

RESEARCH ARTICLE

Sheltered or suppressed? Tree regeneration in unmanaged European forests

Yannek Käber¹  | Christof Bigler¹  | Janneke HilleRisLambers²  | Martina Hobi³  | Thomas A. Nagel⁴  | Tuomas Aakala⁵  | Markus Blaschke⁶  | Peter Brang³  | Bogdan Brzeziecki⁷  | Marco Carrer⁸  | Eugenie Cateau⁹ | Georg Frank¹⁰ | Shawn Fraver¹¹  | Jokin Idoate-Lacasia³  | Jan Holik¹²  | Stanislav Kucbel¹³ | Anja Leyman¹⁴  | Peter Meyer¹⁵  | Renzo Motta¹⁶  | Pavel Samonil¹²  | Lucia Seebach¹⁷  | Jonas Stillhard³  | Miroslav Svoboda¹⁸  | Jerzy Szwagrzyk¹⁹  | Kris Vandekerckhove¹⁴  | Ondrej Vostarek¹⁸  | Tzvetan Zlatanov²⁰  | Harald Bugmann¹ 

¹Forest Ecology Institute of Terrestrial Ecosystems ETH Zürich, Zurich, Switzerland; ²Plant Ecology Institute of Integrative Biology ETH Zürich, Zurich, Switzerland; ³Swiss Federal Institute for Forest, Snow and Landscape Research, Zurich, Switzerland; ⁴University of Ljubljana, Ljubljana, Slovenia; ⁵University of Eastern Finland, Joensuu, Finland; ⁶Bavarian State Institute for Forestry, Freising, Germany; ⁷Department of Silviculture, Warsaw University of Life Sciences, Warszawa, Poland; ⁸TeSAF Dep., University of Padova, Legnaro, Italy; ⁹Reserves Naturelles de France, Quetigny, France; ¹⁰Austrian Federal Research Centre for Forests, Natural Hazards and Landscape (BFW), Wien, Austria; ¹¹School of Forest Resources, University of Maine, Orono, Maine, USA; ¹²Silva Tarouca Research Institute, Brno, Czech Republic; ¹³Department of Silviculture, Faculty of Forestry, Technical University in Zvolen, Zvolen, Slovakia; ¹⁴Research Institute for Nature and Forest, Brussels, Belgium; ¹⁵Northwest German Forest Research Institute, Göttingen, Germany; ¹⁶University of Torino, Torino, Italy; ¹⁷Forest Research Institute of Baden-Württemberg, Freiburg, Germany; ¹⁸Czech University of Life Sciences Prague, Praha, Czech Republic; ¹⁹University of Agriculture in Krakow, Krakow, Poland and ²⁰Institute of Biodiversity and Ecosystem Research, Bulgarian Academy of Sciences, Sofia, Bulgaria

Correspondence

Yannek Käber

Email: yannek.kaeber@usys.ethz.ch;
y.kaeber@posteo.de

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Abstract

1. Tree regeneration is a key demographic process influencing long-term forest dynamics. It is driven by climate, disturbances, biotic factors and their interactions. Thus, predictions of tree regeneration are challenging due to complex feedbacks along the wide climatic gradients covered by most tree species. The stress gradient hypothesis (SGH) provides a framework for assessing such feedbacks across species ranges, suggesting that competition between trees is more frequent under favourable conditions, whereas reduced competition (i.e. positive interactions) is more likely under climatic stress. Moreover, tree life-history strategies (LHS) may shed light on how and whether the SGH explains regeneration of different tree species.
2. To address these topics, we developed statistical models based on >50,000 recruitment events observed for 24 tree species in an extensive permanent plot network (6540 plots from 299 unmanaged European temperate, boreal and sub-alpine forests) covering a wide climatic gradient.

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3. We found that the effects of Leaf Area Index (as a proxy for competition) on tree recruitment changed along climatic gradients but in a species-specific manner. Competition predominates, with its intensity decreasing under stressful conditions for most species, as predicted by the SGH. However, positive interactions were only evident for a few species. Additionally, the ability of the SGH to explain patterns of competition and positive interactions across the gradients differed among species, with some differences and exceptions that may be related to varying LHS.
4. *Synthesis.* Our study shows that competition between trees toward climatic stress decreases systematically but depends on species stress tolerance to climate and shade. These findings explain within- and between-species differences in tree recruitment patterns in European temperate forests. Moreover, our findings imply that projections of forest dynamics along wide climatic gradients and under climate change must accommodate both competition and positive interactions, as they strongly affect rates of community turnover.

KEYWORDS

biogeography and macroecology, competition, facilitation, forest ecology, global change ecology, plant population and community dynamics, stress-gradient hypotheses

1 | INTRODUCTION

Tree regeneration, defined as the transition between generations of adult tree populations, is key to species turnover in long-term forest dynamics (cf. Whittaker, 1972). Tree regeneration determines the species' capability to maintain existing populations and occupy new habitats. If we understand the processes affecting tree regeneration on a larger scale, we will ultimately understand how changing climates will shape future forest ecosystem dynamics and species composition (Lloret et al., 2012). Additionally, tree species responses to climate and disturbances will shape the role of forests for provisioning ecosystem services such as maintaining biodiversity, providing clean water, regulating climate or capturing and storing carbon from the atmosphere (Felipe-Lucia et al., 2018). Therefore, understanding tree regeneration is crucial for mitigating the impacts of climate change and increasing forest disturbances (IPCC, 2022; Seidl et al., 2014) by improving projections of ecosystem resilience that ultimately will guide management policies and practices.

Disentangling the drivers of tree regeneration is challenging because multiple processes governed by abiotic (i.e. climate and soil) and biotic factors are involved and interact (Price et al., 2001). Many of them are difficult to measure, and their complex interactions are poorly understood (Clark et al., 1999). Tree regeneration is particularly important for the migration of tree species under changing climatic conditions (Qiu et al., 2021). Nevertheless, emerging positive and negative interactions potentially change the pace of tree species range shifts (i.e. leading and trailing range edges; HilleRisLambers et al., 2013) with major implications for projections of future forest dynamics. For example, if competition instead of climate determines

regeneration, range shifts will be slower. Conversely, less competition or positive interactions at leading range edges could accelerate regeneration responses to climate change (Brown & Vellend, 2014; Ettinger & HilleRisLambers, 2017). Altogether, competitive context and climatic conditions affect regeneration in ways that result in complex feedbacks and render tree regeneration an extremely stochastic process (cf. Shoemaker et al., 2020).

Unfortunately, we generally lack the information needed to fully understand the large-scale drivers of tree regeneration. Tree regeneration is influenced by processes acting on multiple spatial and temporal scales (Hart et al., 2017; Levin, 1992), making it challenging to translate the mechanisms of small-scaled subprocesses, competition, and climatic responses to larger scales where climatic variation becomes more visible because the stochasticity of small-scaled processes averages out (König et al., 2022; Price et al., 2001; Ren et al., 2022). Trade-offs between temporal and spatial coverage of tree regeneration data at larger scales (e.g. large-scaled spatial data on potential mother trees versus small-scaled spatial and temporal data on germination and early seedling growth and survival; cf. Clark et al., 1999) add another layer of complexity to the many processes involved. Furthermore, data on tree regeneration often rely on observations in managed forests. Since management typically aims to promote particular tree species, demographic processes derived from managed forests may be poorly generalizable (Schelhaas et al., 2018). Joint efforts that allow for the analysis of protected forests like ForestGeo (Anderson-Teixeira et al., 2015; Davies et al., 2021) or the new European Forest Reserves Initiative (EuFoRla, www.euforia-project.org) are thus essential to overcome the scarcity of data on natural long-term forest dynamics.

Despite these challenges, we have gained some insights on the relative effects of climate and competition on regeneration across climate gradients by analysing tree recruitment (i.e. ingrowth), which we define as evidence for successful regeneration. For example, findings from empirical studies and analyses of tree recruitment on cross-regional scales within Europe suggest that climatic signals are often weak, whereas the effects of stand density (represented by basal area) on tree recruitment are much more stronger (Käber et al., 2021; Klopčič et al., 2012; Nagel et al., 2021; Zell et al., 2019). Studies in other forests have found that competition dominates species performance under favourable climatic conditions, whereas climatic effects become pivotal under stressful conditions along elevational gradients (Ettinger et al., 2011), and facilitation could lead to idiosyncratic range shifts under climate change (Kroiss & HilleRisLambers, 2015; Mamantov et al., 2021) but see Grossiord (2020). In this context, tree regeneration may serve as a benchmark for a species when habitat conditions of existing tree populations change, and it is particularly important for their migration into more suitable habitats. In short, most studies on tree recruitment along climatic gradients emphasize the importance of competition for anticipating community trajectories under climate change (Ettinger & HilleRisLambers, 2017) and show that interpolation of climatic effects on species performance without considering biotic interactions is problematic because feedbacks between climate and biotic factors may play out differently under unprecedented climatic conditions (Lenoir et al., 2010; Meier et al., 2010). Although many of these studies of tree recruitment across climate gradients have found support for the stress gradient hypothesis (SGH; Figure 1) and contributed insight into regeneration, none are conducted across continental scales, and thus do not allow us to assess how general these patterns are at the larger spatial scales necessary to understand climate change impacts.

Interactions between a species' climatic stress tolerance and its shade tolerance may determine the recruitment of tree species under different climatic conditions. Life-history strategies (LHS; Grime, 1977, 2006) can summarize these interactions of different traits (e.g. tolerance to drought [*Pinus sylvestris*] versus shade [*Picea abies*]). The SGH and LHS may explain such variation in tree recruitment driven by the interaction between biotic and abiotic factors (Maestre et al., 2009; Figure 1). Predictions of the SGH along climatic stress gradients are continuous; that is, positive interactions (e.g. microclimate amelioration) and negative interactions (e.g. competition for resources) may be evident at the same time, albeit with different intensity (cf. Malkinson & Tielbörger, 2010). Extending the SGH by considering species LHS and different types of climatic stress allows for predictions on how species match the SGH with varying LHS (cf. Maestre et al., 2009). Based on species tolerance to climatic stress and shade (Leuschner & Ellenberg, 2017, p. 185; Niinemets & Valladares, 2006), specific expectations of recruitment patterns along climatic gradients emerge for different species (Figure 1). In the conceptual model shown here the Leaf Area Index (LAI) of a forest stand is a proxy for competition that aggregates over multiple processes. Specifically, LAI is related to negative interactions such as

competition for light (Waring, 1983) and for below-ground resources (Naithani et al., 2013). These relations qualify LAI as a robust measure for competition and to a very limited extent for other biotic interactions affecting tree recruitment such as browsing and microclimate amelioration (Borkowski et al., 2017; De Frenne et al., 2021). Consequently, we expect competition to be stronger in forests with high LAI compared to forests with low LAI.

In this study, we test whether the SGH applies to tree recruitment in European unmanaged forests and whether LHS explain differences between tree species, by analysing how LAI modulates tree recruitment along gradients of temperature and moisture availability. Specifically, we contrast expectations (Figure 1) and empirically derived recruitment patterns under low and high LAI for 24 major tree species from warm to cold and from wet to dry conditions. This allows us to address the following research questions:

1. *Is competition less dominant when abiotic stress is high?* We expect that competition determines tree recruitment under favourable conditions because low abiotic stress allows for a high performance of the adult trees, which tends to suppress tree recruitment. In contrast, competition is reduced under climatic stress because tolerance to stress becomes more important and interactions between trees are less relevant (Bertness & Callaway, 1994).
2. *Are positive interactions more common under cold stress than under drought stress?* Stress induced by low temperature is expected to lead to more positive interactions compared to stress induced by drought (cf. Maestre et al., 2009).
3. *Do life history strategies explain recruitment patterns?* Shade-tolerant and stress-tolerant species experience less competition or more positive interactions under stress, whereas shade-intolerant species experience competition regardless of the environment (Figure 1).

2 | METHODS

2.1 | Forest reserve data

We used repeated tree census data collected in forest reserves and unmanaged (or protected) forests across Europe, which were compiled in the framework of the EuFoRia network. The sampled forests have not been managed for at least one decade, but most for much longer, and some are primary forests. From the EuFoRia network, all plots with dendrometric measurements in plots of at least 0.02 ha size, with repeated measurements, and with a lower diameter at breast height (DBH) threshold of at least 7 or 10 cm were selected (cf. Table A2 for the distribution of DBH thresholds across the original forest inventory plots). The selected data contain more than 1 million tree diameter measurements from 6539 forest inventory plots covering 299 strict forest reserves (Figure 2), with records dating back to 1936 (Białowieża National Park, Poland) and the latest records from 2020. The census periods range from 3 to 37 years,

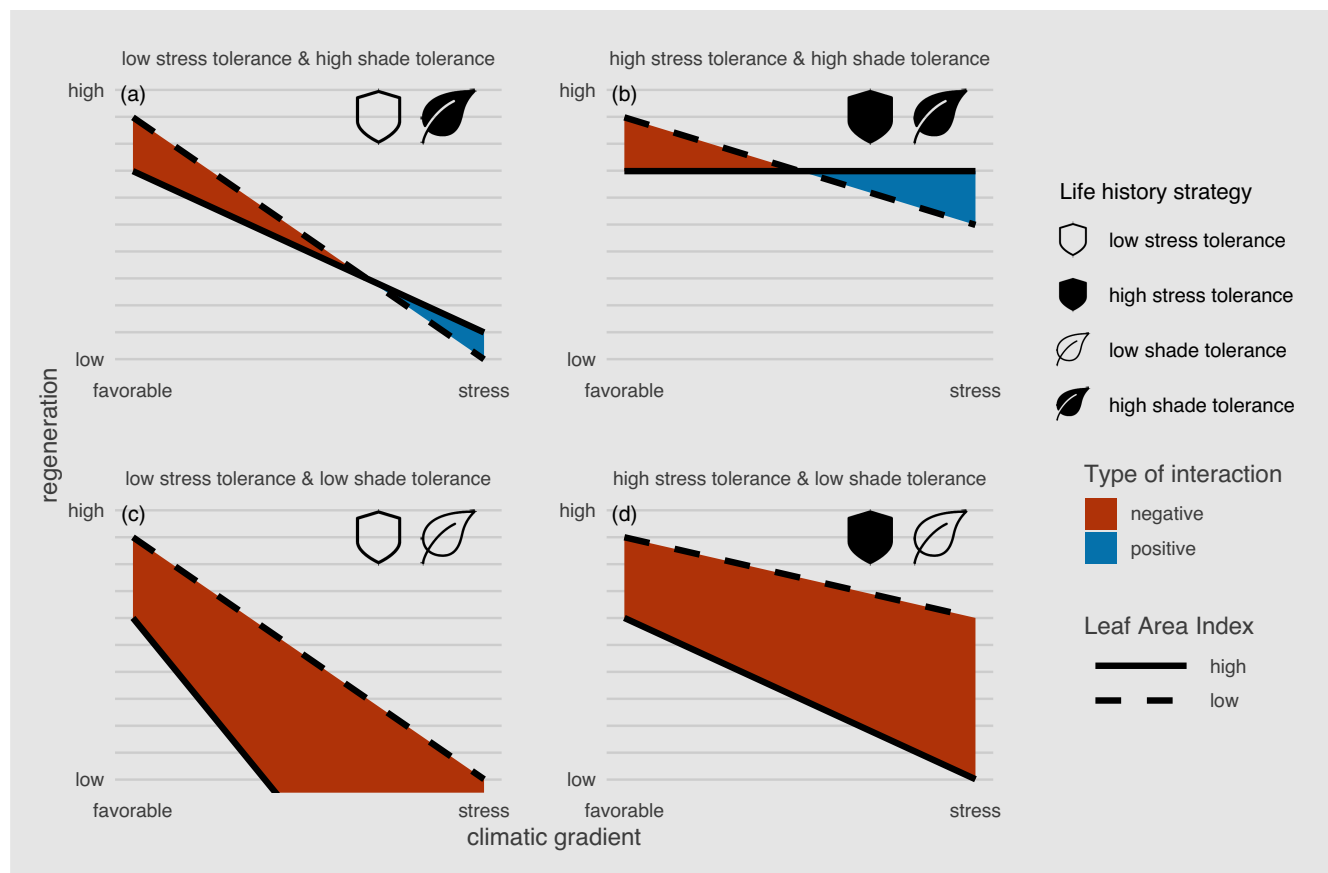
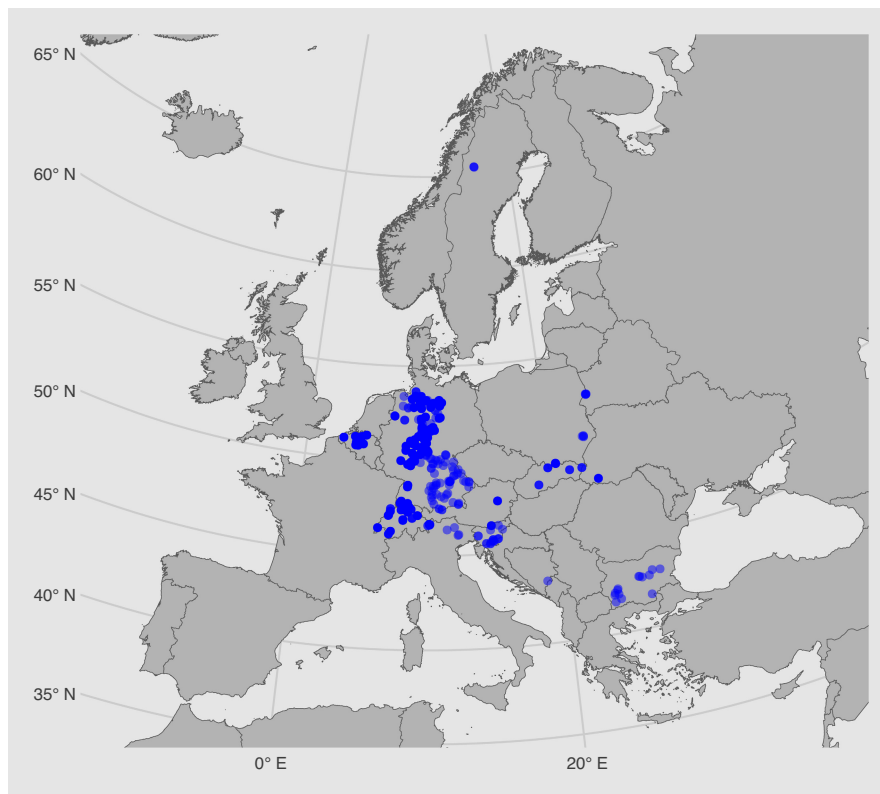


FIGURE 1 Modification of the Stress Gradient Hypotheses (SGH) based on Life History Strategies (LHS). The SGH states that (i) abiotic factors (e.g. climate or soil) determine species performance at the edges of climatic gradients, (ii) negative interactions (competition) determine performance under favourable climatic conditions, and (iii) positive interactions are more likely under stressful climatic conditions (Bertness & Callaway, 1994; Callaway & Walker, 1997). Thus, the original SGH (a) predicts reduced performance with increasing climatic stress, with effects of neighbours (here captured as Leaf Area Index (LAI): high LAI [solid line] vs. low LAI [dashed line]) transitioning from negative interactions (competition) under favourable conditions to positive interactions under stressful conditions—as in (a, b). LHS traits can modify the nature of this relationship. For example, traits conferring shade tolerance can lead to lower negative effects of climatic stress, especially in the absence of competition (a) (e.g. *Tsuga heterophylla* in Ettinger & HilleRisLambers, 2017). Species that are shade-tolerant and tolerant to climatic stress exhibit both reduced effects of stress on recruitment and high effects of competition across the entire climatic gradient (b) (e.g. *Abies amabilis* in Ettinger & HilleRisLambers, 2017). Lower shade tolerance is expected to heighten competition effects across the entire climatic gradient, reducing the likelihood of positive interactions (c) (cf. Körner (2021) for potential mechanisms that limit species distribution range under cold stress) but climatic stress tolerance can still lower the combined negative effects of competition and climatic stress (d) (Maestre et al., 2009). Shade-induced stress is possible along entire climatic gradients, whereas cold and drought stress appears toward their ends. Thus, according to the SGH varying levels of species tolerance to shade (upper vs. lower panels) and climatic stress (left vs. right panels) are expected to systematically modulate the interaction between trees along climatic gradients. These different trait configurations may translate into different strategies for one species, depending on the type of climatic stress. For example, *Fagus sylvatica* is highly tolerant to shade but sensitive to low temperatures and drought (a). *Quercus* spp. is shade-intolerant and tolerant to drought (d) but intolerant to cold conditions (c). The opposite is true for *Picea abies*, which is considered tolerant to shade and low temperatures (b) but not to drought (a). Other species with very low shade tolerance, such as *Betula* spp. and *Pinus sylvestris*, are tolerant to cold or to cold and drought, respectively (d). Consequently, shade-tolerant and shade-intolerant species may feature different strategies depending on the type of climatic stress (i.e. horizontal switches between panels).

with an average of 14 years. The individual plot size ranges from 0.02 to 5.52 ha, of which 4515 plots are sampling plot inventories on regular grids across individual reserves with an average plot size of ca. 0.05 ha. 2024 plots feature inventories that cover larger areas with an average plot size of ca. 0.3 ha. The size measurement threshold for trees differs between plots, ranging from 0 to 10 cm DBH. Individual trees are identifiable between inventories, thus allowing for sequential comparisons of DBH growth and status changes (i.e. tree

recruitment and death). The data were further aggregated and processed to facilitate the empirical analysis. A critical step during data processing was merging small plots and splitting large plots within individual reserves to obtain consistent observation units representing a similar plot size, which we aimed to be ca. 1 ha (Appendix A1). The final data set contained 691 units, each covering on average 1 ha of forest area with observations of tree recruitment at a DBH of 7 cm (see Appendix A1 for details). The 24 most abundant species

FIGURE 2 Location of the forest reserves in Europe. Blue dots show all plots with an inventory-specific diameter at breast height (DBH) threshold ≤ 7 cm DBH. A map including plots with a DBH > 7 cm DBH is shown in [Figure A2](#).



across all plots were selected, of which we focus on 11 species in the main text. These 11 species were selected because they were best covered by the observations. In the main text, the analysis of tree recruitment at a DBH of 7 cm is presented, the corresponding analysis for a DBH of 10 cm can be found in the Appendix (cf. [Figure A2](#)).

2.2 | Definition of variables

Tree recruitment, often also termed ingrowth, was defined as the number of trees that surpass the DBH threshold of 7 or 10 cm between two consecutive inventories for the first time (in the first inventory the trees must have been smaller than the threshold of 7 or 10 cm). Thus, the observation of tree recruitment is evidence for successful regeneration at a specific DBH measurement threshold (cf. the transition from saplings to canopy trees in the concept of seed and sapling rain in Clark et al., 1999). Competition and facilitation are often quantified based on pairwise interactions between species (Adler et al., 2018), but observations of ecosystems in which negative and positive interactions occur usually feature complex patterns that are caused by manifold interactions among species (Wilson & Keddy, 1986). Therefore, we used the sum of the LAI over all tree species as a proxy for the magnitude of all interactions between the focal recruit and all neighbours, instead of distinguishing between intra- and interspecific LAI. LAI was calculated according to Bugmann (1994) for each plot i and inventory year t as

$$\text{LAI}_{i,t} = 0.5 \times \sum_{j=1}^{N_{\text{species}}} \sum_{k=1}^{N_{\text{trees}}} C_j \times A_{1,j} \times \text{DBH}_{k,j,t}^{A_{2,j}}, \quad (1)$$

where C_j is foliage area per unit foliage weight, and $A_{1,j}$ and $A_{2,j}$ are allometric parameters for the foliage weight of each species j . Subsequently, the average of the LAI from two consecutive inventories was used to obtain the LAI for each inventory period and ultimately divided through plot size (ha). All parameters were taken from Bugmann (1994). For species where no allometric parameters were available, the average of the parameters for the genus was used, or if no parameters were available on the genus level, which was only 0.2% of the total observed basal area, the average of the allometric parameters over all species was used.

Climate data were derived from the CHELSA dataset version 2 (Karger et al., 2017) with a horizontal resolution of 30 arc seconds. Specifically, we used the monthly precipitation sum and monthly average temperature. Topographic data were derived from the Copernicus digital elevation model EU-DEM (EU-DEM, 2020) with a spatial resolution of 25 m, which was further processed with QGIS (QGIS Development Team, 2022) to calculate the slope and aspect on a spatial resolution of 100 m. All climatic variables were calculated for the growing season, which we defined as the period from April to October. The seasonal degree-day sum (DDS) is the integral under the temperature curve when ignoring temperatures below 5.5°C (Allen, 1976; Fischlin et al., 1995). As a proxy for moisture availability, we used the site water balance (SWB; cf. Speich, 2019). The calculation of the SWB is explained in detail in Appendix A1.

2.3 | Tree recruitment models

We specified a species-specific tree recruitment model based on a negative binomial distribution to predict counts of tree recruitment

with climatic variables, LAI, and the interaction between climate and LAI. The purpose of this model was to predict the number of recruited trees based on climate and stand-level effects (i.e. LAI), which allows for the quantification of the difference between the number of recruited trees in dense versus open forest stands along climatic gradients (Figure 3).

We fitted four candidate models for each species. The candidate models covered four combinations with and without second-degree polynomials for the explanatory variables. Thus, these models allowed for strictly linear and more flexible relationships between the climatic site variables (DDS and SWB) and tree recruitment. Among the four models, the one with the lowest Bayes information criterion (BIC; Schwarz, 1978) was selected. We preferred BIC over the Akaike information criterion (Sakamoto et al., 1986) because it favours less complex models. Preferring BIC was particularly important for models of less frequent tree species, where many candidate models were too complex (i.e. included too many parameters).

The number of recruited trees was modelled with a negative binomial distribution defined as

$$\text{NegBinomial2}(y_{i,t} | \mu_{i,t}, \phi) = \binom{y_{i,t} + \phi - 1}{y_{i,t}} \left(\frac{\mu_{i,t}}{\mu_{i,t} + \phi} \right)^{y_{i,t}} \left(\frac{\phi}{\mu_{i,t} + \phi} \right)^{\phi}, \quad (2)$$

$$\begin{aligned} \log(\mu_{i,t}) = & \underbrace{\log(S_i \times \Delta t_{i,t})}_{\text{competition}} + \underbrace{\beta_0 + \beta_1 \text{DDS}_{i,t} + \beta_2 \text{DDS}_{i,t}^2 + \beta_3 \text{SWB}_{i,t} + \beta_4 \text{SWB}_{i,t}^2}_{\text{abiotic effects}} \\ & + \underbrace{\beta_5 \text{LAI}_{i,t} + \beta_6 \text{DDS}_{i,t} \text{LAI}_{i,t} + \beta_7 \text{DDS}_{i,t}^2 \text{LAI}_{i,t} + \beta_8 \text{SWB}_{i,t} \text{LAI}_{i,t} + \beta_9 \text{SWB}_{i,t}^2 \text{LAI}_{i,t}}_{\text{interaction of competition and abiotic effects}}. \end{aligned} \quad (3)$$

Note that the model terms represent the full model. The other candidate models included only one of the polynomial terms, or none. The term $\log(S_i \times \Delta t_{i,t})$ refers to the model offset based on the

size S of plot i and the census interval Δt of plot i in year t . The offset for plot size was necessary because aggregated or split plots did not exactly sum up to 1 ha. The fitted coefficients are denoted with β . All methods were implemented in the R programming language (R Core Team, 2020), and model fitting was done with the glmmTMB package version 1.1.3 (Brooks et al., 2017). Ultimately, we used the DHARMa package (Hartig, 2021) to ensure that the scaled residuals met the model assumptions. We considered including random effects and spatial autocorrelation in the models. Unfortunately, these more complex models had convergence issues or could not be fitted because of computational constraints. Because of these issues we were unable to resolve the problem of spatial autocorrelation in the residuals. However, the conclusions of our analysis did not change when we applied a more conservative modelling approach with subsets of the data. For more details, see Appendix A7.

2.4 | Competition effects of LAI on tree recruitment

Competition and positive interactions were quantified by predicting the number of recruited trees per ha and year for open versus dense forest stands (Figure 3a). LAI was modelled with a log-linear regression to obtain realistic stands along the gradient of DDS and SWB. Low LAI and high LAI were defined as the 2.5% and 97.5% limits of the prediction interval, respectively (see Appendix A1). For each combination of DDS and SWB within the observed range of the species, the extent of interaction (I) among trees during recruitment was defined as

$$I = N.\text{recr}_{\text{highLAI}} - N.\text{recr}_{\text{lowLAI}}, \quad (4)$$

where $N.\text{recr}$ is the predicted number of recruits under high LAI and low LAI, respectively (Figure 3a). Positive interactions ($I > 0$)

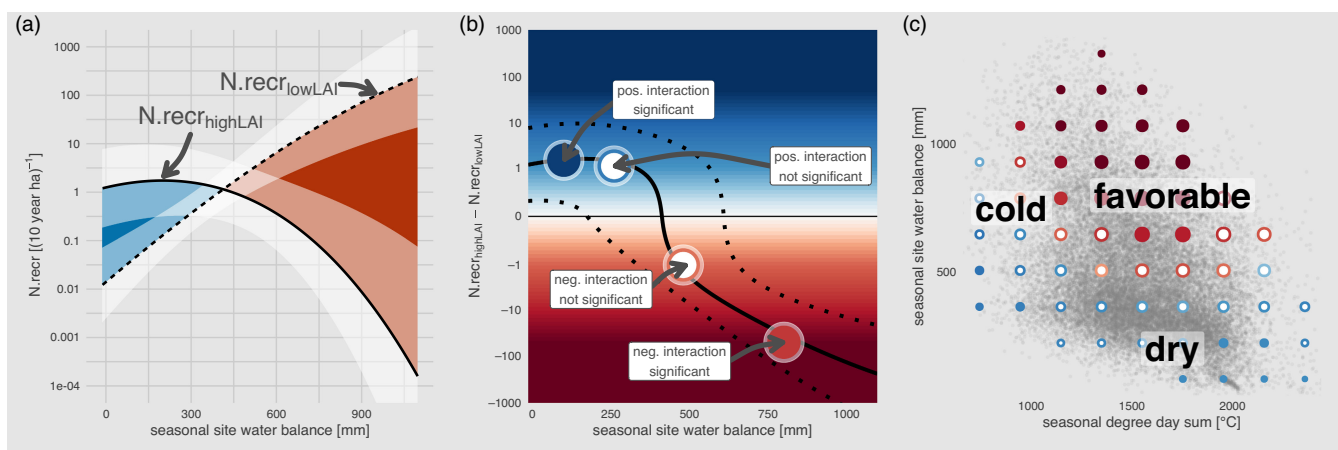


FIGURE 3 Quantification of competition with the example of *Abies alba* showing (a) tree recruitment per ha and 10 years for high Leaf Area Index (LAI; solid line) versus low LAI (dashed line) on a gradient of seasonal site water balance. Competition shown in red and positive interaction in blue. (b) Difference between tree recruitment for high LAI and low LAI (solid line), including the 95% interval (dotted line). The open dots (non-significant) and the filled dots (significant) explain the labelling of the dots in (c). (c) Simulated interaction along the gradients seasonal degree-day sum and seasonal site water balance. The size of the points corresponds to the probability of tree recruitment and was simulated with a logistic regression model (cf. Appendix A2).

represent net facilitation, and negative interactions ($I < 0$) represent net competition. An effect was considered significant if the 95% confidence interval of the interaction did not include zero (Figure 3b). Additionally, we simulated the probability that at least one tree was recruited based on the logistic model to visualize the relation between overall recruitment probability and the interaction effect. All simulation results were synthesized in one graph (Figure 3c). To put the simulated results into perspective, we included samples of the site factors from the European Atlas of Forest Tree Species (San-Miguel-Ayanz et al., 2016) as shown in Figure 3c, using a draw of 10,000 random locations where the relative probability of presence (de Rigo et al., 2016) of a tree species was larger than 50%. Note that the actual number of samples was lower than 10,000 for tree species where not enough locations were associated with a relative probability of presence larger than 50%.

3 | RESULTS

The models showed that tree recruitment was sensitive to LAI for most species (Figure 4), indicating that competition was predominant. High LAI generally reduced recruitment but these effects changed significantly along the climatic gradients of DDS and SWB for most species (Figures 4 and 5). For some shade- to very shade-tolerant species such as *Abies alba*, *Carpinus betulus* and *Tilia cordata*, higher recruitment occurred under high LAI in some cases. Thus, interactions between LAI and abiotic factors were evident for most species. There were only a few rare species for which we found no significant differences between low and high LAI within the observed climatic envelope (cf. Table 1; Figure A10). Here, we focus on the results for the 11 most frequent species. Results for all species are presented in the Appendix.

Contrary to the expectation that tree recruitment should decrease toward stressful conditions (Figure 1), several species showed polynomial responses or higher recruitment rates toward such conditions (Figures 4 and 5). For example, 2nd degree polynomial responses to DDS were evident for *Fagus sylvatica*, *Quercus* spp., *Picea abies*, *Abies alba* and *Carpinus betulus*, and to SWB for *Betula* spp. Under low LAI, *Betula* spp. and *Pinus sylvestris* featured a positive relationship with cold and dry conditions. *Picea abies* showed a distinct optimum toward cold conditions and a weak monotonic positive effect of drier conditions, and *Quercus* spp. was also positively affected by drier conditions. High LAI was more often associated with positive effects on tree recruitment toward climatic stress than low LAI. These positive responses were particularly evident for some shade-tolerant tree species: *Abies alba* and *Carpinus betulus* to drought, and *Picea abies* to low temperature and drought. In summary, the results showed that the direction of climatic effects often differed between open stands (low LAI) and dense stands (high LAI) and revealed complex species-specific patterns between LAI, abiotic factors, and tree recruitment.

3.1 | Is competition less dominant when abiotic stress is high?

Competition, defined here as the net effect of LAI on tree recruitment being negative, is the most frequent pattern across all 24 species and along both climatic gradients. Competition was less dominant under cold stress for most species (Figures 4a and 5), yet various species showed increases and decreases in competition under drought (Figures 4b and 5). However, the level of competition along stress gradients was species-specific. For example, along the temperature gradient *Betula* spp. and *Larix decidua* showed no change in interaction, whereas *Pinus sylvestris* and *Tilia cordata* featured higher levels of competition toward low temperatures (Figures 4 and 5; Figure A6; Table 1). Along the moisture gradient, *Picea abies* showed no change in interaction, whereas other species (e.g. *Fagus sylvatica*, *Betula* spp., *Pinus sylvestris*) experienced more competition toward dry conditions.

3.2 | Are positive interactions more common under cold stress than under drought stress?

Positive interactions (i.e. recruitment being higher under high LAI compared to low LAI) or a significant reduction in competition were more common in cold compared to dry climates. Most tree species experienced a significant reduction in competition or sometimes positive interactions toward cold stress, whereas fewer tree species showed positive interactions under drought stress (Figure 4). *Pinus sylvestris* was the only tree species that featured a significant increase in competition under cold conditions (Figure 4a). *Acer pseudoplatanus* and *Betula* spp. experienced competition under cold conditions but without an increase in competition (Figure 4a). Moreover, additive effects of DDS and SWB affected the interactions and their significance—for example for *Abies alba*, *Tilia cordata*, and *Quercus* spp.—as shown in Figure 5.

3.3 | Do life history strategies explain recruitment patterns?

Species that are tolerant to shade and climatic stress experienced positive interactions more frequently than those only tolerant to climatic stress. Some, but not exclusively, shade-intolerant tree species showed similarly positive interactions during recruitment along the climatic gradients (Figure 4; Table 1). Specifically, *Picea abies*, which is tolerant to shade and low temperatures, and *Abies alba*, which is very tolerant to shade but less tolerant to low temperatures, experienced overall positive or decreased competition under cold stress during recruitment, respectively (Figure 4a). Under drier conditions, the shade- and drought-tolerant species *Tilia cordata* was associated with positive interactions (Figure 4b). In contrast, drought-tolerant species that are less shade tolerant, such as *Pinus sylvestris* or *Quercus* spp., experienced increased competition toward

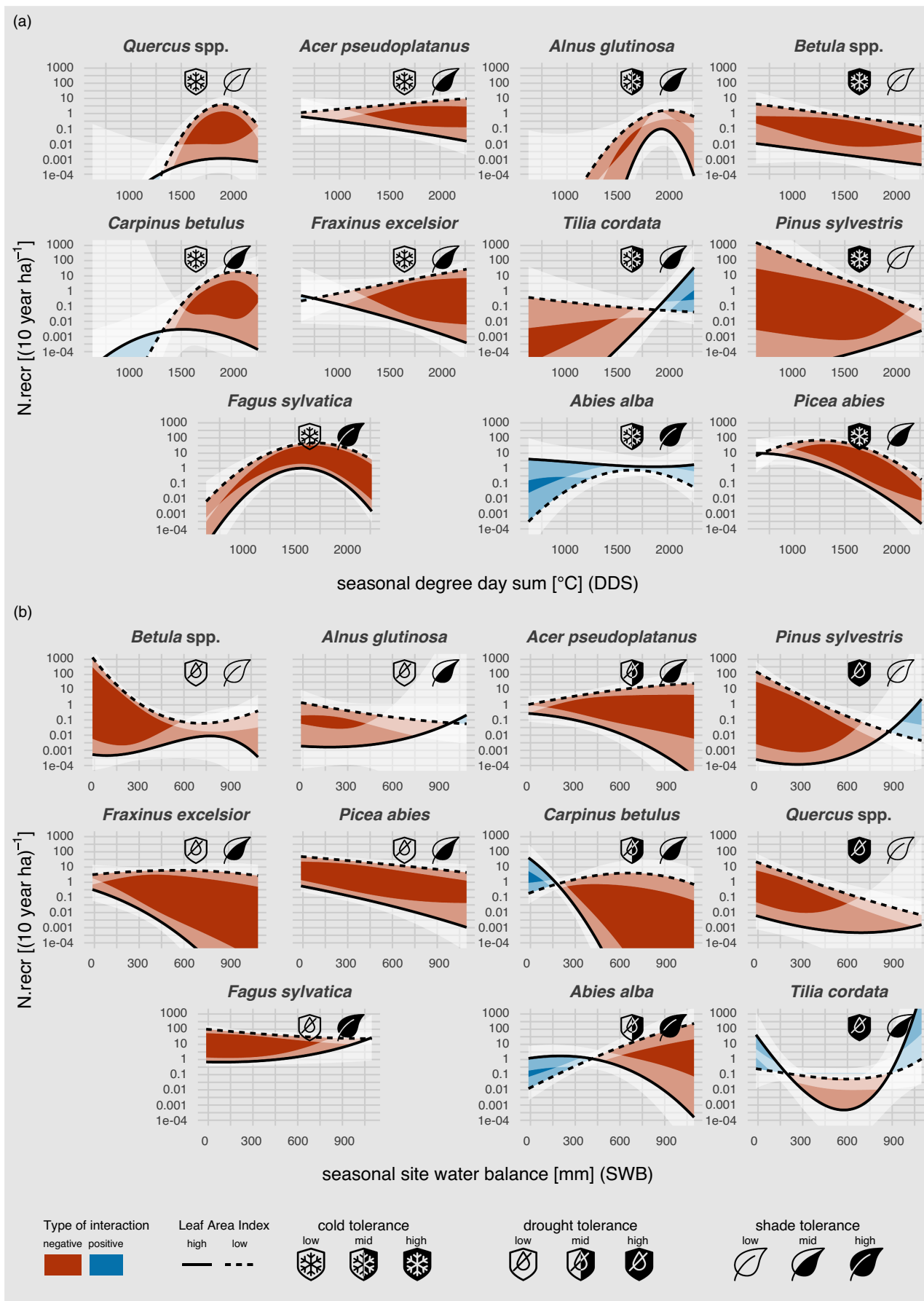


FIGURE 4 Predicted number of recruits per ha and 10 years along the gradients of seasonal degree-day sum (a) and seasonal site water balance (b) for low Leaf Area Index (LAI; dashed line) and high LAI (solid). The 95% confidence intervals are shown by the white transparent areas. Positive and negative interactions (competition) are indicated by blue and red filling, respectively. The symbols at the top right of each panel show the species' tolerance to stress (shield) and shade (leaf), from low tolerance (no fill) to high tolerance (filled). In both (a, b), species are ranked first by stress tolerance and then by shade tolerance. For detailed model results for all species cf. Appendix A3; fitted model coefficients are shown in Appendix A6.

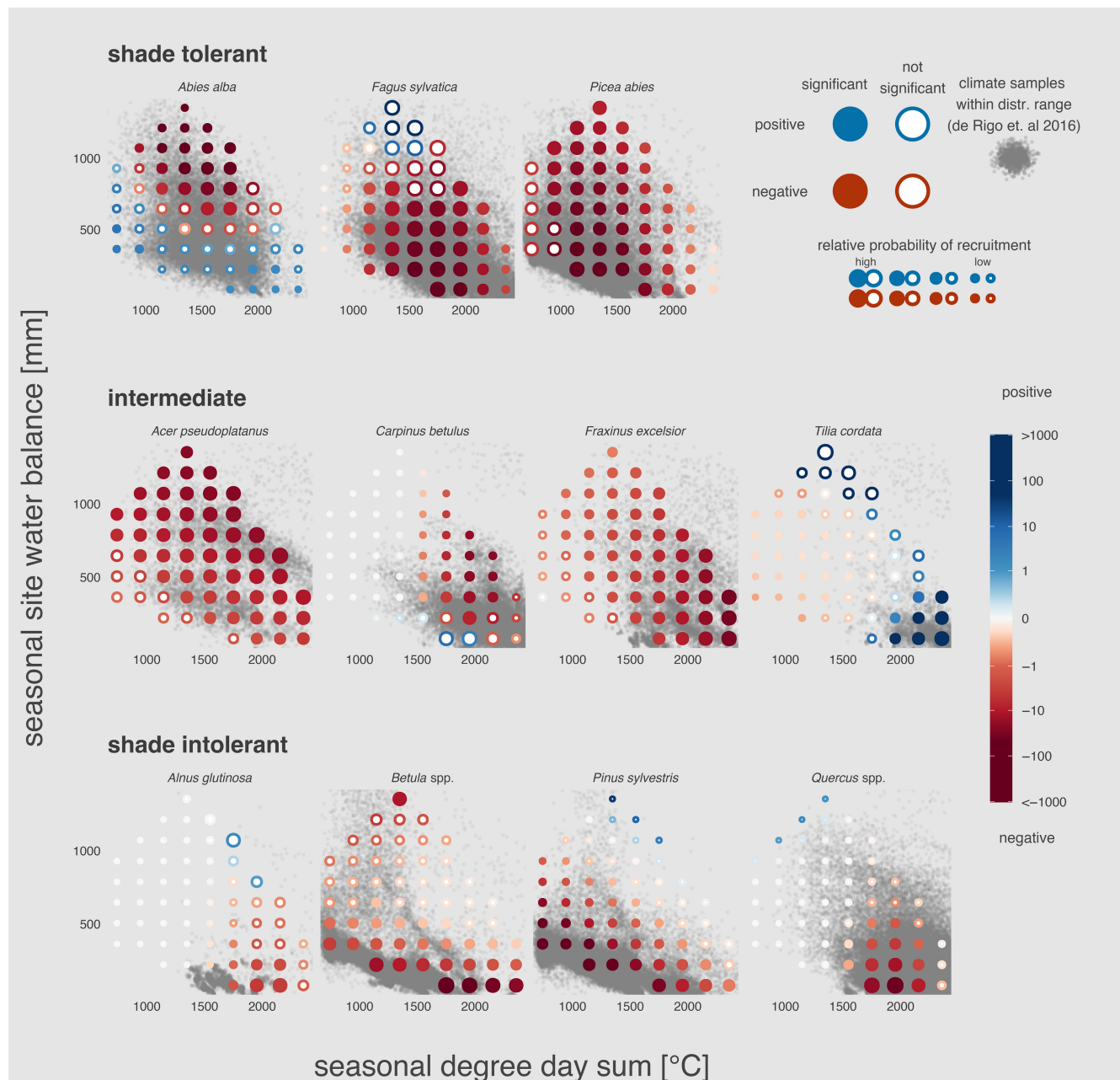


FIGURE 5 Simulated difference between the number of recruits at diameter at breast height 7 cm in stands with high versus low Leaf Area Index (blue to red colour gradient) along the climatic gradients of site water balance (y-axis) and seasonal degree-day sum (x-axis) for 11 major European tree species ranked by shade tolerance (for all species see Figure A10). The size of the points shows the recruitment probability. Only points where observations exist are shown here to avoid extrapolation. If a difference is not significant, the point is filled white. The dark grey dots in the background layer represent 10,000 samples of climatic conditions throughout Europe where the species' general occurrence probability is >50%, derived from the EU-forest data set (de Rigo et al., 2016). Detailed results for all species are shown in Appendix A6 and fitted model coefficients are shown in Appendix A5, Table A4 and Figure A9.

TABLE 1 Comparison of expected changes in interactions according to the stress gradient hypothesis (SGH) and life-history strategies (LHS; Figure 1) versus empirically derived changes (Figures 4 and 5) during recruitment along stress gradients. Expectations are according to the species' juvenile tolerance to shade and stress (Leuschner & Ellenberg, 2017). 'Increase' denotes that competition increases with increasing stress, 'Decrease' denotes that competition decreases with increasing stress, and 'Indifferent' denotes that no significant change is evident or the patterns are unclear. The interpretation of this table, for example for *Fagus sylvatica* under drought stress is: *Fagus sylvatica* is expected to experience decrease in competition under drought stress because its shade tolerance should enable it to experience positive interactions. The empirical pattern does not match this expectation and therefore *Fagus sylvatica* is placed in the upper right panel which indicates that it does not behave according to the SGH and its LHS as described in Figure 1.

		Expected change in competition with increasing drought stress				Expected change in competition with increasing cold stress	
		Increase	Decrease			Increase	Decrease
Empirical pattern	Increase	<i>Betula</i> spp. <i>Pinus sylvestris</i> <i>Quercus</i> spp.	<i>Alnus glutinosa</i> <i>Fagus sylvatica</i>	Empirical pattern	Increase	<i>Pinus sylvestris</i>	<i>Tilia cordata</i>
	Decrease		<i>Abies alba</i> <i>Acer pseudoplatanus</i> <i>Carpinus betulus</i> <i>Fraxinus excelsior</i>		Decrease		<i>Abies alba</i> <i>Acer pseudoplatanus</i> <i>Carpinus betulus</i> <i>Fraxinus excelsior</i> <i>Picea abies</i>
	Indifferent		<i>Picea abies</i> <i>Tilia cordata</i>		Indifferent	<i>Betula</i> spp. <i>Quercus</i> spp.	<i>Fagus sylvatica</i> <i>Alnus glutinosa</i>

dry conditions (Figure 4b). *Pinus sylvestris* was also associated with increased competition under cold stress. The very light-demanding *Betula* spp. and *Larix decidua* showed similar recruitment rates for low and high LAI along the temperature gradient (Figure 4a; Figure A4). All species but *Picea abies* experienced a change in interaction along the moisture gradient (Figure 4b). Altogether, while LHS partly explains these variations, some patterns remain unclear and may only be understood at the species level.

4 | DISCUSSION

Our analysis shows that the expectations regarding tree recruitment derived from the SGH and LHS (Bertness & Callaway, 1994; Leuschner & Ellenberg, 2017; Maestre et al., 2009) are partially supported by empirical patterns across a wide range of unmanaged European temperate forests. Competition (i.e. negative effects of stand LAI on tree recruitment) decreases toward stressful environments for many species. Generally, shade-tolerant species are associated with a decrease in competition under climatic stress during regeneration, and positive interactions are more common compared to species that lack shade tolerance. Furthermore, distinct differences between species' cold stress and drought stress are evident from the results (Table 1).

4.1 | Competition can but does not always decrease with high climatic stress

According to the SGH, competition is expected to decrease, and positive interactions to dominate in stressful climates (Bertness &

Callaway, 1994). Our results do not fully support this. Instead, we show that competition is common along the entire stress gradient for many tree species, yet decreasing competition toward dry conditions and low temperatures does indicate facilitation for some species. Still, it is important to note that while the emerging patterns show net competition, facilitation and competition may cancel out, and the share of competition decreases (Malkinson & Tielbörger, 2010). Our finding that competition decreases toward climatic stress is consistent with other studies on plant interactions (He et al., 2013) and tree regeneration (Adams et al., 2022; Ettinger & HilleRisLambers, 2017; Klanderud et al., 2021). Assuming that decreases in competition are caused by facilitation effects, we partly confirm the predictions of the SGH for most species (Table 1). It is also important to acknowledge that we investigated tree recruitment and its patterns on a relatively coarse level (i.e. our analysis aggregates over many subprocesses; cf. Pickett et al., 1987), making it challenging to identify specific underlying processes. Therefore, our results are not providing a proof for the SGH, but rather indicate that the emerging patterns are not contradicting the predictions of the SGH.

4.2 | Competition is less common at cold than at dry range edges

In our analysis, a higher level of competition is evident under dry compared to cold conditions. This supports the predictions of the refined SGH (Maestre et al., 2009), that is that interactions along drought gradients are non-linear with moderate drought inducing facilitation but extreme drought preventing it (Andivia et al., 2018; Grant et al., 2014). It is furthermore consistent with other studies on

tree species interactions along gradients of water availability (Bel-luau et al., 2021; Grossiord, 2020; Jucker et al., 2014) and emphasizes the importance of distinguishing between stress caused by low temperature and different levels of drought (Kunstler et al., 2021; Maestre et al., 2009). However, firm conclusions at the species level would require a finer-scaled analysis along drought gradients (Lortie & Callaway, 2006). Overall, our results show distinct differences regarding changes in competition under dry versus cold conditions.

It is reasonable to expect that the ameliorating effects of neighbouring trees on microclimate are becoming weaker and are switching to competition for water under extreme drought (Haberstroh & Werner, 2022; Kitzberger et al., 2000). Therefore, our findings regarding the differences between cold- and drought-induced stress are plausible as competition for water resources negatively affects tree recruitment. Cold stress, however, is typically not resource-driven, and therefore facilitation, for example through microclimate amelioration or resistance against a heavy snow load is fostered (cf. Maestre et al., 2009). Similar effects were reported for *Tsuga mertensiana* and *Abies amabilis* along elevational gradients in North America (Ettinger & HilleRisLambers, 2017).

4.3 | LHS partially explain differences between tree species along stress gradients

Overall, we also found partial support for our expectations of how LHS explains differences among species. For species with low shade tolerance, negative competitive interactions often increased along temperature and moisture gradients. In contrast, moderately shade tolerant species commonly experienced high competition across their entire distribution, regardless of climate. This difference suggests that shade-tolerant tree species often gain a competitive advantage by enduring low levels of light or by high crown plasticity, enabling these species to benefit, for example from a favourable microclimate (De Frenne et al., 2021). Conversely, stress-tolerant but less shade-tolerant species require fewer resources to recruit successfully compared to stress-intolerant species (Maestre et al., 2009), but they also need higher light levels, which makes them more sensitive to competition. Distinguishing between the intensity and importance of competition (Welden & Slauson, 1986) is pivotal to understanding the implications of these results. Especially shade-intolerant, fast-growing tree species experience intense competition, yet this is not necessarily an impediment for their large-scale recruitment success provided that sufficient seeds, large dispersal distances, or recurring disturbances allow them to recruit somewhere.

An important exception to these patterns is *Fagus sylvatica*, and its dominance in European forests is ubiquitous (Meier et al., 2011). It is necessary to distinguish between interactions with *Fagus sylvatica* and those with other species to evaluate whether LHS and the SGH explain its variation of recruitment along climatic gradients. In favourable conditions or without disturbances, recruitment is likely to be suppressed by *Fagus sylvatica*, which may explain the reduced competition for *Fagus sylvatica* in favourable conditions because of

lower negative neighbouring effects on intraspecific recruitment compared to other species. Such patterns have also been shown by Dieler and Pretzsch (2013) and are supported by Li et al. (2021), who found that *Fagus sylvatica* is primarily subject to intraspecific competition. However, interspecific interactions become more important when conditions are becoming stressful for *Fagus sylvatica*. This may also explain increased competition toward drought stress for shade-intolerant species such as *Pinus sylvestris*, *Fraxinus excelsior* or *Betula* spp., indicating that these species are entirely excluded under favourable conditions regardless of LAI due to the lack of potential seed trees and, potentially, the lack of disturbance. Unfortunately, the effects of disturbance and dispersal on tree recruitment are not represented in the data to sufficiently inform empirical models.

Finally, LAI does not allow to differentiate among the many constituent factors other than light, such as soil biota (Defosse et al., 2011), dispersal (Journé et al., 2022), or herbivory (Smit et al., 2007). Yet, our analysis shows that particularly species' shade tolerance explains changes in the interplay between stand density (i.e. LAI) and tree recruitment along a stress gradient for most species. Still, tree recruitment patterns remain complex, and simple classifications of LHS (cf. Brzeziecki & Kienast, 1994) or generally and globally posited patterns for competition and growth (Kunstler et al., 2016) do not appear to apply to tree recruitment in unmanaged temperate forests in Europe.

4.4 | Implications for climate change

Climate change will result in warmer (Figure 4a, right direction of the x-axis) and more drought-prone (Figure 4b, left direction of the x-axis) conditions for temperate forests in central Europe. Yet, it is uncertain how quickly forests will respond to climate change because their response depends on climate and competition (HilleRisLambers et al., 2013). At the same time, the effects of competition are expressed differently for individual species along the climatic gradients, that is, some species such as *Quercus* spp. may respond more slowly to climate change as they benefit from a warmer and drier climate but can recruit only if sufficient light is available (cf. Kašpar et al., 2021). Other species, such as *Abies alba* or *Tilia cordata*, are likely to respond more quickly because they experience reduced competition or even facilitation toward warm and dry conditions. However, it is not only the interactions between trees that determine accelerating and decelerating effects in species range shifts. Fecundity (Sharma et al., 2022), plant-herbivore interactions (Liu & He, 2019), dispersal limitations (Liang et al., 2018) and disturbances (Nagel et al., 2021) are also important. Disturbances, in particular, are expected to be more frequent under climate change (Seidl et al., 2014) and thus could have overall positive effects on tree species with low shade tolerance, such as *Pinus sylvestris* or *Betula pendula* (cf. Seidl & Turner, 2022).

Further research should focus on identifying the mechanisms and species traits that determine negative (i.e. competitive) and positive (i.e. facilitative) effects on scale-dependent processes such as

tree recruitment. Identifying such mechanisms is possible, for example by evaluating process models with data (Hartig et al., 2012). However, it is impossible to constrain mechanistic models and establish ecological principles without sufficient data on highly stochastic demographic processes across large temporal and spatial scales in forests. Thus, the long-term monitoring of strictly protected forests must be continued, and further monitoring plots should be established, particularly in parts of the climatic gradient that are currently data-poor. Extending the climatic gradient to drier and colder conditions is crucial to identify species-specific thresholds for demographic processes and ultimately overcome the limitations induced by the currently critically low sample sizes for many tree species.

The main finding of our analysis is that species interactions during tree recruitment are sensitive to climatic conditions, with major implications for projections of long-term forest dynamics under both current and future climatic conditions. However, the patterns elucidated here do not directly translate into potential recruitment strategies under climate change because future drought regimes will probably differ from those underlying the patterns shown here (Bevacqua et al., 2022). Nevertheless, the sensitivity of recruitment strategies to different stress gradients and the relevance of LHS is evident from our results, lending strong quantitative support to the refined SGH (Maestre et al., 2009).

We explored patterns across climatic gradients and gradients of LAI, which allows us to predict how competition may mediate effects of climate. Projections of future species ranges without considerations of interactions predict increased habitat suitability throughout Europe for *Fagus sylvatica* under climate change (Mauri et al., 2022). However, our results suggest that changing climatic conditions and disturbance regimes in Europe will reduce the competitive advantage of currently dominant tree species such as *Fagus sylvatica* or *Picea abies* (Hanewinkel et al., 2013). In that case, the recruitment patterns of other tree species may change drastically. If so, drought-adapted tree species (e.g. *Pinus sylvestris*, *Quercus* spp., or *Acer pseudoplatanus*) could become more dominant and substantially modulate recruitment conditions of many tree species, with substantial implications for future forest structure, composition and functioning. The most important implication of this result is that future forest communities will not only be shaped by climate. Current forest structure and disturbances are key to species range shifts.

AUTHOR CONTRIBUTIONS

Yannek Käber and Harald Bugmann conceived the idea; Yannek Käber led the writing of the paper, conducted the analysis, created the graphics and led the harmonization of the data; Yannek Käber, Christof Bigler, Harald Bugmann, Janneke HilleRisLambers, Jokim Idoate-Lacasia, Martina Hobi, Peter Brang and Thomas A. Nagel developed the concept and framing of the paper; Christof Bigler contributed to the development of the analysis; Thomas A. Nagel, Tuomas Aakala, Markus Blaschke, Peter Brang, Bogdan Brzeziecki, Marco Carrer, Eugénie Cateau, Georg Frank, Shawn Fraver, Jokim Idoate-Lacasia, Jan Holik, Stanislav Kucbel, Anja Leyman, Peter Meyer, Renzo Motta, Pavel Samonil, Lucia Seebach, Jonas Stillhard,

Miroslav Svoboda, Jerzy Szwagrzyk, Kris Vandekerckhove, Ondrej Vostarek and Tzvetan Zlatanov contributed data and substantially supported the process of data harmonization; all authors contributed to paper writing.

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CONFLICT OF INTEREST STATEMENT

The authors declare that there is no conflict of interest.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

Code along with the data required to reproduce all results is archived in a Dryad repository <https://doi.org/10.5061/dryad.hx3ffbqkx> (Käber, 2023).

ORCID

Yannek Käber  <https://orcid.org/0000-0002-7041-9849>

Christof Bigler  <https://orcid.org/0000-0003-3757-6356>

Janneke HilleRisLambers  <https://orcid.org/0000-0001-5523-0354>

Martina Hobi  <https://orcid.org/0000-0003-3537-9738>

Thomas A. Nagel  <https://orcid.org/0000-0002-4207-9218>

Tuomas Aakala  <https://orcid.org/0000-0003-0160-6410>

Markus Blaschke  <https://orcid.org/0000-0001-9361-8966>

Peter Brang  <https://orcid.org/0000-0003-0766-9826>

Bogdan Brzeziecki  <https://orcid.org/0000-0001-5786-3075>

Marco Carrer  <https://orcid.org/0000-0003-1581-6259>

Shawn Fraver  <https://orcid.org/0000-0003-1614-9072>

Jokim Idoate-Lacasia  <https://orcid.org/0009-0005-4709-0861>

Jan Holik  <https://orcid.org/0000-0002-7949-9689>

Anja Leyman  <https://orcid.org/0000-0002-0292-6582>
 Peter Meyer  <https://orcid.org/0000-0003-4200-4993>
 Renzo Motta  <https://orcid.org/0000-0002-1631-3840>
 Pavel Samonil  <https://orcid.org/0000-0002-7722-8797>
 Lucia Seebach  <https://orcid.org/0000-0001-9238-7852>
 Jonas Stillhard  <https://orcid.org/0000-0001-8850-4817>
 Miroslav Svoboda  <https://orcid.org/0000-0003-4050-3422>
 Jerzy Szwagrzyk  <https://orcid.org/0000-0001-8741-7383>
 Kris Vandekerckhove  <https://orcid.org/0000-0003-1954-692X>
 Ondrej Vostarek  <https://orcid.org/0000-0002-0657-0114>
 Tzvetan Zlatanov  <https://orcid.org/0000-0003-4205-3429>
 Harald Bugmann  <https://orcid.org/0000-0003-4233-0094>

REFERENCES

- Adams, A. E., Besozzi, E. M., Shahrokhi, G., & Patten, M. A. (2022). A case for associational resistance: Apparent support for the stress gradient hypothesis varies with study system. *Ecology Letters*, 25, 202–217.
- Adler, P. B., Smull, D., Beard, K. H., Choi, R. T., Furniss, T., Kulmatiski, A., Meiners, J. M., Tredennick, A. T., & Veblen, K. E. (2018). Competition and coexistence in plant communities: Intraspecific competition is stronger than interspecific competition. *Ecology Letters*, 21, 1319–1329.
- Allen, J. C. (1976). A modified sine wave method for calculating degree days. *Environmental Entomology*, 5, 388–396.
- Anderson-Teixeira, K. J., Davies, S. J., Bennett, A. C., Gonzalez-Akre, E. B., Muller-Landau, H. C., Joseph Wright, S., Abu Salim, K., Almeyda Zambrano, A. M., Alonso, A., Baltzer, J. L., Basset, Y., Bourg, N. A., Broadbent, E. N., Brockelman, W. Y., Bunyavejchewin, S., Burslem, D. F. R. P., Butt, N., Cao, M., Cardenas, D., ... Zimmerman, J. (2015). CTFS-ForestGEO: A worldwide network monitoring forests in an era of global change. *Global Change Biology*, 21, 528–549.
- Andivia, E., Madrigal-González, J., Villar-Salvador, P., & Zavala, M. A. (2018). Do adult trees increase conspecific juvenile resilience to recurrent droughts? Implications for forest regeneration. *Ecosphere*, 9, e02282.
- Belluau, M., Vitali, V., Parker, W. C., Paquette, A., & Messier, C. (2021). Overyielding in young tree communities does not support the stress-gradient hypothesis and is favoured by functional diversity and higher water availability. *Journal of Ecology*, 109, 1790–1803.
- Bertness, M. D., & Callaway, R. (1994). Positive interactions in communities. *Trends in Ecology & Evolution*, 9, 191–193.
- Bevacqua, E., Zappa, G., Lehner, F., & Zscheischler, J. (2022). Precipitation trends determine future occurrences of compound hot-dry events. *Nature Climate Change*, 12, 1–6.
- Borkowski, J., Dobrowolska, D., Dąbrowski, W., Banul, R., & Zatuski, D. (2017). Young conifer stands form a deer browsing refuge for an oak admixture: Silvicultural implications for forest regeneration under herbivore pressure. *European Journal of Forest Research*, 136, 787–800.
- Brooks, M. E., Kristensen, K., van Benthem, K. J., Magnusson, A., Berg, C. W., Nielsen, A., Skaug, H. J., Machler, M., & Bolker, B. M. (2017). glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *The R Journal*, 9, 378–400.
- Brown, C. D., & Vellend, M. (2014). Non-climatic constraints on upper elevational plant range expansion under climate change. *Proceedings of the Royal Society B: Biological Sciences*, 281(1794), 20141779. <https://doi.org/10.1098/rspb.2014.1779>
- Brzeziecki, B., & Kienast, F. (1994). Classifying the life-history strategies of trees on the basis of the Griman model. *Forest Ecology and Management*, 69, 167–187.
- Bugmann, H. (1994). *On the ecology of mountainous forests in a changing climate: A simulation study* [PhD thesis, ETH Zurich].
- Callaway, R. M., & Walker, L. R. (1997). Competition and facilitation: A synthetic approach to interactions in plant communities. *Ecology*, 78, 1958–1965.
- Clark, J. S., Beckage, B., Camill, P., Cleveland, B., HilleRisLambers, J., Lichter, J., McLachlan, J., Mohan, J., & Wyckoff, P. (1999). Interpreting recruitment limitation in forests. *American Journal of Botany*, 86, 1–16.
- Davies, S. J., Abiem, I., Abu Salim, K., Aguilar, S., Allen, D., Alonso, A., Anderson-Teixeira, K., Andrade, A., Arellano, G., Ashton, P. S., Baker, P. J., Baker, M. E., Baltzer, J. L., Basset, Y., Bissengou, P., Bohlman, S., Bourg, N. A., Brockelman, W. Y., Bunyavejchewin, S., ... Zuleta, D. (2021). ForestGEO: Understanding forest diversity and dynamics through a global observatory network. *Biological Conservation*, 253, 108907.
- De Frenne, P., Lenoir, J., Luoto, M., Scheffers, B. R., Zellweger, F., Aalto, J., Ashcroft, M. B., Christiansen, D. M., Decocq, G., De Pauw, K., Govaert, S., Greiser, C., Gril, E., Hampe, A., Jucker, T., Klimes, D. H., Koelemeijer, I. A., Lembrechts, J. J., Marrec, R., ... Hylander, K. (2021). Forest microclimates and climate change: Importance, drivers and future research agenda. *Global Change Biology*, 27, 2279–2297.
- de Rigo, D., Caudullo, G., Houston Durrant, T., & San-Miguel-Ayanz, J. (2016). The European atlas of Forest tree species: Modelling, data and information on forest tree species. In A. Mauri (Ed.), *European atlas of forest tree species* (pp. 40–45). Publications Office of the European Union.
- Defossez, E., Courbaud, B., Marcais, B., Thuiller, W., Granda, E., & Kunstler, G. (2011). Do interactions between plant and soil biota change with elevation? A study on *Fagus sylvatica*. *Biological Letters*, 7, 699–701.
- Dieler, J., & Pretzsch, H. (2013). Morphological plasticity of European beech (*Fagus sylvatica* L.) in pure and mixed-species stands. *Forest Ecology and Management*, 295, 97–108.
- Ettinger, A., Ford, K. R., & HilleRisLambers, J. (2011). Climate determines upper, but not lower, altitudinal range limits of Pacific Northwest conifers. *Ecology*, 92, 1323–1331.
- Ettinger, A., & HilleRisLambers, J. (2017). Competition and facilitation may lead to asymmetric range shift dynamics with climate change. *Global Change Biology*, 23, 3921–3933.
- EU-DEM. (2020). EU-DEM v1.1. EU-DEM v1.1. Copernicus Land Monitoring Service. <https://land.copernicus.eu/imagery-in-situ/eu-dem/eu-dem-v1.1?tab=mapview>
- Felipe-Lucia, M. R., Soliveres, S., Penone, C., Manning, P., van der Plas, F., Boch, S., Prati, D., Ammer, C., Schall, P., Gossner, M. M., Bauhus, J., Buscot, F., Blaser, S., Blüthgen, N., de Frutos, A., Ehbrecht, M., Frank, K., Goldmann, K., Hänsel, F., ... Allan, E. (2018). Multiple forest attributes underpin the supply of multiple ecosystem services. *Nature Communications*, 9, 4839.
- Fischlin, A., Bugmann, H., & Gyalistras, D. (1995). Sensitivity of a forest ecosystem model to climate parametrization schemes. *Environmental Pollution*, 87, 267–282.
- Grant, K., Kreyling, J., Heilmeyer, H., Beierkuhnlein, C., & Jentsch, A. (2014). Extreme weather events and plant-plant interactions: Shifts between competition and facilitation among grassland species in the face of drought and heavy rainfall. *Ecological Research*, 29, 991–1001.
- Grime, J. P. (1977). Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *The American Naturalist*, 111, 1169–1194.
- Grime, J. P. (2006). *Plant strategies, vegetation processes, and ecosystem properties*. John Wiley & Sons.
- Grossiord, C. (2020). Having the right neighbors: How tree species diversity modulates drought impacts on forests. *New Phytologist*, 228, 42–49.

- Haberstroh, S., & Werner, C. (2022). The role of species interactions for forest resilience to drought. *Plant Biology*, 24, 1098–1107.
- Hanewinkel, M., Cullmann, D. A., Schelhaas, M.-J., Nabuurs, G.-J., & Zimmermann, N. E. (2013). Climate change may cause severe loss in the economic value of European forest land. *Nature Climate Change*, 3, 203–207.
- Hart, S. P., Usinowicz, J., & Levine, J. M. (2017). The spatial scales of species coexistence. *Nature Ecology & Evolution*, 1, 1066–1073.
- Hartig, F. (2021). *DHARMA: Residual diagnostics for hierarchical (multi-level/mixed) regression models*. <https://www.cran.r-project.org>
- Hartig, F., Dyke, J., Hickler, T., Higgins, S. I., O'Hara, R. B., Scheiter, S., & Huth, A. (2012). Connecting dynamic vegetation models to data—An inverse perspective. *Journal of Biogeography*, 39, 2240–2252.
- He, Q., Bertness, M. D., & Altieri, A. H. (2013). Global shifts towards positive species interactions with increasing environmental stress. *Ecology Letters*, 16, 695–706.
- HilleRisLambers, J., Harsch, M., Ettinger, A., Ford, K. R., & Theobald, E. J. (2013). How will biotic interactions influence climate change-induced range shifts? *Annals of the New York Academy of Sciences*, 1297, 112–125.
- IPCC. (2022). Climate change 2022: Impacts, adaptation, and vulnerability. Contribution of working group II to the sixth assessment report of the intergovernmental panel on climate change.
- Journé, V., Andrus, R., Aravena, M.-C., Ascoli, D., Berretti, R., Berveiller, D., Bogdziewicz, M., Boivin, T., Bonal, R., Caignard, T., Calama, R., Camarero, J. J., Chang-Yang, C. H., Courbaud, B., Courbet, F., Curt, T., das, A. J., Daskalaki, E., Davi, H., ... Clark, J. S. (2022). Globally, tree fecundity exceeds productivity gradients. *Ecology Letters*, 00, 1–12.
- Jucker, T., Bouriaud, O., Avacaritei, D., Dănilă, I., Duduman, G., Valladares, F., & Coomes, D. A. (2014). Competition for light and water play contrasting roles in driving diversity-productivity relationships in Iberian forests. *Journal of Ecology*, 102, 1202–1213.
- Käber, Y. (2023). Data and code from: Sheltered or suppressed? Tree regeneration in unmanaged European forests. *Dryad, Dataset*. <https://doi.org/10.5061/dryad.hx3fbgkx>
- Käber, Y., Meyer, P., Stillhard, J., Lombaerde, E. D., Zell, J., Stadelmann, G., Bugmann, H., & Bigler, C. (2021). Tree recruitment is determined by stand structure and shade tolerance with uncertain role of climate and water relations. *Ecology and Evolution*, 11, 12182–12203.
- Karger, D. N., Conrad, O., Böhner, J., Kawohl, T., Kreft, H., Soria-Auza, R. W., Zimmermann, N. E., Linder, H. P., & Kessler, M. (2017). Climatologies at high resolution for the earth's land surface areas. *Scientific Data*, 4, 170122.
- Kašpar, J., Tumajer, J., Šamonil, P., & Vašíčková, I. (2021). Species-specific climate-growth interactions determine tree species dynamics in mixed central European mountain forests. *Environmental Research Letters*, 16, 034039.
- Kitzberger, T., Steinaker, D. F., & Veblen, T. T. (2000). Effects of climatic variability on facilitation of tree establishment in northern Patagonia. *Ecology*, 81, 1914–1924.
- Klanderud, K., Meineri, E., Goldberg, D. E., Michel, P., Berge, A., Guittar, J. L., & Vandvik, V. (2021). Vital rates in early life history underlie shifts in biotic interactions along bioclimatic gradients: An experimental test of the stress gradient hypothesis. *Journal of Vegetation Science*, 32, e13006.
- Klopčič, M., Poljanec, A., & Boncina, A. (2012). Modelling natural recruitment of European beech (*Fagus sylvatica* L.). *Forest Ecology and Management*, 284, 142–151.
- König, L. A., Mohren, F., Schelhaas, M.-J., Bugmann, H., & Nabuurs, G.-J. (2022). Tree regeneration in models of forest dynamics—Suitability to assess climate change impacts on European forests. *Forest Ecology and Management*, 520, 120390.
- Körner, C. (2021). The cold range limit of trees. *Trends in Ecology & Evolution*, 36, 979–989.
- Kroiss, S. J., & HilleRisLambers, J. (2015). Recruitment limitation of long-lived conifers: Implications for climate change responses. *Ecology*, 96, 1286–1297.
- Kunstler, G., Falster, D., Coomes, D. A., Hui, F., Kooyman, R. M., Laughlin, D. C., Poorter, L., Vanderwel, M., Vieilledent, G., Wright, S. J., Aiba, M., Baraloto, C., Caspersen, J., Cornelissen, J. H. C., Gourlet-Fleury, S., Hanewinkel, M., Herault, B., Kattge, J., Kurokawa, H., ... Westoby, M. (2016). Plant functional traits have globally consistent effects on competition. *Nature*, 529, 204–207.
- Kunstler, G., Guyennon, A., Ratcliffe, S., Rüger, N., Ruiz-Benito, P., Childs, D. Z., Dahlgren, J., Lehtonen, A., Thuiller, W., Wirth, C., Zavala, M. A., & Salguero-Gomez, R. (2021). Demographic performance of European tree species at their hot and cold climatic edges. *Journal of Ecology*, 109, 1041–1054.
- Lenoir, J., Gégout, J.-C., Guisan, A., Vittoz, P., Wohlgemuth, T., Zimmermann, N. E., Dullinger, S., Pauli, H., Willner, W., & Svenning, J. C. (2010). Going against the flow: Potential mechanisms for unexpected downslope range shifts in a warming climate. *Ecography*, 33, 295–303.
- Leuschner, C., & Ellenberg, H. (2017). *Ecology of Central European forests: Vegetation ecology of Central Europe* (Vol. I). Springer International Publishing.
- Levin, S. A. (1992). The problem of pattern and scale in ecology: The Robert H. MacArthur award lecture. *Ecology*, 73, 1943–1967.
- Li, Y., Mayfield, M. M., Wang, B., Xiao, J., Kral, K., Janik, D., Holik, J., & Chu, C. (2021). Beyond direct neighbourhood effects: Higher-order interactions improve modelling and predicting tree survival and growth. *National Science Review*, 8, nwaa244.
- Liang, Y., Duveneck, M. J., Gustafson, E. J., Serra-Diaz, J. M., & Thompson, J. R. (2018). How disturbance, competition, and dispersal interact to prevent tree range boundaries from keeping pace with climate change. *Global Change Biology*, 24, e335–e351.
- Liu, Y., & He, F. (2019). Incorporating the disease triangle framework for testing the effect of soil-borne pathogens on tree species diversity. *Functional Ecology*, 33, 1211–1222.
- Lloret, F., Escudero, A., Iriondo, J. M., Martínez-Vilalta, J., & Valladares, F. (2012). Extreme climatic events and vegetation: The role of stabilizing processes. *Global Change Biology*, 18, 797–805.
- Lortie, C. J., & Callaway, R. M. (2006). Re-analysis of meta-analysis: Support for the stress-gradient hypothesis. *Journal of Ecology*, 94, 7–16.
- Maestre, F. T., Callaway, R. M., Valladares, F., & Lortie, C. J. (2009). Refining the stress-gradient hypothesis for competition and facilitation in plant communities. *Journal of Ecology*, 97, 199–205.
- Malkinson, D., & Tielbörger, K. (2010). What does the stress-gradient hypothesis predict? Resolving the discrepancies. *Oikos*, 119, 1546–1552.
- Mamantov, M. A., Gibson-Reinemer, D. K., Linck, E. B., & Sheldon, K. S. (2021). Climate-driven range shifts of montane species vary with elevation. *Global Ecology and Biogeography*, 30, 784–794.
- Mauri, A., Girardello, M., Strona, G., Beck, P. S. A., Forzieri, G., Caudullo, G., Manca, F., & Cescatti, A. (2022). EU-Trees4F, a dataset on the future distribution of European tree species. *Scientific Data*, 9, 37.
- Meier, E. S., Edwards, T. C., Jr., Kienast, F., Dobbertin, M., & Zimmermann, N. E. (2011). Co-occurrence patterns of trees along macro-climatic gradients and their potential influence on the present and future distribution of *Fagus sylvatica* L. *Journal of Biogeography*, 38, 371–382.
- Meier, E. S., Kienast, F., Pearman, P. B., Svenning, J.-C., Thuiller, W., Araújo, M. B., Guisan, A., & Zimmermann, N. E. (2010). Biotic and abiotic variables show little redundancy in explaining tree species distributions. *Ecography*, 33, 1038–1048.
- Nagel, T. A., Firm, D., & Rozman, A. (2021). Intermediate disturbances are a key driver of long-term tree demography across old-growth temperate forests. *Ecology and Evolution*, 11, 16862–16873.

- Naithani, K. J., Baldwin, D. C., Gaines, K. P., Lin, H., & Eissenstat, D. M. (2013). Spatial distribution of tree species governs the spatio-temporal interaction of Leaf Area Index and soil moisture across a forested landscape. *PLoS One*, 8, e58704.
- Niinemets, Ü., & Valladares, F. (2006). Tolerance to shade, drought, and waterlogging of temperate northern hemisphere trees and shrubs. *Ecological Monographs*, 76, 521–547.
- Pickett, S. T. A., Collins, S. L., & Armesto, J. J. (1987). A hierarchical consideration of causes and mechanisms of succession. *Vegetatio*, 69, 109–114.
- Price, D. T., Zimmermann, N. E., van der Meer, P. J., Lexer, M. J., Leadley, P., Jorritsma, I. T. M., Schaber, J., Clark, D. F., Lasch, P., McNulty, S., Wu, J., & Smith, B. (2001). Regeneration in gap models: Priority issues for studying forest responses to climate change. *Climatic Change*, 51, 475–508.
- QGIS Development Team. (2022). *QGIS geographic information system*. QGIS Association.
- Qiu, T., Sharma, S., Woodall, C. W., & Clark, J. S. (2021). Niclas shifts from trees to fecundity to recruitment that determine species response to climate change. *Frontiers in Ecology and Evolution*, 9, 719141.
- R Core Team. (2020). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing.
- Ren, H., Svenning, J.-C., Mi, X., Lutz, J. A., Zhou, J., & Ma, K. (2022). Scale-dependent species–area relationship: Niche-based versus stochastic processes in a typical subtropical forest. *Journal of Ecology*, 110, 1883–1895.
- Sakamoto, Y., Ishiguro, M., & Kitagawa, G. (1986). *Akaike information criterion statistics. Mathematics and its applications* (1986th ed.). Kluwer Academic.
- San-Miguel-Ayanz, J., de Rigo, D., Caudullo, G., Durrant, T. H., & Mauri, A. (2016). *European atlas of forest tree species*. Publication Office of the European Union.
- Schelhaas, M.-J., Fridman, J., Hengeveld, G. M., Henttonen, H. M., Lehtonen, A., Kies, U., Krajnc, N., Lerink, B., Ní Dhúbháin, Á., Polley, H., Pugh, T. A. M., Redmond, J. J., Rohner, B., Temperli, C., Vayreda, J., & Nabuurs, G. J. (2018). Actual European forest management by region, tree species and owner based on 714,000 re-measured trees in national forest inventories. *PLoS One*, 13, e0207151.
- Schwarz, G. (1978). Estimating the dimension of a model. *Annals of Statistics*, 6, 461–464.
- Seidl, R., Schelhaas, M.-J., Rammer, W., & Verkerk, P. J. (2014). Increasing forest disturbances in Europe and their impact on carbon storage. *Nature Climate Change*, 4, 806–810.
- Seidl, R., & Turner, M. G. (2022). Post-disturbance reorganization of forest ecosystems in a changing world. *Proceedings. National Academy of Sciences. United States of America*, 119, e2202190119.
- Sharma, S., Andrus, R., Bergeron, Y., Bogdziewicz, M., Bragg, D. C., Brockway, D., Cleavitt, N. L., Courbaud, B., das, A. J., Dietze, M., Fahey, T. J., Franklin, J. F., Gilbert, G. S., Greenberg, C. H., Guo, Q., Hille Ris Lambers, J., Ibanez, I., Johnstone, J. F., Kilner, C. L., ... Clark, J. S. (2022). North American tree migration paced by climate in the west, lagging in the east. *Proceedings of the National Academy of Sciences of the United States of America*, 119, e2116691118.
- Shoemaker, L. G., Sullivan, L. L., Donohue, I., Cabral, J. S., Williams, R. J., Mayfield, M. M., Chase, J. M., Chu, C., Harpole, W. S., Huth, A., HilleRisLambers, J., James, A. R. M., Kraft, N. J. B., May, F., Muthukrishnan, R., Satterlee, S., Taubert, F., Wang, X., Wiegand, T., ... Abbott, K. C. (2020). Integrating the underlying structure of stochasticity into community ecology. *Ecology*, 101, e02922.
- Smit, C., Vandenbergh, C., den Ouden, J., & Müller-Schärer, H. (2007). Nurse plants, tree saplings and grazing pressure: Changes in facilitation along a biotic environmental gradient. *Oecologia*, 152, 265–273.
- Speich, M. J. R. (2019). Quantifying and modeling water availability in temperate forests: A review of drought and aridity indices. *IForest*, 12, 1–16.
- Waring, R. H. (1983). Estimating Forest growth and efficiency in relation to canopy leaf area. In A. MacFadyen & E. D. Ford (Eds.), *Advances in ecological research* (pp. 327–354). Academic Press.
- Welden, C. W., & Slauson, W. L. (1986). The intensity of competition versus its importance: An overlooked distinction and some implications. *The Quarterly Review of Biology*, 61, 23–44.
- Whittaker, R. H. (1972). Evolution and measurement of species diversity. *Taxon*, 21, 213–251.
- Wilson, S. D., & Keddy, P. A. (1986). Measuring diffuse competition along an environmental gradient: Results from a shoreline plant community. *The American Naturalist*, 127, 862–869.
- Zell, J., Rohner, B., Thürig, E., & Stadelmann, G. (2019). Modeling ingrowth for empirical forest prediction systems. *Forest Ecology and Management*, 433, 771–779.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Appendix S1. Further analysis and detailed description of methods.

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