneration in the equilibrium state only. It is equally important to understand how these models project tree regeneration after changes in forest structure by disturbances ([Seidl and Turner 2022](#ref-seidl2022)), or under different management strategies ([Lindner, Lasch, and Erhard 2000](#ref-lindner2000)). However, this will require an entirely different set of observed data, and potentially not all models of forest dynamics would be able to assess the relationship of these aspects on tree regeneration, e.g. due to the lack of disturbance or appropriate management modules.

We recommend to investigate in detail the implications of the current modeling strategies for tree regeneration and, ultimately, simulated forest stand structure. This applies particularly to the erroneous patterns of excess tree regeneration and later excess mortality, by focusing on a wider range of tree sizes and the related regeneration dynamics. We also recommend, especially for the landscape-level models, the inclusion of explicit spatial considerations regarding tree regeneration ([Beckage and Clark 2003](#ref-beckage2003)); this, however, is a serious challenge regarding appropriate datasets, as inventory data have wide coverage, but by definition do not allow for the assessment of spatial interaction effects.

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

## Conclusions

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

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

Regarding mortality in the early phase of tree life, many models that feature a particularly high overestimation of regeneration levels are compensating for this by a larger tree mortality. Often, this compensation is not sufficient to reduce the high regeneration levels to realistic values. Overall, 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.

# 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. Brůna, 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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# Conflict of interest statement

The authors declare no conflicts of interest.

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# Table

# 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 (overperdicted, 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.

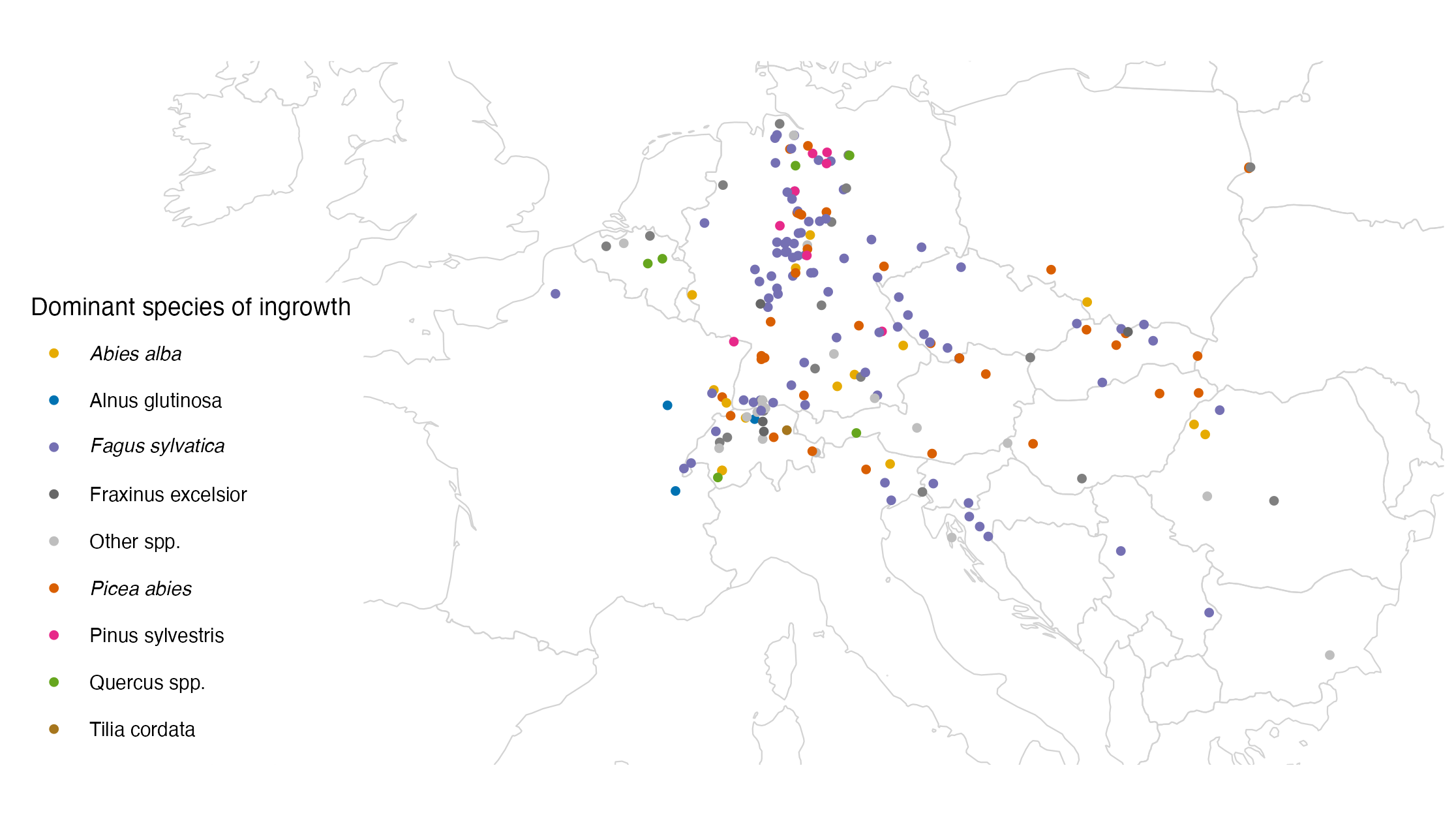
**Figure 5.** Ratio of tree regeneration rates between the 7 and 10 cm thresholds. Dashed blue lines mark a ratio equal to 1, indicating no decrease in tree regeneration between 7 and 10 cm, and a ratio equal to 1.77, corresponding to the Reineke self-thinning ratio under even-aged conditions.

**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 ([simulated - observed] / 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.

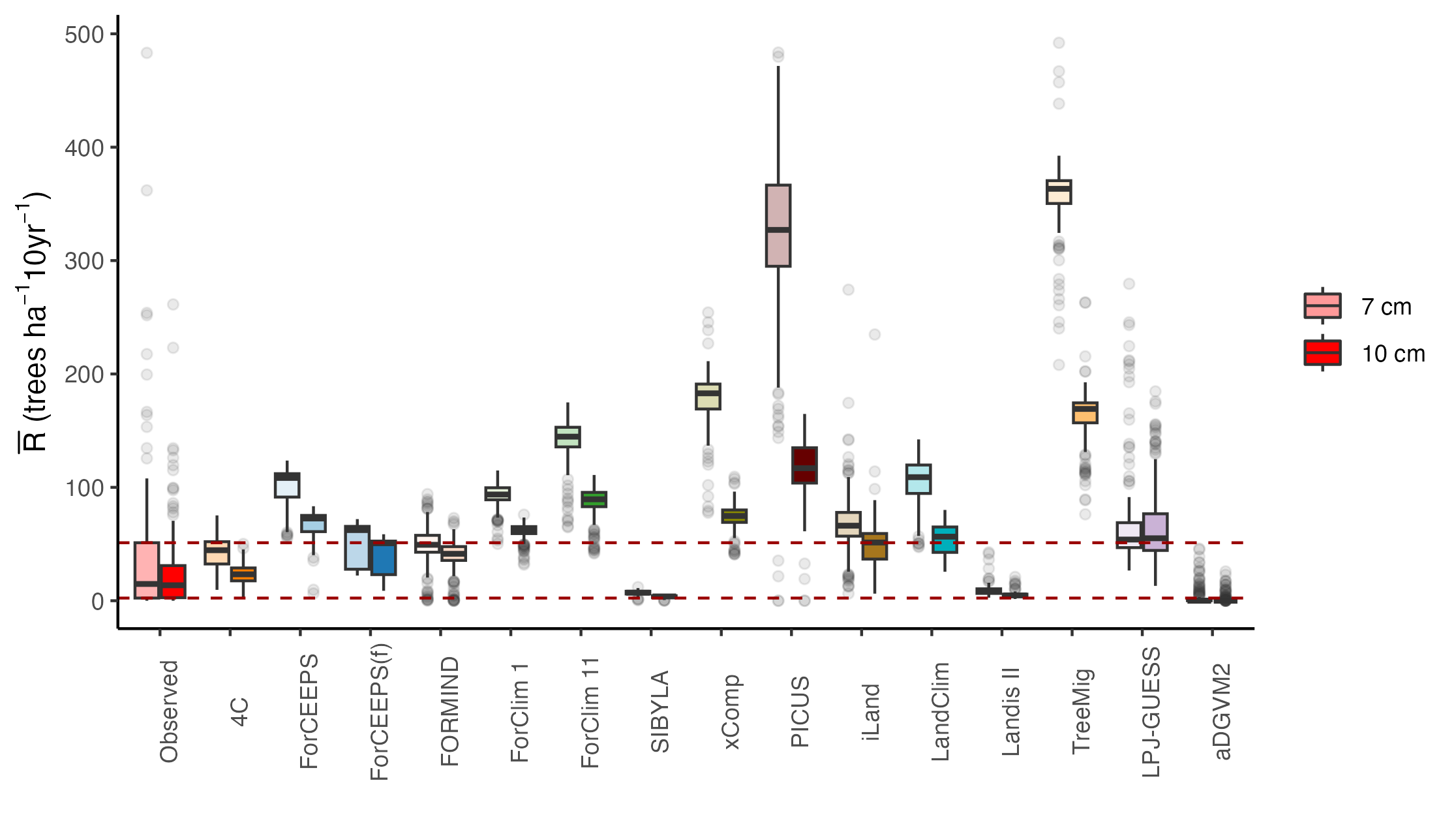
**Figure 7.** Mean regeneration values across the 200 samples per site with the y-axis scaled differently by model, for the 200 sites against gradients of (a) total basal area; (b) climatic water balance; (c) seasonal degree-day sum. The values were split into ten bins; the red lines represent a GAM 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.

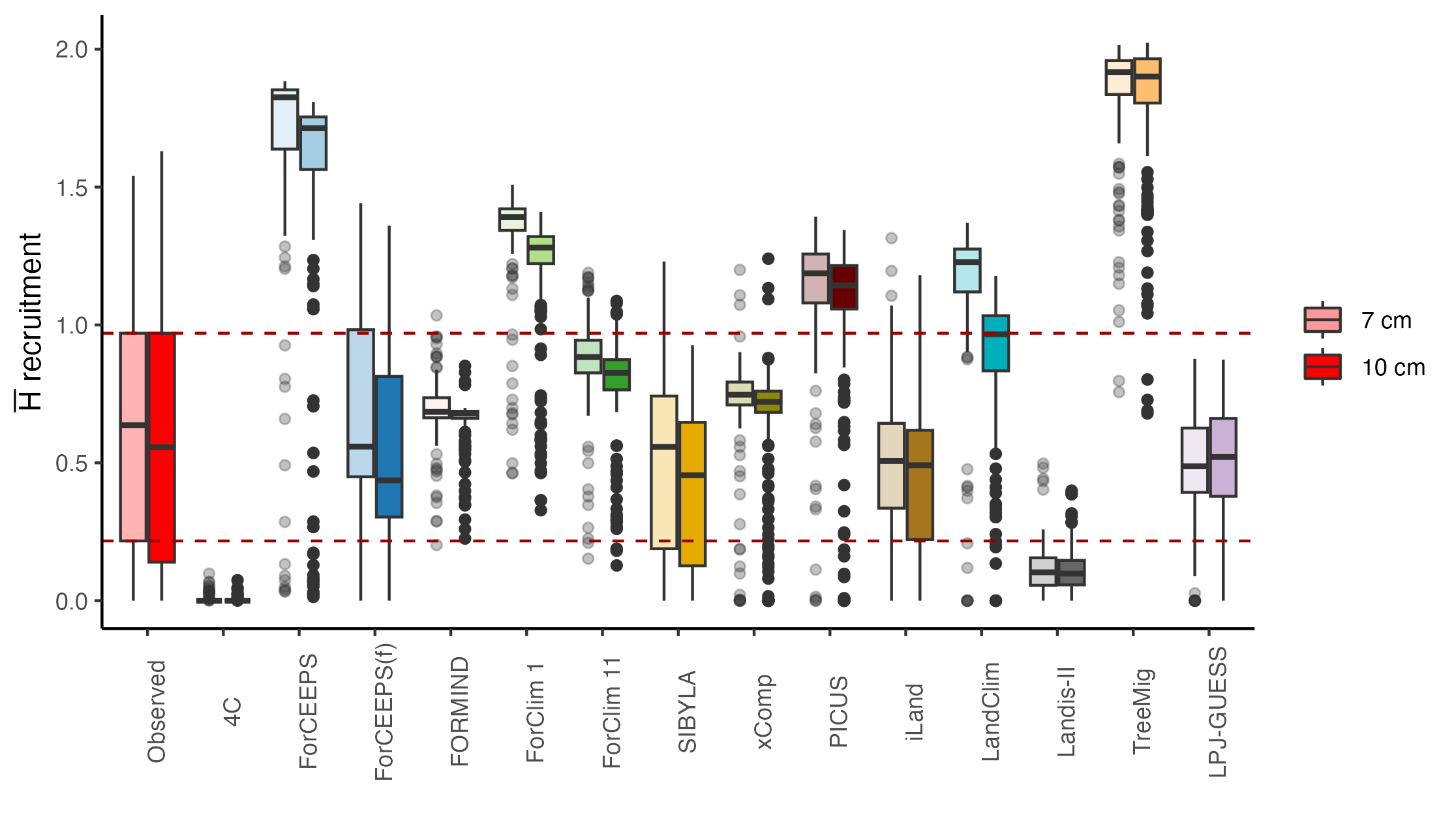
# Figures



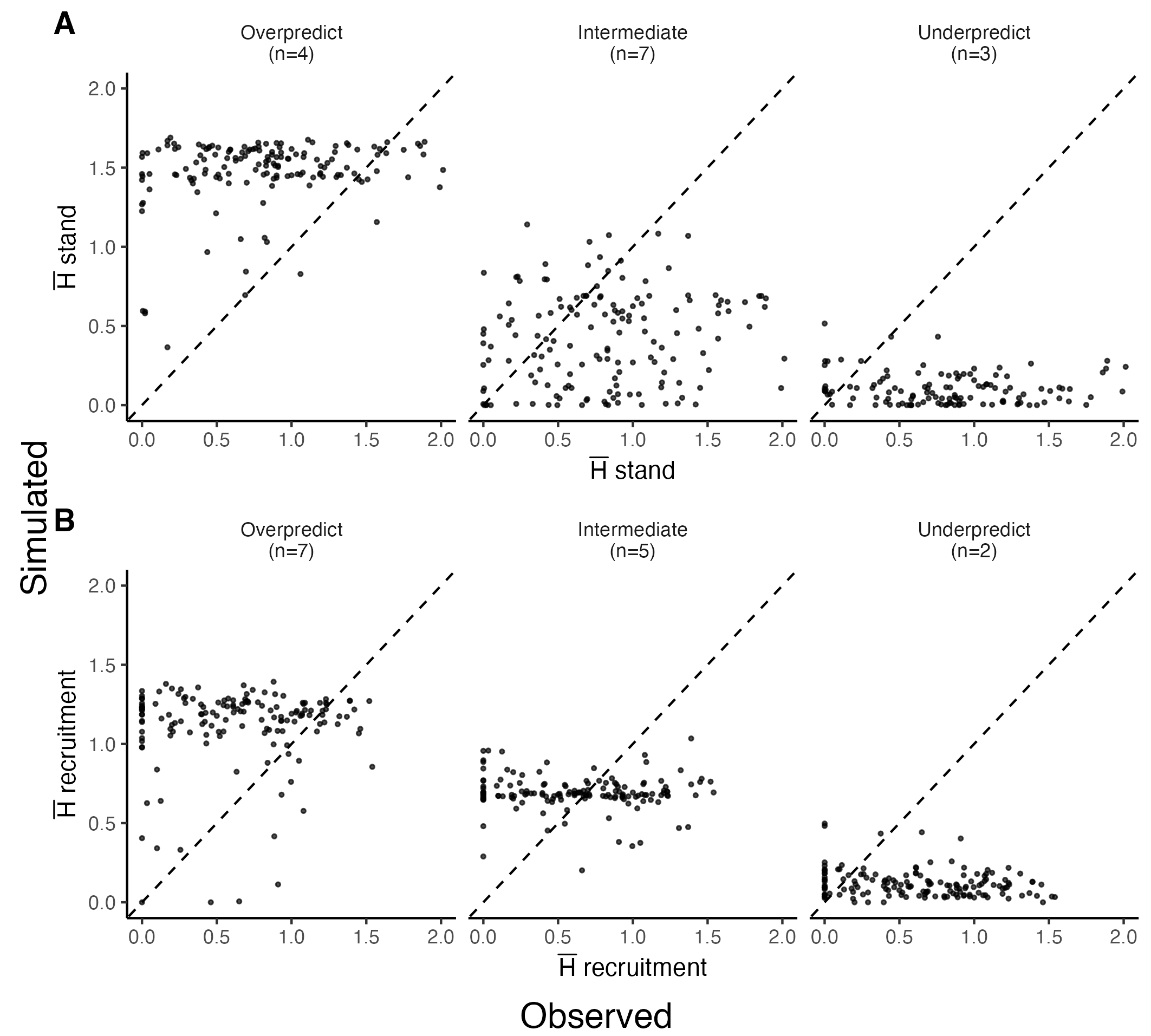
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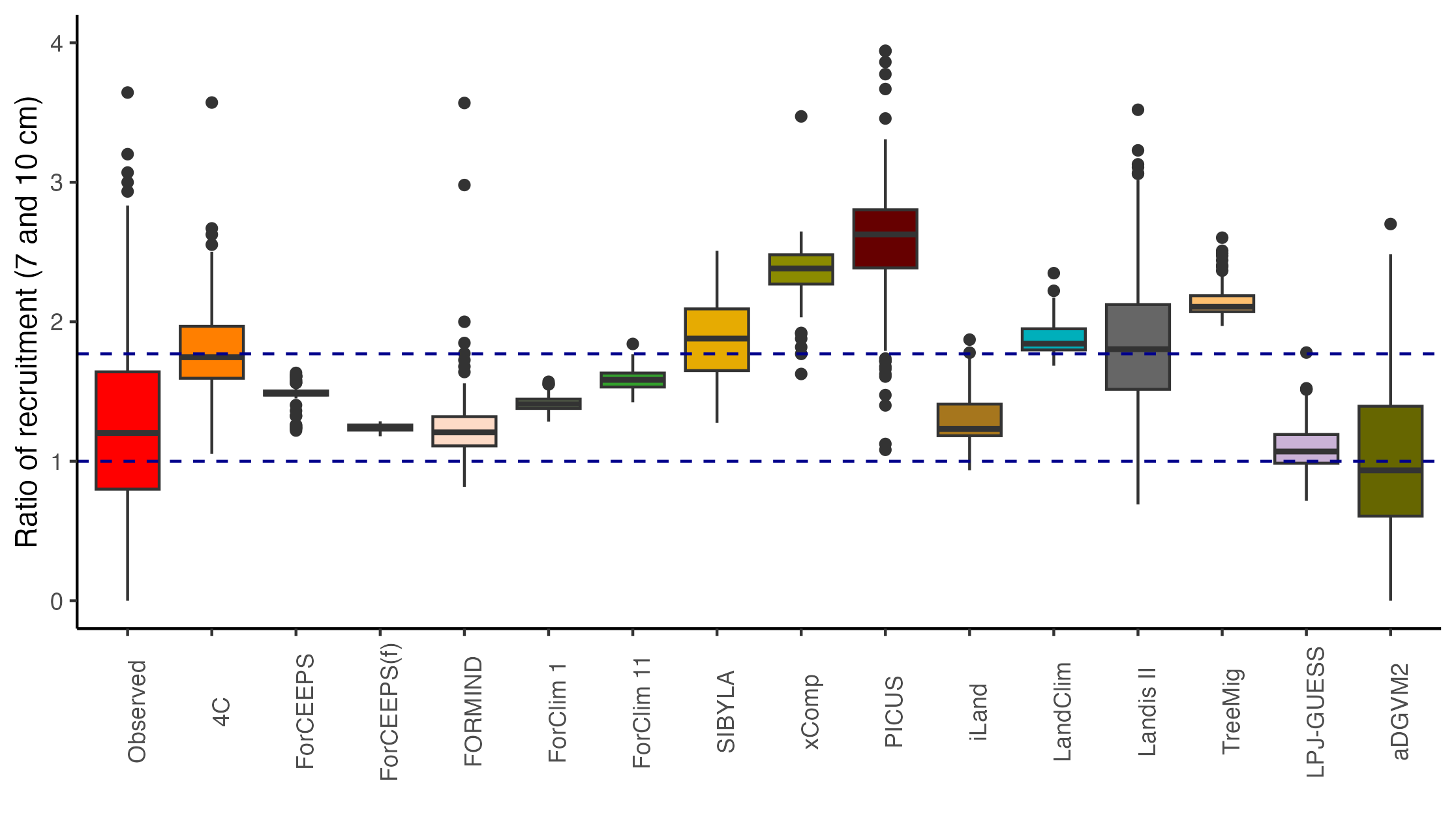
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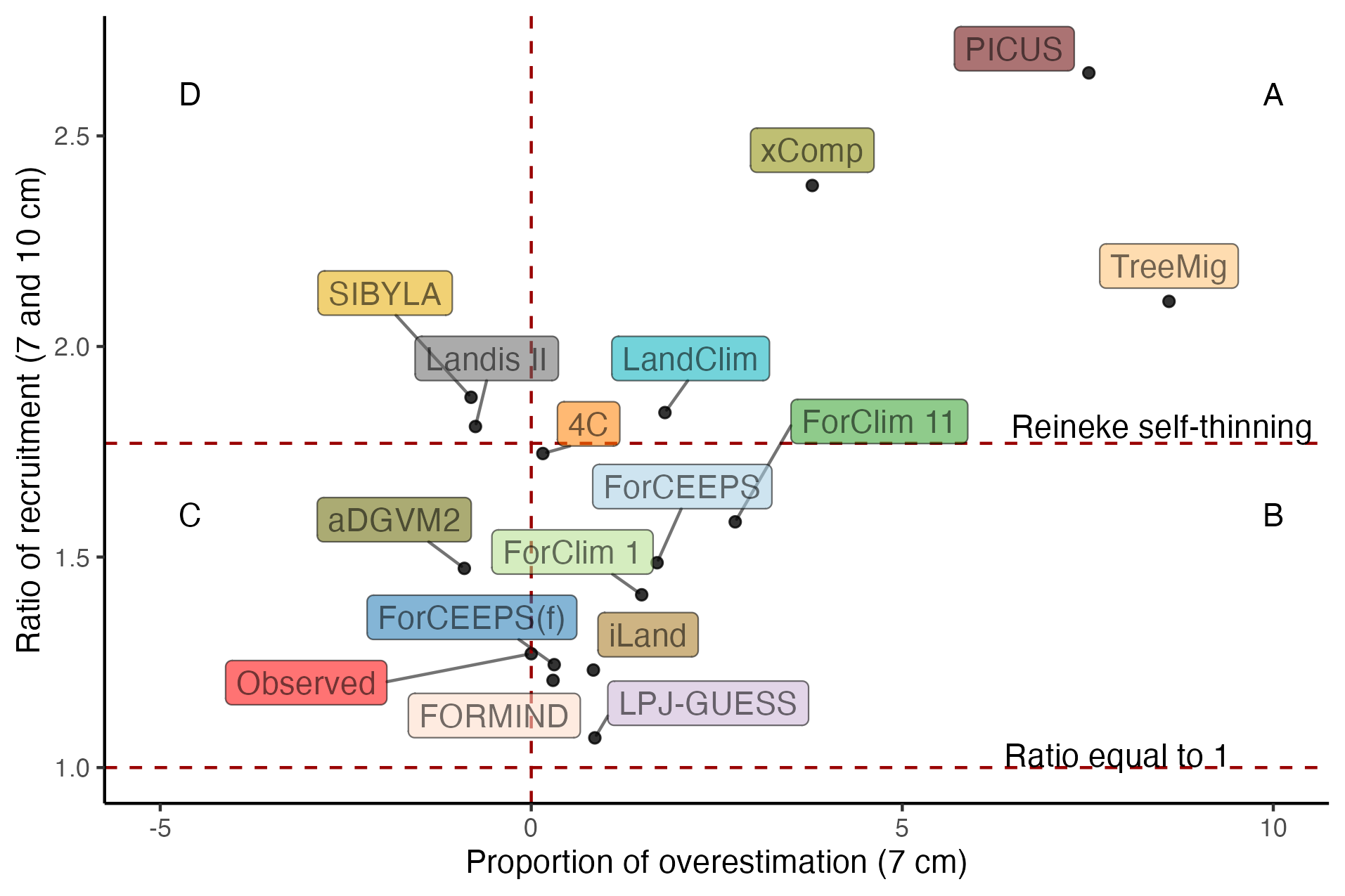
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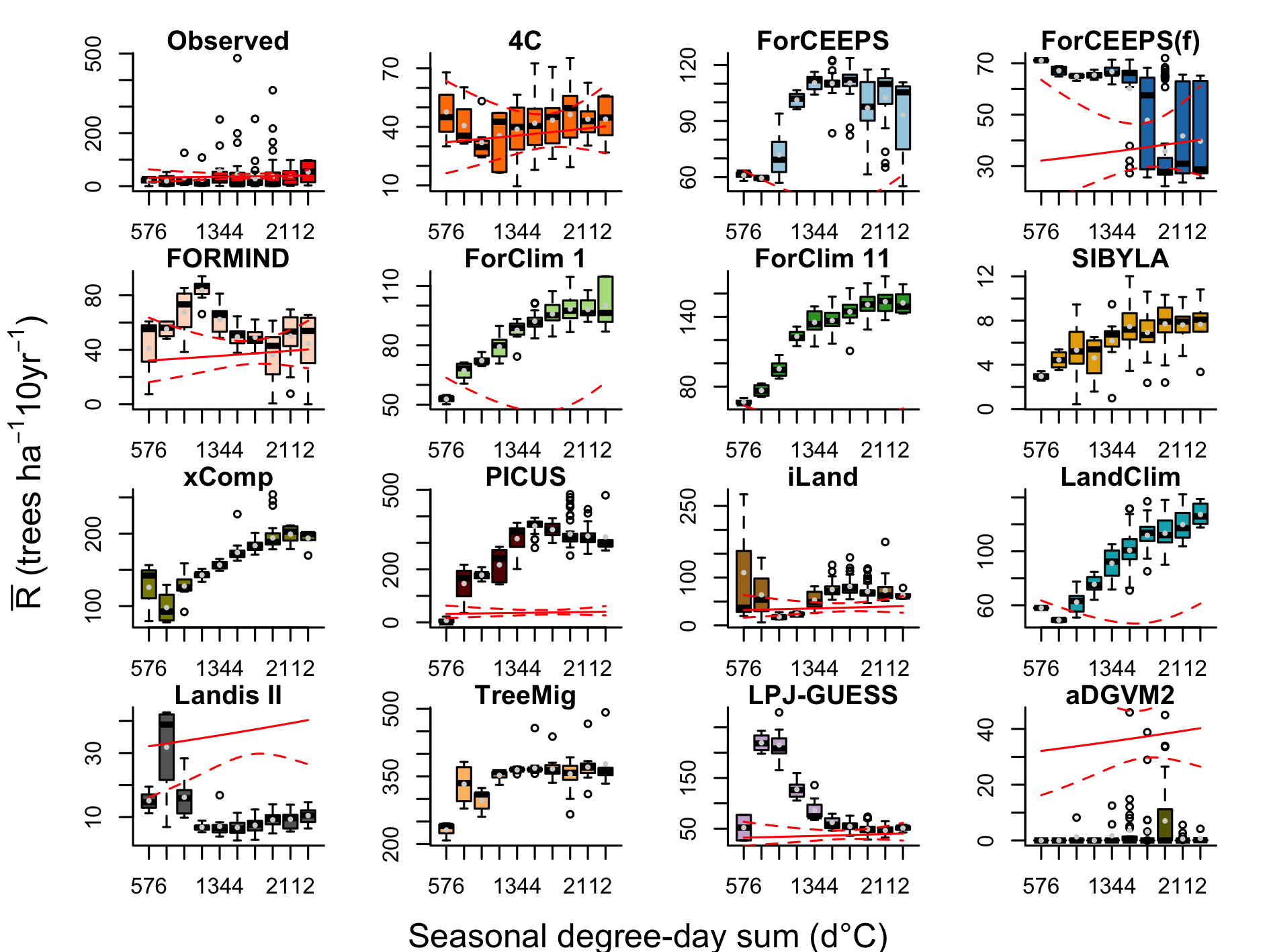
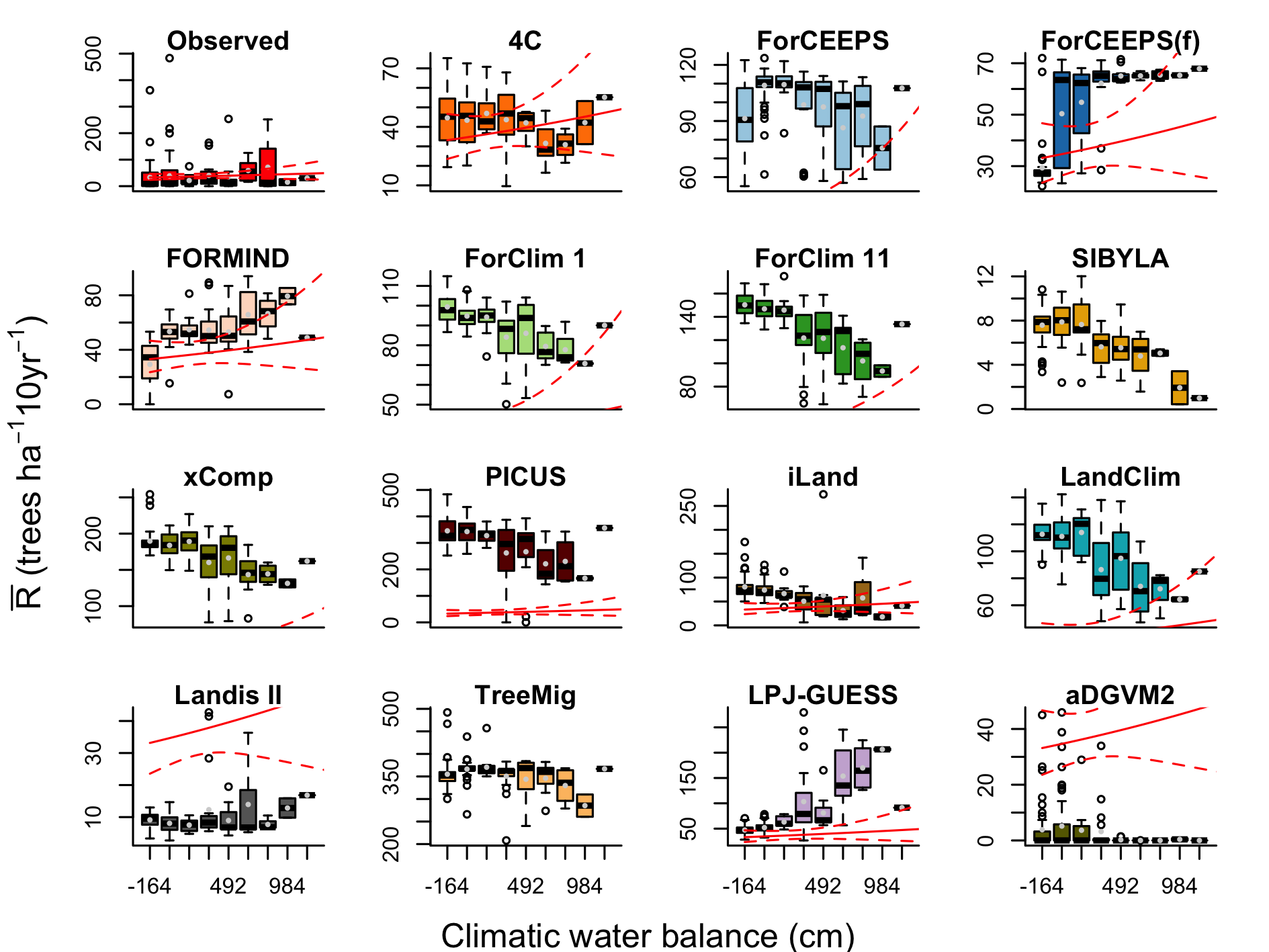
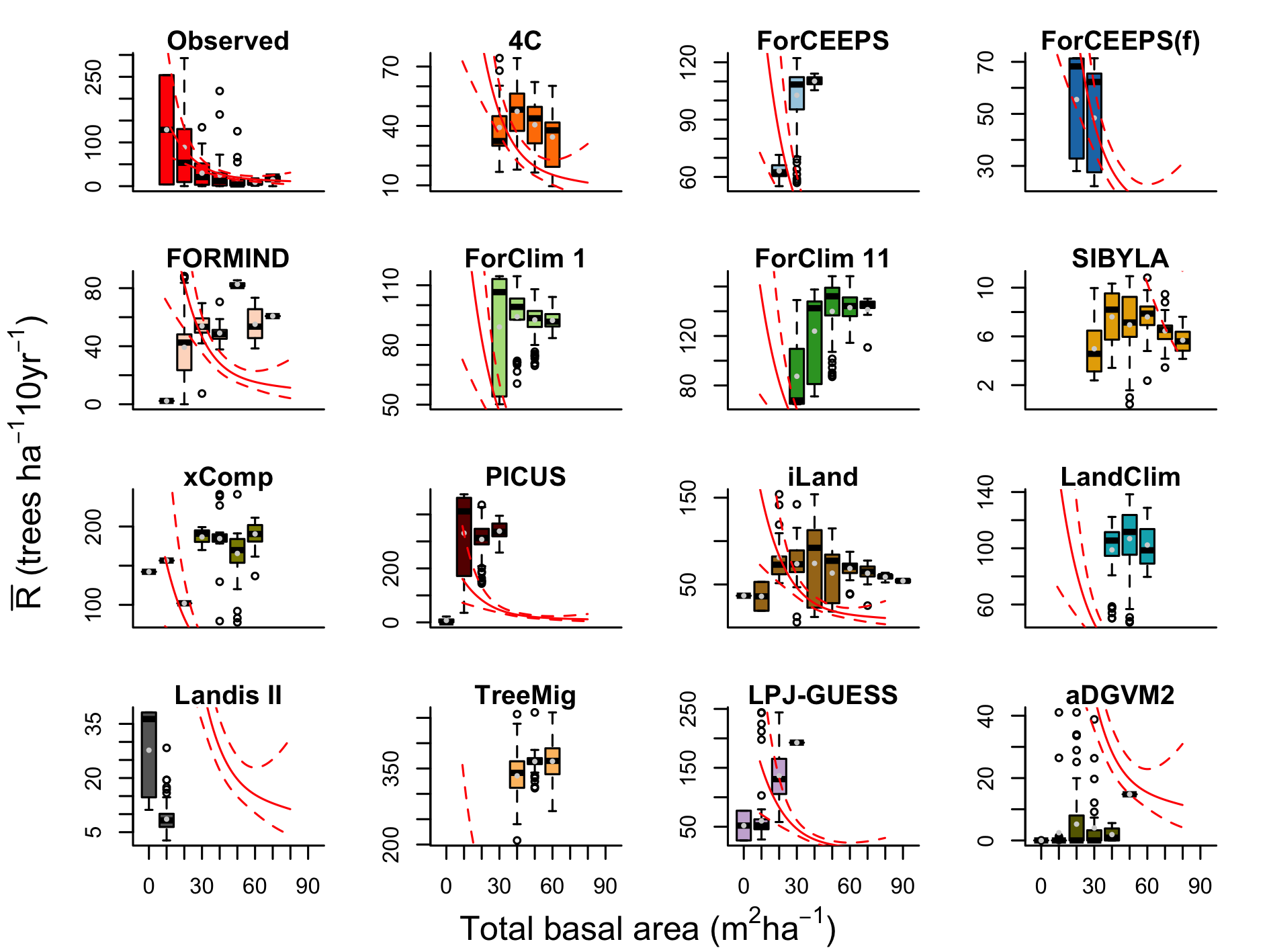
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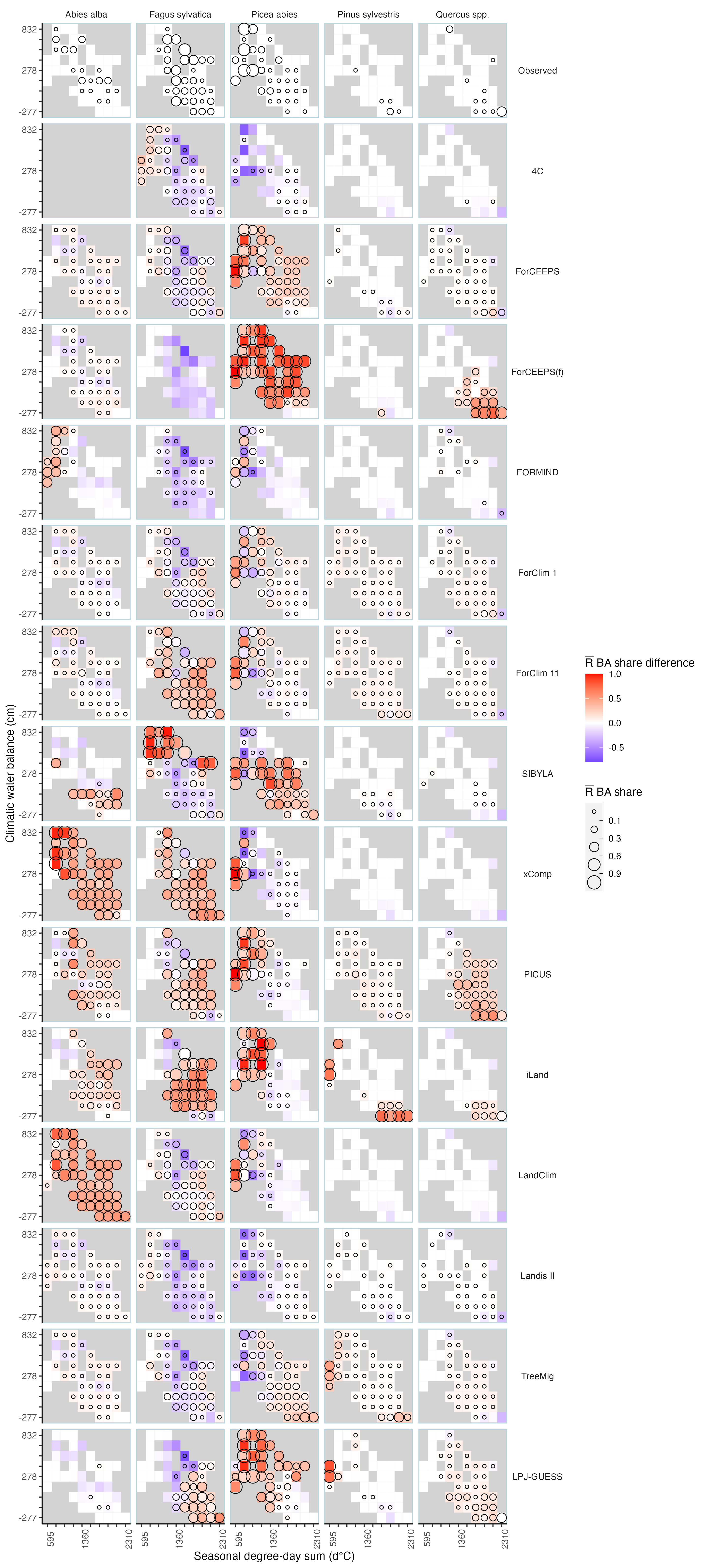


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