

Mixing tree species at different spatial scales: The effect of alpha, beta and gamma diversity on disturbance impacts under climate change

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Abstract

1. Single species forest systems often suffer from low resistance and resilience to perturbations. Consequently, fostering tree species diversity is discussed as an important management approach to address the impacts of changing climate and disturbance regimes. Yet, the effect of the spatial grain of tree species mixtures remains unknown.
2. We asked whether increasing tree species diversity between stands (beta diversity) has the same effect as increasing tree species diversity within stands (alpha diversity) at similar overall levels of richness (gamma diversity). We conducted a multi-model simulation experiment under climate change, applying two forest landscape models (iLand and LandClim) across two contrasting landscapes of Central Europe. We analysed the effect of different levels and configurations of diversity on the disturbance impact and the temporal stability of biomass stocks and forest structure.
3. In general, increasing levels of diversity decreased disturbance impacts. Positive diversity effects increased with increasing severity of climate change. Beta diversity buffered disturbance impacts on landscape-level biomass stocks more strongly than alpha diversity. The effects of the spatial configuration on forest structure were more variable. Diversity effects on temporal stability were less pronounced compared to disturbance impacts, and mixture within and between stands had comparable effects on temporal stability.
4. Diversity effects were context-dependent, with patterns varying between landscapes and indicators. Furthermore, we found a strong species identity effect, with increasing diversity being particularly beneficial in conifer-dominated systems of the European Alps. The two models agreed on the effects of different levels and configurations of tree species diversity, underlining the robustness of our findings.
5. *Synthesis and application.* Enhancing tree species diversity can buffer forest ecosystems against increasing levels of perturbation. Mixing tree species between stands is at least as effective as mixing tree species within stands. Given the managerial advantages of between-stand mixtures (e.g. reduced need to control

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competition to maintain diversity, higher timber quality, lower logistic effort), we conclude that forest management should consider enhancing diversity at multiple spatial scales.

KEYWORDS

beta diversity, biodiversity, climate change, disturbances, forest, forest management, resilience, species diversity

1 | INTRODUCTION

Global change increases the pressure on forest ecosystems through changed environmental conditions, which, in turn, alter ecological processes substantially (Trumbore et al., 2015). One of the most climate-sensitive processes in forest ecosystems is disturbance (Seidl et al., 2020; Sommerfeld et al., 2018). As a consequence, forests that have developed under historic disturbance regimes may change drastically in the future due to the emergence of novel disturbance regimes (Turner, 2010). In addition, the societal demand for ecosystem services changes at an accelerating pace, challenging ecosystem managers to adapt forests so that they are able to deliver broad portfolios of ecosystem services. Given the high uncertainty in future environmental conditions and societal demands, fostering tree species diversity has been recommended as a particularly suitable management approach (Griess et al., 2012; Knoke et al., 2008; Neuner et al., 2015). Diverse forests facilitate the provisioning of a wide range of ecosystem services (Gamfeldt & Roger, 2017) and increase the resistance and resilience to changing disturbance regimes (Silva Pedro et al., 2015). Consequently, increasing tree species diversity is frequently proposed as an important forest management strategy to ensure ecosystem service provisioning and forest multi-functionality (Messier et al., 2015; van der Plas et al., 2018).

Theory suggests that a high diversity of species varying in their ecological responses leads to stable systems in a changing environment (Mori et al., 2013; Peterson et al., 1998). If the performance of one tree species declines or even fails under a certain set of conditions, other species with different traits better adapted to the emerging environmental drivers will ensure ecosystem functioning. In the face of increasing disturbances, for instance, diverse ecosystems are more likely to include species that are resistant to a specific disturbance agent (insurance hypothesis; Yachi & Loreau, 1999). Furthermore, trait diversity among different tree species determines their ability to respond to changing climate and disturbance regimes. Diverse traits increase the probability of a positive response to disturbances, thereby enhancing the speed of recovery and thus rendering the ecosystem more resilient (Mori et al., 2013).

Building on these theoretical considerations, a number of quantitative studies have shown that tree species diversity increases the resistance of forest ecosystems to disturbances (see the reviews of Jactel et al., 2017; Knoke et al., 2008). In addition, there is mounting evidence that diverse forests are often more resistant to climatic

extremes such as drought (Grossiord, 2019; Lebourgeois et al., 2013; Metz et al., 2016; Pretzsch et al., 2013). Furthermore, also the resilience to disturbances increases in diverse forests (Honkaniemi et al., 2020; Silva Pedro et al., 2015).

While there is growing evidence for the benefits of diverse forests in a changing world, the effects of the spatial grain of mixing tree species have not yet been investigated systematically. Most analyses to date focus on tree species diversity within forest stands, that is, the smallest entity of forest management (in Europe typically 0.5–10 ha in size). While the effects of within-stand diversity (alpha diversity) have been explored previously (e.g. del Río et al., 2017; Guyot et al., 2016; Huang et al., 2018; Rothe & Binkley, 2001), tree species diversity between stands (beta diversity) has received relatively little attention. Beta diversity has been identified as an important element of ecosystem functioning (Mori et al., 2018; Schuler et al., 2017) and is a key element for the provisioning of multiple ecosystem goods and services at the landscape scale (Van Der Plas et al., 2016). Furthermore, landscape configuration is increasingly recognized as an important element of ecosystem resilience (Honkaniemi et al., 2020; Lamy et al., 2016). Also, evidence is mounting that focusing forest management solely on alpha diversity might not be sufficient for conserving biodiversity (Schall et al., 2018; Schuler et al., 2019). In broader terms, the effect of the spatial grain of tree species mixtures remains an unresolved issue in applied ecology (Ammer, 2019).

In the context of ecosystem management, increasing diversity between stands rather than within stands can have operational advantages: First, high levels of species diversity might be easier to achieve between stands compared to within stands, since interspecific competition often leads to the dominance of one species over the others in mixed stands (Larocque et al., 2013). Maintaining high levels of tree species diversity within forest stands thus often requires considerable regulatory actions by management (e.g. via tending and thinning), which is labour-intensive and costly (Larocque et al., 2013). Second, timber production in mixed stands can be complicated by yielding many different assortments and a low amount of timber per assortment, which is a drawback for timber logistics and sales. Lastly, high-quality stemwood is often difficult to achieve in stands of high alpha diversity (Höwler et al., 2019; Zingg & Ramp, 1997) while straight and self-pruned stems of low taper often emerge naturally under intraspecific competition (Kint et al., 2010).

One reason for the scarcity of studies on diversity beyond the stand scale is the inherent difficulty of systematic investigations at

larger spatial scales. Field experiments that manipulate diversity at different spatial scales in forests are often not feasible due to resource limitations resulting from the extended observation times required by such experiments. Furthermore, studying diversity effects requires replicated experiments that control for the influence of confounding factors, yet such experiments are well-nigh impossible due to the inability to replicate real landscapes (Keane et al., 2015; Phillips, 2007). Simulation models are an important tool of scientific inquiry in this context, as they can extend the spatial scope of field experiments to the landscape scale and efficiently implement replicated large-scale experiments over extended time periods under otherwise fully controlled conditions (He, 2008; Scheller & Mladenoff, 2007). Furthermore, computer simulation allows us to investigate the effects of no-analogue future environmental conditions, for example, in terms of novel climate and disturbance regimes (Bugmann, 2014). Simulation-based studies are, however, inherently limited by the uncertainties with regard to our quantitative understanding of ecological processes (Huber et al., 2020). An important way to address these uncertainties is to apply multiple different models under identical forcing, as multi-model studies give an indication of the process uncertainty in models and increase the robustness of the model-derived inference (Bugmann et al., 2019; Petter et al., 2020; Valle et al., 2009).

Therefore, we conducted a simulation experiment applying two well-established forest landscape models (i.e. iLand and LandClim) in two contrasting forest landscapes of Central Europe, aiming to study the effects of tree species diversity at different spatial scales across a wide environmental gradient. Specifically, we investigated whether the effects of tree species diversity vary with the spatial grain at which species are mixed. We focused on the response of above-ground forest biomass and the abundance of large trees (i.e. the number of trees >30 cm dbh/ha), two indicators tightly linked to ecosystem service supply in the two study regions. We evaluated how diversity modulates the impact of different climate and disturbance scenarios on these indicators. We also investigated the temporal stability in these indicators, as this aspect of ecosystem service provisioning is gaining importance in practical forest management (Albrich et al., 2018). Our overarching research questions were as follows:

1. Does tree species diversity at the landscape scale (gamma diversity) reduce disturbance impacts and increase the temporal stability of biomass stocks and the abundance of large trees under climate change in Central Europe? Based on theoretical considerations (Yachi & Loreau, 1999, insurance hypothesis) and previous research (del Río et al., 2017; Jactel et al., 2017), we expected a significant positive effect (i.e. lower impacts, higher stability) of tree species diversity.
2. What is the effect of the spatial configuration of tree species diversity, that is, is there a difference in disturbance impact and temporal stability if tree species are mixed within stands (alpha diversity) or between stands (beta diversity)? Here we tested the Null hypothesis that for a given level of tree species diversity

the spatial configuration of the species on the landscape does not matter. Alternatively, if local processes are the main driver of positive diversity effects, we would expect alpha diversity to yield higher positive effects than beta diversity at a given level of gamma diversity.

2 | MATERIALS AND METHODS

2.1 | Study landscapes

To investigate the effects of tree species diversity across a wide ecological gradient, we studied two contrasting forest landscapes in Central Europe (Figure 1). The Rosalia landscape (1,231 ha, 47.70 N, 16.30 E) is located at the easternmost edge of the Alps in Austria at the border of the Pannonic plains of central Eastern Europe. The landforms are dominated by pre-alpine ridges running in north-south direction with generally low topographic complexity and an elevation range from 374 to 728 m a.s.l. Historic mean annual temperature (1981–2010) decreases with elevation from 9.4 to 8.0°C, while mean annual precipitation increases with elevation from 717 to 916 mm. The potential natural vegetation is dominated by European beech (*Fagus sylvatica* L.) with silver fir (*Abies alba* Mill.) as admixed species (Kilian et al., 1994). The Dischma landscape (924 ha, 46.78 N, 9.87 E) is located in Eastern Switzerland and represents a mountain landscape of the Central Alps with harsh climate conditions and high topographic complexity. Elevation ranges from 1,545 to 2,738 m a.s.l. Historic mean annual temperature decreases from 4.4°C at low elevations to -0.6°C at the natural treeline (located at approximately 2,300 m a.s.l. under historic climate, see Gehrig-Fasel et al., 2007), with annual precipitation ranging from 1,074 to 1,297 mm. The potential natural vegetation consists of subalpine forests (up to approximately 1,900 m a.s.l.) dominated by Norway spruce (*Picea abies* (L.) Karst.), subalpine forests with Norway spruce and European larch (*Larix decidua* L.), and Swiss stone pine (*Pinus cembra* L.) forests at treeline (Schumacher et al., 2004). Both landscapes are dominated by crystalline bedrock covered by cambisols of varying soil depth and nutrient content. Both landscapes are approximately three orders of magnitude larger than the average disturbance patch size (1.09 ha, Senf & Seidl, 2021), and are thus large enough to be considered quasi-equilibrium landscapes in the context of disturbance analysis (see Urban et al., 1987).

2.2 | Simulation models

We simultaneously employed two process-based forest landscape models in our study, iLand and LandClim, to increase the robustness of our results.

iLand (Seidl et al., 2012) was developed to study the dynamic interactions between forest development, climate and disturbance, and has been successfully applied to address a wide range of ecological and management-oriented questions (e.g. Albrich et al., 2018;

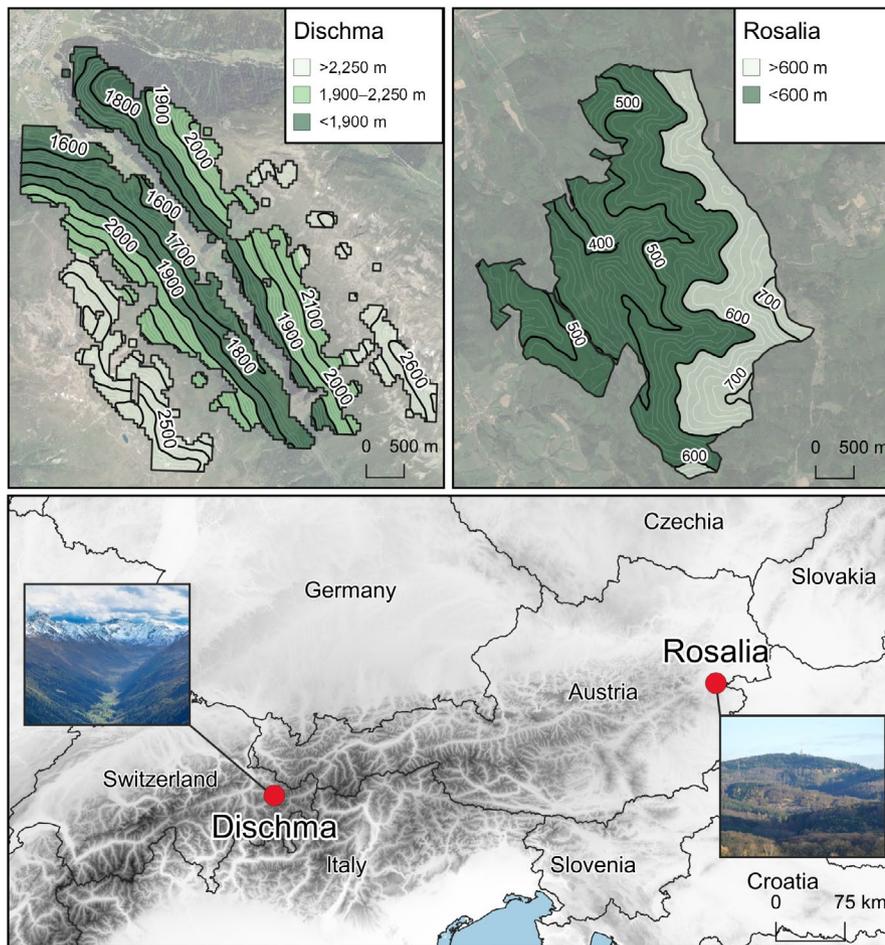


FIGURE 1 Map showing the location of the two study landscapes *Dischma* (CH) and *Rosalia* (AT), and their respective elevation belts

Seidl et al., 2019; Thom et al., 2017). *iLand* is a multi-scale model; it simulates growth, competition and mortality at the level of individual trees, primary production at the stand scale, and processes like seed dispersal and disturbances at the landscape scale. *iLand* is driven by daily climate data and forest structure is updated annually (i.e. demographic processes and disturbances are simulated with an annual time step).

LandClim (Schumacher et al., 2004, 2006) is a stochastic process-based forest landscape model that operates at the grain of tree cohorts, simulated at a spatial resolution of 25×25 m. *LandClim* has been successfully applied in numerous studies in Europe and other parts of the world, demonstrating the utility of the model to study landscape dynamics under a wide range of environmental conditions (e.g. Elkin et al., 2013; Temperli et al., 2013; Thrippleton et al., 2016). *LandClim* is driven by monthly climate data and forest structure is updated annually (even though tree regeneration and disturbances are simulated with a decadal time step).

For a detailed comparison of *LandClim* and *iLand* including a description of the models using the ODD protocol (Grimm et al., 2006), we refer to Petter et al. (2020). The models have been tested and evaluated in the two landscapes in previous studies (Honkaniemi et al., 2020; Petter et al., 2020). To ensure that the models are able to capture the expected tree species dynamics for both landscapes (a crucial ability in the context of the current study), we ran

additional model tests comparing the simulated potential natural vegetation from both models to expected values (see Appendix S11 and Section 2.1 below). These tests showed good agreement of simulated successional patterns with expectations, indicating that both models are well able to reproduce the competitive relationships between tree species across the wide ecological gradients covered by the two study landscapes.

2.3 | Experimental design

We performed a factorial experiment of varying levels ($n = 4$) and spatial configurations ($n = 2$) of tree species diversity with the two models for both landscapes under different climate ($n = 3$) and disturbance ($n = 3$) scenarios. The underlying premises of our experimental design were (a) to simulate the exact same scenarios with both models (which required the harmonization of some elements of the design, for example, with regard to the different time steps of *iLand* and *LandClim*, see also Petter et al., 2020) and (b) to focus on the diversity effects of interest here while controlling for other potential drivers of forest dynamics (e.g. legacy effects from past disturbances and land use; Kulakowski et al., 2017). Specifically, we initialized four levels of tree species diversity (gamma diversity) in two spatial configurations (alpha and beta diversity), see Figure 2a.

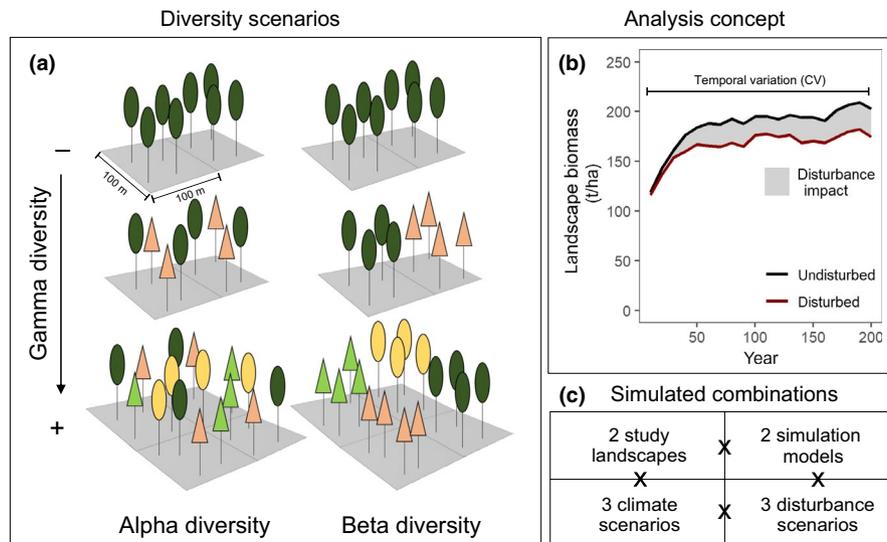


FIGURE 2 Conceptual visualization of the study design. We initialized varying levels of tree species diversity (gamma diversity) in two spatial configurations at a grain of 100×100 m (a). Subsequently, we exposed these initial states to a series of disturbances and derived disturbance impacts by comparing landscape values for biomass stock and forest structure to an undisturbed reference simulation. In addition, we quantified temporal variation in biomass stocks and forest structure by calculating the coefficient of variation over the 200-year simulation period (20 time steps, b). All analyses were conducted in two contrasting landscapes with two simulation models, studying vegetation development under three alternative climate and disturbance scenarios (c)

The grain for the spatial configurations was 100×100 m (henceforth referred to as a stand). For beta diversity, species were varied between stands (with only one species occupying a stand), while for alpha diversity species were mixed within a stand. Based on these initial conditions of landscape composition and configuration, we simulated 200 years of forest development under a common management regime. Furthermore, we exposed the simulated forest to three prescribed sequences of disturbance under three climate scenarios (Figure 2c). Disturbance impacts were derived by comparing landscape-scale response variables to simulations without disturbance (i.e. the reference runs). The individual elements of the study design are described in detail below; Figure 2 provides a graphical overview of our approach.

2.4 | Initialization

We initialized simulations with different levels of gamma diversity in tree species: *no* diversity (initializing only the most productive species over the entire landscape), *low* diversity (initializing only species that obtain dominance in natural forest development) and *high* diversity (initializing dominant and co-dominant species). The level of dominance of each species in natural forest development was determined by simulating forest succession from bare ground over 2,000 years in both landscapes and with both models under historic climate (see Appendix S11). To account for changing species dominance with elevation, both landscapes were divided into elevation belts: for the Dischma landscape, we considered three elevation belts (1,545–1,899 m; 1,900–2,249 m; 2,250–2,738 m), while for the Rosalia landscape two elevational belts (374–599 m; 600–728 m)

were distinguished (Figure 1). We defined dominant (co-dominant) species as those reaching a proportion of at least 35% (3%) of total biomass in a particular elevation belt at any point in time during succession (see Appendices S11 and S12). This ensured that both early and late seral species were included in the design. As we expected climate change to alter the species pool of both landscapes and shift the competitive balance between species, we added a fourth gamma diversity scenario, referred to as the *high+* scenario. For this scenario, we ran succession simulations also under climate change (see details below) and again determined all species that reached a level of at least 3% of total biomass. The initialization of the *high+* scenario was identical to the *high* diversity scenario, but in the course of the simulation the species pool was extended by the additional species that reached at least co-dominance in the succession runs under climate change. The *high+* scenario thus had the highest gamma diversity of all simulated diversity scenarios (see Appendix S12).

All levels of gamma diversity were initialized in two spatial configurations: alpha diversity and beta diversity. For the alpha diversity configuration, all tree species from the species pool were mixed within stands. For the beta diversity configuration, each of the 100×100 m stands consisted of only one species, with species varying between stands (see Figure 2). In total, we simulated seven combinations of gamma diversity and spatial configuration in each landscape (3 levels of gamma diversity \times 2 spatial configurations + 1 no diversity scenario).

The initial age of each stand was sampled with replacement from a uniform distribution ranging from 0 to 100 years in the Rosalia landscape and from 0 to 150 years in the Dischma landscape. These values represent realistic rotation periods under current management in the two landscapes. The resulting forest structure corresponds to a 'normal forest' (Assmann, 1961), in which all stand ages

are represented equally across the landscape. The effects of different age class distributions were tested in a sensitivity analysis, and the results were found to be robust to changes in age class distribution (Appendices SI9 and SI10). Stand structure (i.e. stem density in 5 cm dbh classes, tree height and height–diameter-ratio) for specific initialization ages was derived from model runs with iLand (i.e. the structurally more detailed of the two models) for all species in all stands of both landscapes.

2.5 | Forest management

Forest management was implemented in both models based on a common set of rules, describing a rotation forestry system (e.g. Bianchi et al., 2020). Simulated management interventions were thinnings (removing 20% of basal area of a stand), clear-cutting and planting. We assumed a rotation period R of 100 years in Rosalia and 150 years in Dischma, based on the different growing conditions in both study landscapes. Thinnings were scheduled at $R \times 0.35$ (i.e. stand age 35 in Rosalia and stand age 53 in Dischma) and $R \times 0.55$ (i.e. stand age 55 in Rosalia and stand age 83 in Dischma). After the final cut at the end of the rotation period, each stand was replanted with the species composition prescribed by the respective diversity scenario. During a rotation period, species composition varied due to the simulated growth dynamics of the models.

2.6 | Climate

We simulated each diversity scenario for 200 years under three climate scenarios, representing a constant historic climate as well as two contrasting climate change scenarios. The latter represent moderate climate change (RCP4.5, see IPCC, 2014) with a peak of CO₂ emissions around 2040, and a Business-As-Usual scenario with increasing greenhouse gas emissions throughout the 21st century (RCP8.5, see IPCC, 2014). Historic climate conditions were sampled with replacement from past climate data (1981–2010) to obtain a stationary 200-year climate record. Climate change scenarios followed the trajectory of the respective RCP scenario for the first

100 years of the simulation period (representing climate development throughout the 21st century). For the second 100-year period, we assumed a hypothetical stabilization of climate, and randomly sampled years from the period 2070 to 2099, an approach that is often taken in long-term simulations of climate change impacts (e.g. Elkin et al., 2013). For details on the climate scenarios, see Table 1.

2.7 | Disturbances

Disturbances were simulated in a two-step approach, granting a consistent forcing between the two models while dynamically considering disturbance responses in the context of the simulated forest state. In a first step, we created sequences of disturbance events by sampling the size (patch area), location and timing of disturbances. In a second step, disturbance severity (i.e. which trees died within a disturbance perimeter) was determined dynamically within the simulation models.

Each simulation run was driven by a different sequence of disturbance events. Year of disturbance was sampled with replacement from a uniform distribution ranging from 1 to 200 (i.e. the first and last year of the simulation period, respectively). Disturbance size was sampled from an empirically derived disturbance size distribution representative for Central Europe (Senf et al., 2017, see Appendix SI3). The location of each disturbance patch was selected randomly on the landscape, and the spatial grain of disturbance was 1 ha, thus matching the resolution of the simulated stands (see Section 2.4 above). We simulated three disturbance scenarios: historic disturbance, future disturbance and no disturbance. The three scenarios differed in disturbance frequency, as determined by the disturbance rotation period (i.e. the average time it takes for the cumulative area of disturbance to reach the size of the study landscape), which was set to 400 years in the *historic* disturbance scenario (Čada et al., 2016; Thom et al., 2013), and to 200 years in the *future* disturbance scenario (Schumacher & Bugmann, 2006). This implies that in the future disturbance scenario twice as many disturbance events occurred compared to the historic disturbance scenario, which is within the range of expectations for Central European forest ecosystems (Schumacher &

TABLE 1 Mean annual precipitation, temperature and CO₂ concentration for both study landscapes (Dischma, Rosalia) and the three climate scenarios investigated (historic, RCP4.5, RCP8.5)

Study landscape	Rosalia			Dischma		
	Historic (1981–2010)	RCP4.5 (2070–2099)	RCP8.5 (2070–2099)	Historic (1981–2010)	RCP4.5 (2070–2099)	RCP8.5 (2070–2099)
GCM-RCM combination	–	EC-EARTH and KNMI-RACMO22E	EC-EARTH and KNMI-RACMO22E	–	HadGEM2-ES	HadGEM2-ES
Mean annual temperature [°C]	8.51	10.40 (+1.89)	12.13 (+3.62)	1.69	5.36 (+3.67)	8.02 (+6.33)
Mean annual precipitation [mm]	810	883 (+73)	835 (+25)	1,179	1,130 (–49)	1,012 (–167)
CO ₂ concentration [ppm]	369	537	927	369	537	927

Bugmann, 2006; Thom et al., 2013). The effect of different disturbance rotation periods was investigated in a sensitivity analysis, which showed that main patterns were robust to changes in disturbance rotations (Appendix SI8). Each scenario was replicated 20 times to account for the stochastic variability in the timing, location and size of disturbances. For each replication, we generated a unique sequence of disturbance events that was used in both models. This approach ensured that both iLand and LandClim simulated the same disturbance patches in the same year and location. Our simulations thus solely focus on disturbance responses rather than on future projections of disturbance activity.

Disturbance severity (i.e. the number of trees killed within a disturbance perimeter) was contingent on the simulated vegetation state in the different diversity scenarios considered. Specifically, we employed the empirically derived disturbance impact model of Schmidt et al. (2010), which quantifies the susceptibility of Central European forests to storm events (i.e. the most important agent of natural disturbance in Europe's forests; Schelhaas et al., 2003; Seidl et al., 2014). The model (see Appendix SI4) predicts probability of tree mortality dependent on tree species and tree height. Simulated disturbance impacts thus reflect emergent differences in susceptibility (as determined by the development of vegetation structure and composition) in the different scenarios. The effect of different disturbance impact models is shown in Appendix SI12.

In total, 5,040 simulation runs with a duration of 200 years were conducted (2 models \times 2 landscapes \times [3 levels of gamma diversity \times 2 spatial configurations +1 \times no diversity] \times 3 climate scenarios \times 3 disturbance scenarios \times 20 replicates).

2.8 | Analyses

We quantified the effects of tree species diversity under different climate and disturbance regimes on two response variables for both disturbance impact and temporal variation. The two response variables were above-ground biomass (t/ha) and the average number of trees >30 cm dbh/ha. Biomass was selected because it is a widely used variable for quantifying disturbance effects in ecosystems, integrating over disturbance impact and recovery (Temperli et al., 2013). Furthermore, forest biomass stocks are closely related to important ecosystem services such as timber production and carbon storage (Mina et al., 2017). The number of large trees is an indicator of forest structure. It was selected because the presence of large trees is a characteristic feature of current forest ecosystems in Central Europe (Albrich et al., 2020), yet future projections suggest a shift towards smaller trees (McDowell et al., 2020). Furthermore, large trees are also important in the context of the provisioning of regulating services that are of particular relevance in mountain ecosystems (Frehner et al., 2005). Disturbance impact was quantified as relative (biomass) or absolute (forest structure) difference to the corresponding no disturbance run (i.e. the run with the same climate, spatial configuration and gamma diversity level, without disturbances; see Figure 2 and Equations 1 and 2). Temporal variation was

quantified by calculating the coefficient of variation of the response variables (i.e. biomass t/ha and trees >30 cm dbh/ha) over the 200-year simulation period in 20 time steps.

$$\text{biomass impact (\%)} = \left(1 - \frac{\text{biomass}_{\text{disturbed}}[\text{t/ha}]}{\text{biomass}_{\text{undisturbed}}[\text{t/ha}]} \right) \times 100, \quad (1)$$

$$\text{structural impact (trees > 30 cm dbh/ha)} = \frac{\text{tree}_{\text{disturbed}}[\text{n/ha}] - \text{trees}_{\text{undisturbed}}[\text{n/ha}]}{\text{trees}_{\text{undisturbed}}[\text{n/ha}]} \quad (2)$$

To test for differences in species dominance between the two spatial configurations of tree diversity, we also calculated the realized gamma diversity of the landscape at the end of the simulation period (i.e. simulation year 200). Realized gamma diversity was expressed as the exponent of the Shannon Entropy over the biomass of all species (i.e. effective number of species; see Jost, 2006), with a theoretical maximum equal to the size of the species pool if all species are represented equally on the landscape. All data analysis and visualization were accomplished with R version 4.0.2 (R Core Team, 2020).

3 | RESULTS

3.1 | Realized gamma diversity

As expected, the realized gamma diversity emerging from the simulations was lower than the theoretical maximum in most diversity scenarios and spatial configurations (Figure 3). In the scenario *high+*, realized gamma diversity at the end of the 200-year simulation period reached on average 84% (Figure 3a,c) and 92% (Figure 3b,d) of the theoretical maximum in Dischma (under RCP8.5) and Rosalia (under historic climate), respectively. The qualitative differences between the four diversity scenarios were well reflected in the realized gamma diversity. The effective number of species ranged from 1 in the no diversity scenarios to 8.9 in the *high+* scenarios of the high-elevation Dischma landscape under climate change (scenario RCP8.5). Climate change strongly increased realized gamma diversity in Dischma (Figure 3a,c), but slightly decreased realized gamma diversity in Rosalia (Figure 3b,d). We found no notable differences in realized gamma diversity between the two spatial configurations (alpha and beta) and the three disturbances scenarios (no disturbance, historic disturbance and future disturbance). Both models were able to maintain high levels of species diversity over the full 200-year simulation period and agreed well on the patterns of realized diversity.

3.2 | Effects of tree species diversity on disturbance impacts

Increasing tree species diversity at the landscape scale (gamma diversity) generally reduced disturbance impact for both indicators investigated (biomass, structure; Figure 4). A notable exception to this pattern was the Rosalia landscape, where lowest disturbance impacts

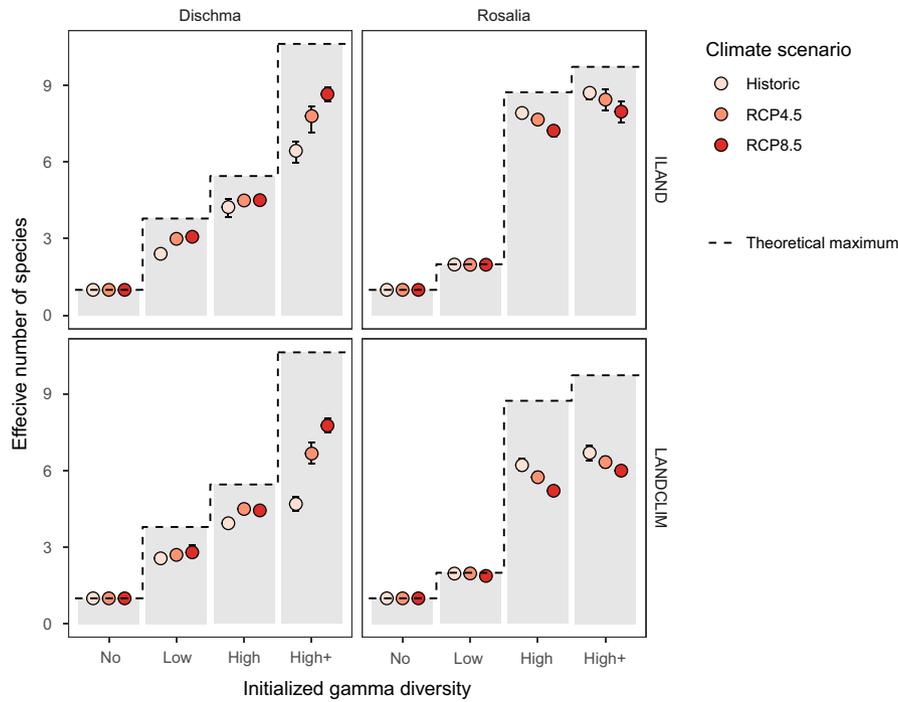


FIGURE 3 Realized gamma diversity (i.e. effective number of species at the landscape level) in the different diversity scenarios after 200 years of simulation. Results are shown for the two study landscapes (columns) and the two models (rows) under the three climate scenarios (colours) investigated. Data points show mean values over the three disturbance scenarios (no disturbance, historic disturbance and future disturbance), two spatial arrangements and 20 replicates. Error bars show the range of the data. The effective number of species was calculated as the exponent of Shannon Entropy based on biomass shares, which reaches a theoretical maximum at an equal representation of all species from the species pool on the landscape (indicated by the dashed line and shaded bars)

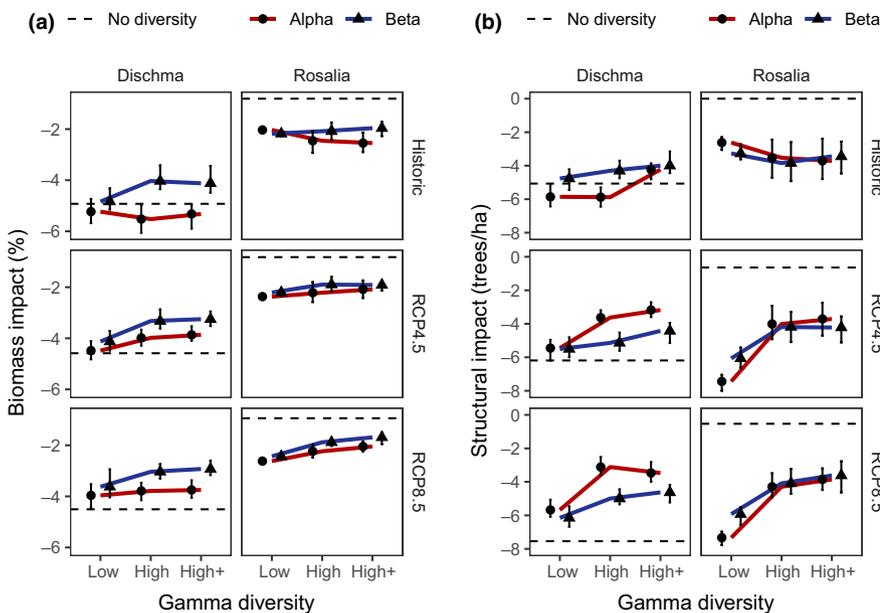


FIGURE 4 Disturbance impacts on biomass (a) and forest structure (b) for two spatial configurations of tree species diversity (alpha and beta) along a gradient of gamma diversity. Effects are displayed separately for the two study landscapes (Dischma and Rosalia) and three climate scenarios (historic, RCP4.5, RCP8.5). The data points are mean values over two disturbance frequencies (400- and 200-year disturbance rotation), two models (iLand, LandClim), 20 time steps and 20 replicates. The error bars show the range of the data. Individual results for the two simulation models can be found in the Supporting Information (Appendix S16)

were simulated for the no diversity scenario (representing pure beech forests over the entire landscape) compared to the scenarios of higher species diversity (Figure 4). Disturbance impacts were generally more pronounced in the conifer-dominated Dischma landscape compared to the broadleaved-dominated Rosalia landscape. Overall, climate change amplified the positive effect of increasing diversity in both landscapes

(Figure 4). Furthermore, we found that the effect of spatial configuration was context-dependent, with patterns varying between landscapes and indicators. Biomass impacts were generally lower when species were mixed between stands (beta scenario). Conversely, disturbance impacts on forest structure were lower in the alpha scenario in Dischma, and did not differ between configuration scenarios in Rosalia (Figure 4).

3.3 | Effects of tree species diversity on temporal variation

The temporal variation in biomass stocks and forest structure generally increased with increasing intensity of climate change in both landscapes (Figure 5). The role of tree species diversity on temporal variation was strongly context-dependent: For biomass stocks, the *low* and *no* diversity scenario were most stable under historic climate

while under future climate scenarios of higher tree species diversity were more stable. Forest structure was generally more variable in simulations under the *low* diversity scenario compared to scenarios with higher gamma diversity. Overall, however, differences between gamma diversity scenarios were small relative to the variation within each scenario. Furthermore, we did not detect differences in the simulated temporal variation between the two spatial configurations (i.e. alpha and beta diversity; see Appendix S15).

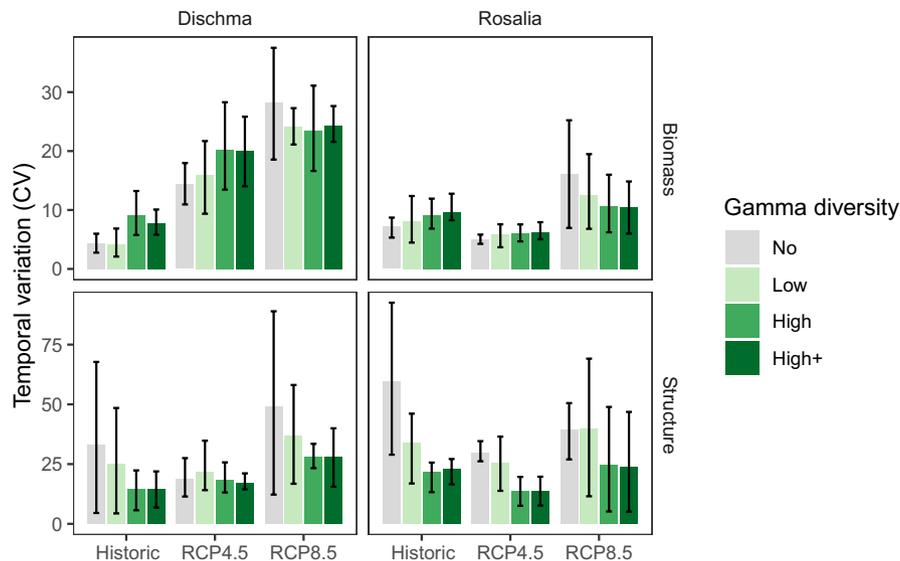
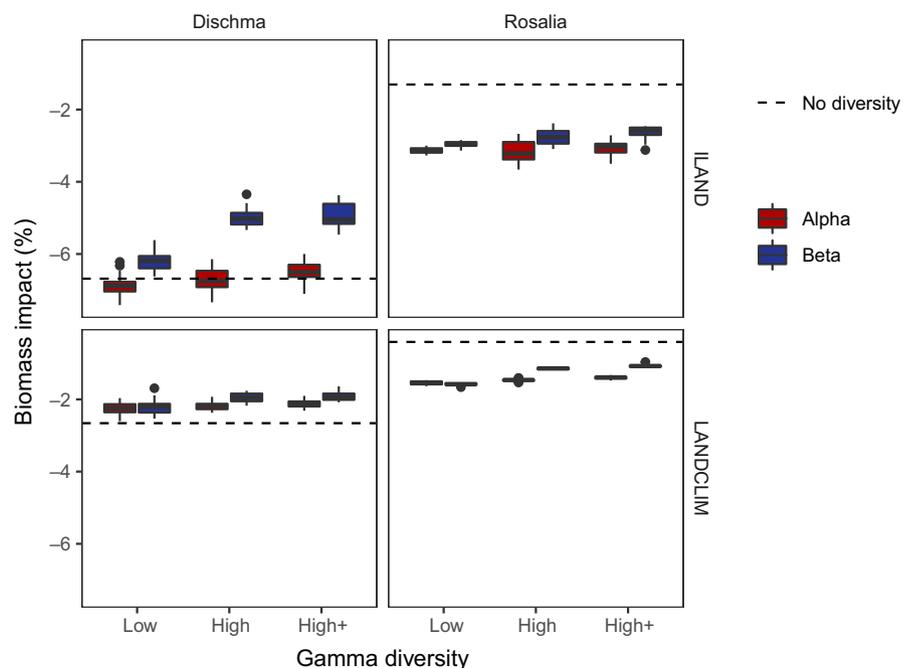


FIGURE 5 Temporal variation, expressed as the coefficient of variation over time in biomass stocks (top) and forest structure (bottom) under three different climate scenarios and four levels of gamma diversity. The bars show mean values, with the whiskers indicating the range over two models (iLand and LandClim), two spatial configurations (alpha and beta), three disturbance scenarios (no disturbance, 400-year disturbance rotation and 200-year disturbance rotation) and 20 replicates. Temporal variation was calculated over the 200-year simulation period in 10-year time steps. We did not detect differences in the simulated temporal variation between the two spatial configurations (i.e. alpha and beta diversity), which is why they are pooled together here (see Appendix S15). Individual results for the two simulation models are found in the Supplementary Information (Appendix S17)

FIGURE 6 Differences in disturbance impact between the two models (iLand and LandClim) and the two spatial configurations (alpha and beta). Biomass impact is the relative difference in average biomass stocks compared to simulations without disturbance (see Figure 2). Values are averaged over two disturbance scenarios (200- and 400-year rotation period), three climate scenarios (historic, RCP4.5 and RCP8.5) and 20 replicates. Note the different scaling of the y-axes. See Supporting Information Table Appendices S16 and S17 for a comparison between models regarding the simulated temporal variation and the disturbance impact on forest structure



3.4 | Model effects

iLand and LandClim were mostly consistent in their projections of the effects of gamma diversity and spatial configuration (alpha and beta scenarios, Figure 6). They agreed on biomass impacts generally decreasing with increasing gamma diversity. Furthermore, both models were consistent in simulating lower disturbance impacts on biomass stocks under beta mixtures compared to alpha mixtures.

We did, however, also detect differences between the two models (Appendices S16 and S17). iLand generally simulated a denser forest structure (trees >30 cm dbh/ha) and thus higher biomass stocks. Consequently, also disturbance impacts were more pronounced in iLand compared to LandClim for both indicators investigated. Furthermore, model differences were generally greater for forest structure than biomass stocks: While disturbances decreased the number of trees >30 cm dbh/ha in iLand, their numbers even increased slightly under some scenarios in LandClim (Appendix S16). Temporal variation of biomass stocks and forest structure increased with climate change and decreased with species diversity, consistently across both models. However, buffering effects of species diversity were more pronounced in LandClim compared to iLand.

4 | DISCUSSION

4.1 | Increasing tree species diversity at different spatial scales

We found evidence that higher levels of tree species diversity can reduce disturbance impacts on biomass stocks and forest structure in two contrasting forest landscapes of Central Europe, representing broadleaved-dominated lowland ecosystems and conifer-dominated mountain ecosystems. Our results thus generally confirm our first hypothesis of positive biodiversity effects on forest ecosystems under changing climate and disturbance regimes, and are in line with previous research (Griess et al., 2012; Jactel et al., 2017; Knoke et al., 2008; Silva Pedro et al., 2015). However, we went one step beyond previous studies by testing whether the spatial grain of mixing modulates diversity effects (see also Griess & Knoke, 2013 for an economic investigation). Our results indicate that positive diversity effects arise irrespective of whether species are mixed within or between stands, in line with our null hypothesis regarding the influence of spatial configuration. However, our analyses also highlight that diversity effects are strongly context-specific, and differ with study landscape and response variable. With regard to the impacts of disturbances on biomass stock, for instance, we found that species mixtures between stands (beta scenario) are more resistant than simulations in which species are mixed within a stand (alpha scenario), especially in the conifer-dominated Dischma landscape. This finding is consistent with a previous analysis investigating the effects of landscape configuration and composition on the resilience of Norway spruce (Honkaniemi et al., 2020).

An important insight from our analysis is the strong effect of species identity on diversity effects, that is, the effect being strongly contingent on the presence of certain species and their particular traits (see also Blaško et al., 2020; De Wandeler et al., 2018; Hantsch et al., 2013; Schwarz et al., 2015). In our simulations, the effects of diversity differed considerably depending on the species being present in the local species pool. In Dischma, for instance, the species serving as baseline in the 'no diversity' scenario is Norway spruce, which is more susceptible to disturbance compared to other species of the species pool (Schmidt et al., 2010). Thus, enhancing species diversity with, for example, European larch and Silver birch resulted in a considerable reduction of disturbance impacts on the landscape (Figure 4). In contrast, the tree species simulated in the 'no diversity' scenario in Rosalia is European beech, which is more resistant to disturbance than most of the naturally co-occurring species (Schmidt et al., 2010). Here, adding species such as Silver fir and Norway spruce to the mix increased disturbance impacts. Our results therefore underline that species identity is a key element in determining the interactions between forest composition and the disturbance regime of a given landscape. Specifically, we found that species identity effects can reverse the patterns expected under the insurance hypothesis (Yachi & Loreau, 1999).

In addition to identity effects and the resulting differences between landscapes, we also found differences in the response to the spatial configuration between the two indicators studied. For biomass stocks, increasing beta diversity had consistently stronger positive effects than increasing alpha diversity while the effect of increasing gamma diversity was moderately positive. For forest structure (i.e. trees >30 cm in dbh/ha), the effect of increasing gamma diversity was more pronounced, yet effects of spatial configuration differed between the two landscapes. In Dischma, the prevalence of large trees was less affected by disturbances in within-stand mixtures of species (alpha scenario) under climate change while in Rosalia both the alpha and beta scenario performed similarly under all climate scenarios. This suggests that especially under the high-elevation conditions of Dischma, increasing resource availability for tree growth linked to climate change (e.g. resulting from longer growing seasons, cf. Delbart et al., 2008; Menzel et al., 2006) can be utilized better when tree species are mixed within a stand (complementary resource use, Larocque et al., 2013; Morin et al., 2018). Overall, the differences between indicators highlight that diversity effects are strongly contingent on the functions and services under consideration, suggesting that there is no universally best mixture, and that the social-ecological context is a matter of central importance.

Temporal variation of biomass stocks and forest structure generally increased with increasing intensity of climate change. We found that single species systems of the currently most productive species (i.e. Norway Spruce in Dischma and European beech in Rosalia) had highly stable biomass stocks under historic climate conditions. Under severe climate change, however, these were the most volatile systems, suggesting that forest dynamics could become significantly more variable in the future (McDowell et al., 2020; Seidl et al., 2017;

Sommerfeld et al., 2018). However, temporal variation of biomass stocks and forest structure also increased in response to climate change in scenarios of higher tree species diversity, suggesting that increasing tree species alone will not be enough to buffer Central European forests from the impacts of climate change.

4.2 | Methodological considerations

We conducted a simulation experiment investigating the effects of alpha, beta and gamma diversity on disturbance impacts and temporal variation of biomass stocks and forest structure. Using models, we were able to study spatiotemporal scales that are beyond the realm of experimental research. A novelty of our analysis is that it is based not on one but on two well-established forest landscape models (Keane et al., 2015). Multi-model inference is frequently used in other fields of science (Eyring et al., 2007; Tebaldi & Knutti, 2007), and is increasingly applied in ecology (McDowell et al., 2013; Renwick et al., 2018; Reyer et al., 2017). However, in ecological studies, multi-model analyses have to date largely focused on methodological questions (e.g. Bugmann et al., 2019; Ichii et al., 2010) while questions of applied ecology are commonly addressed only with a single model. We emphasize that using multiple models also in the context of applied questions considerably increases the robustness of the management implications deduced from such studies (see below). The consistency in the general patterns and effects between iLand and LandClim suggests that our results are robust, and that model-specific uncertainties are not impeding the general conclusions of our study.

We nonetheless identified differences between the two models, particularly with regard to disturbance impacts on both biomass stocks and forest structure, which were generally stronger in iLand than in LandClim. These differences can mostly be attributed to different spatial (iLand: individual tree, LandClim: tree cohort) and temporal (iLand: year, LandClim: decade) resolutions of the two models, resulting in different simulations of disturbance impacts. Specifically, for the predominantly moderate disturbance severities simulated here, in LandClim forest attributes recover faster than in iLand, as tree regeneration is assumed to completely recolonize a disturbed patch within the first 10-year time step after disturbance if seed trees are nearby (Schumacher et al., 2004). In contrast, regeneration processes in iLand are simulated at finer temporal and spatial grain, which results in slower regeneration trajectories and larger biomass impacts of disturbances. Overall, however, the results were remarkably consistent between the two models, especially when taking into account the strong differences in model architecture (Petter et al., 2020).

While we emphasize that multi-model inference is an important way to quantify model uncertainties (Keane et al., 2015), such an approach has shortcomings as well. Multi-model inference necessarily requires that driver data are harmonized between the models, which can result in simplified simulation designs. An example in the current study is the implementation of natural disturbance. While both models include dynamic modules of natural disturbances,

their differences in process representation were deemed too large to warrant a meaningful comparison. In other words, if forced with their respective dynamic disturbance modules, the inference on our main research questions (how diversity modulates the effects of disturbances on forest biomass and structure) would have likely been masked strongly or even rendered impossible by the differing disturbance trajectories in the models. This element was controlled by the simplified and standardized implementation of wind disturbances in the current application. As a consequence, however, our analysis disregards other, potentially important aspects of the disturbance regime such as other disturbance agents (e.g. biotic disturbances, Kautz et al., 2018), disturbance interactions (Temperli et al., 2013) and edge effects (Mezei et al., 2014). As our approach excludes processes of spatial spread (e.g. of bark beetle populations, Kautz et al., 2011), our finding on the positive effects of fostering beta diversity are likely conservative, as landscape configuration can strongly reduce the spread of biotic disturbance agents (Honkaniemi et al., 2020). Future work could further investigate effects of tree species diversity and configuration using fully dynamic disturbance simulations and considering multiple disturbance agents.

Another important limitation of our study lies in its fixed grain (100 × 100 m) and categorical representation of alpha and beta diversity. While we were able to show that beta diversity can reduce disturbance impacts, we cannot determine at which spatial grain beta diversity effects are optimized. We a priori chose a grain of 1 ha, corresponding roughly to the average stand size and median disturbance patch size in Central Europe (Senf et al., 2017). Future work could analyse the effects of beta diversity over varying stand sizes, to, for example, determine the maximum stand size for which a landscape still benefits from increased beta diversity. Furthermore, to increase contrasts, we assumed minimal alpha diversity in our beta diversity scenario. In reality, alpha and beta diversity do, however, exist on a continuum, and future analyses could quantify potential trade-offs along this continuum explicitly.

4.3 | Implications for forest management

Our results have important implications for forest ecosystem management. We showed that mixing tree species between stands (i.e. fostering beta diversity) can be as effective or even more effective in buffering disturbance impacts under climate change than mixing tree species within a stand (i.e. focusing on alpha diversity). This finding opens up opportunities for forest managers to extend the spatial scope of fostering tree species diversity from the stand to the landscape scale, potentially capitalizing on the many other advantages of beta diversity for ecosystem service provisioning (Blatter et al., 2018; Schall et al., 2018; van der Plas et al., 2018). Our results are thus in line with growing evidence on the importance of beta diversity in ecosystem management (Blatter et al., 2018; Mori et al., 2018; Schall et al., 2018). Moving the focus from mixtures within stands to mixtures between stands could also have many operational advantages for forest

management, as it may reduce the efforts needed to regulate competition between species, improve stem quality and simplify harvesting logistics.

However, our results also document that diversity effects vary with context and indicator, underlining that fostering beta diversity is no silver-bullet solution. Enhancing tree species diversity may not be enough to meet the multiple threats of global change on forests (McDowell et al., 2020), and may need to be accompanied by additional measures such as increasing resistance through improved thinning and reduced rotation periods (Zimová et al., 2020) or increasing resilience through advance regeneration (Johnstone et al., 2016) and enhanced structural diversity (Millar et al., 2007). Nonetheless, fostering tree species diversity across spatial scales is a powerful means to buffer the impacts of changing climate and disturbance regimes, and should thus be considered as a powerful tool in the adaptation toolbox of forest ecosystem managers.

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AUTHORS' CONTRIBUTIONS

J.S., R.S. and H.B. designed the study; J.S., W.R. and T.T. ran simulations with iLand and LandClim; J.S. analysed the data; J.S. wrote the initial draft of the manuscript. All Authors contributed critically to the initial drafts and the revised version, and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data and code are available via the Zenodo Digital Repository <https://doi.org/10.5281/zenodo.4739037> (Sebald et al., 2021).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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