



## RESEARCH ARTICLE

# ‘How to adapt forests?’—Exploring the role of leaf trait diversity for long-term forest biomass under new climate normals

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## Abstract

Forests, critical components of global ecosystems, face unprecedented challenges due to climate change. This study investigates the influence of functional diversity—as a component of biodiversity—to enhance long-term biomass of European forests in the context of changing climatic conditions. Using the next-generation flexible trait-based vegetation model, LPJmL-FIT, we explored the impact of functional diversity on long-term forest biomass under three different climate change scenarios (video abstract: [https://www.pik-potsdam.de/~billing/video/2023/video\\_abstract\\_billing\\_et\\_al\\_LPJmLFIT.mp4](https://www.pik-potsdam.de/~billing/video/2023/video_abstract_billing_et_al_LPJmLFIT.mp4)). Four model set-ups were tested with varying degrees of functional diversity and best-suited functional traits. Our results show that functional diversity positively influences long-term forest biomass, particularly when climate warming is low (RCP2.6). Under these conditions, high-diversity simulations led to an approximately 18.2% increase in biomass compared to low-diversity experiments. However, as climate change intensity increased, the benefits of functional diversity diminished (RCP8.5). A Bayesian multilevel analysis revealed that both full leaf trait diversity and diversity of plant functional types contributed significantly to biomass enhancement under low warming scenarios in our model simulations. Under strong climate change, the presence of a mixture of different functional groups (e.g. summergreen and evergreen broad-leaved trees) was found more beneficial than the diversity of leaf traits within a functional group (e.g. broad-leaved summergreen trees). Ultimately, this research challenges the notion that planting only the most productive and climate-suited trees guarantees the highest future biomass and carbon sequestration. We underscore the importance of high functional diversity and the potential benefits of fostering a mixture of tree functional types to enhance long-term forest biomass in the face of climate change.

## KEYWORDS

biomass, European forests, functional diversity, functional traits, new climate normal, resilience, vegetation modelling

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## 1 | INTRODUCTION

Numerous climate impact studies suggest that forests will undergo substantial changes in the current century (Albrich et al., 2020; Buras & Menzel, 2019; Hanewinkel et al., 2013; McDowell et al., 2020; Svenning & Sandel, 2013; Venäläinen et al., 2020). The projected magnitude and pace of changes in temperature and water availability challenge the capacity of forests to adapt and might trigger large forest dieback (Hartmann et al., 2022). To anticipate such impacts and increase forest resilience several theories and approaches are still discussed (Brang et al., 2014; Jandl et al., 2019; Keenan, 2015).

On the one side of the spectrum, solutions relying on natural ecosystem processes are promoted where forest diversification, plant complementarity and natural forest adaptation potentials are the central elements (Hisano et al., 2018; Sakschewski et al., 2016; Schmitt et al., 2020). Here, environmental and competitive filtering are thought to continuously select the best-performing tree individuals and help forests to adapt to a new climate if natural competition is allowed and plant diversity is high (Sakschewski et al., 2016). In this discussion, functional diversity—as the diversity of functional traits—has been identified as a key to understand ecosystem resilience (Cadotte et al., 2011; Díaz & Cabido, 2001; Grime, 1998). Especially, recent findings indicate that functional diversity can help forests enhance individual productivity (Madrigal-González et al., 2016) or improve tree survival under climate change via functional trait complementarity effects (Billing et al., 2022). However, natural forest adaptation including high functional diversity and alternative silvicultural practices is currently restrained by a number of ecological, economic, logistical, informational, cultural and historical constraints (Puettmann et al., 2015).

On the other side of the spectrum, it is suggested to actively change forest composition, for example by increasing the proportion of tree species estimated to be climate-adapted (Buras & Menzel, 2019; Thurm et al., 2018). Climate-adapted tree species could be introduced as monocultures in isolation or mixed together in order to anticipate climatic changes early on and form climate-adapted forests in the long term. Such adaptation strategies that focus on a narrow range of tree diversity might miss out the positive effects of functional diversity such as portfolio effects and functional redundancy (Liu et al., 2018). This principle suggests that diverse ecosystems featuring high trait portfolios are more resilient, as different species can compensate for those negatively affected by changing conditions, thus maintaining ecosystem functions under stress (Naeem & Li, 1997; Yachi & Loreau, 1999).

Moreover, such tree species selection is often based on climate envelop analysis or species distribution models, which currently do not fully account for tree-to-tree interactions so that unforeseen competitive effects could emerge (Dormann et al., 2018; Wisz et al., 2013; Zurell et al., 2018). Increasing plant stress and competition for sparse resources might change the competitive patterns that we observe today (Ruiz-Benito et al., 2013). Therefore, we need to understand in which way competition among climate-adapted trees affects long-term forest development under a new climate normal.

Controlled long-term forest experiments could be valuable tools to shed light on the open questions of functional diversity and plant competition in future forest development. However, stakeholders need to make informed decisions at present-day. Therefore, computer simulation models are a valuable tool to test for a variety of scenarios in little time (Sakschewski et al., 2016; Schmitt et al., 2020).

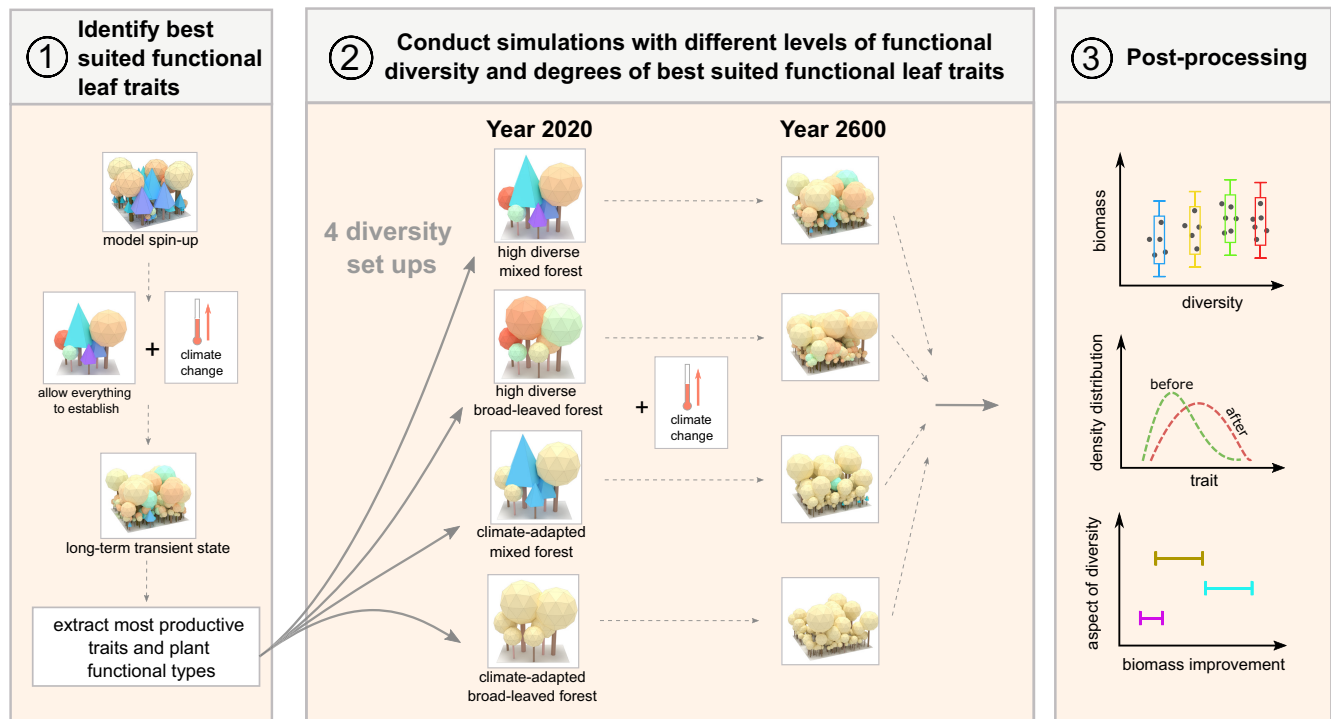
Here, we applied the next-generation flexible trait- and tree individual-based vegetation model LPJmL-FIT ('Lund-Potsdam-Jena managed Land—Flexible Individual Traits' Sakschewski et al., 2015; Thonicke et al., 2020) to six different European regions (from temperate to boreal/alpine conditions) to explore the spectrum of approaches currently discussed to increase long-term forest biomass under climate change. More specifically, we test the influence of functional diversity on long-term forest biomass in four different experimental model set-ups. We vary the amount of functional diversity (functional leaf trait diversity & diversity of plant functional types, PFTs) between full diversity and traits best suited for future climate conditions. Hereby, we define 'best-suited traits' as functional traits of trees that are most abundant under transient climate change simulations, given that the full plant spectrum can establish at any time (see Figure 1, circle 1). Each of the four model setups is tested under a range of different climate change scenarios (transient RCP2.6, RCP4.5, RCP8.5, Figure 1, circle 2) and evaluated by their transient biomass under a new climate normal thereafter (Figure 1, circle 3). We used the simulated data of each simulation experiment to conduct a Bayesian multilevel analysis to quantify the overall effect of functional leaf trait diversity and diversity of PFTs separately depending on the future climate scenario.

## 2 | METHODS

### 2.1 | The model LPJmL-FIT

The dynamic flexible-trait vegetation model LPJmL-FIT ('Lund-Potsdam-Jena managed Land – Flexible Individual Traits') is a process-based model, which simulates the establishment, growth, competition and mortality of individual trees and grasses (Sakschewski et al., 2015; Thonicke et al., 2020). The model is driven by daily climate input data (temperature, precipitation and radiation), atmospheric CO<sub>2</sub> concentration and soil texture, where the latter determines soil hydrology.

Each tree individual belongs to one out of four main PFTs: temperate broad-leaved summergreen (BL-S), temperate broad-leaved evergreen (BL-E), boreal needle-leaved evergreen (B-NL) and temperate needle-leaved evergreen (T-NL). A set of functional trait values is randomly drawn out of PFT-specific ranges based on the TRY database and is assigned during the establishment of a new tree individual and stays constant over their lifetime. This set determines the competitive ability, mortality and productivity under given environmental conditions. Key functional traits that have a strong impact on individual tree performance are specific leaf area (SLA), leaf longevity (LL) and wood density (WD). As a first principle of the model, every



**FIGURE 1** Overview of the study design. First, we identified ‘best-suited’ functional traits and functional types with transient long-term simulations allowing the full plant spectrum to establish (circle 1). Those traits and functional types form the basis for four different simulation setups with varying degree of functional diversity and share of best-suited traits/functional types, which we run until year 2600 forced with transient end-of-century climate (circle 2). Lastly, we evaluated transient biomass for each experiment and climate forcing using different statistical methods (circle 3). A sample simulation experiment can be found in the video abstract (Video 2).

PFT—and, therefore, every plant functional strategy—can establish in every forest patch at any time (Thonicke et al., 2020). The establishment rate of new trees depends on the available forest floor light (Methods S1). Vegetation dynamics are simulated on independent 10m × 10m forest patches, where the individual tree performance depends on an interplay of photosynthetic production, autotrophic respiration and inter-individual competition for light and water. Over time, only performance and competition determine which tree individuals survive and grow, and which die. A visualization of for exemplary forest community assembly at a single site can be found at: [https://www.pik-potsdam.de/~billing/video/2023/spinup\\_LPJmL\\_FIT.mp4](https://www.pik-potsdam.de/~billing/video/2023/spinup_LPJmL_FIT.mp4); Video 1. In this video, each animated tree resembles simulated variables describing individual tree growth, canopy (stem) coloured according to SLA (WD) value assigned at establishment. Finally, simulated tree communities are a result of (a) environmental filtering via the local climate and (b) competitive filtering through the current standing plant community. Understorey herbaceous vegetation is represented by two herbaceous PFTs (temperate C<sub>3</sub> and tropical C<sub>4</sub> grasses). More detail about the key functional traits and their connections in the model can be found in Methods S1.

Through its ecological approach, LPJmL-FIT is especially suitable to investigate the interaction of plant competition, functional traits and their diversity under varying climatic conditions. So far, the model simulates forests without any local human influence like management. Therefore, modelling results should be seen in the context of natural dynamics. In earlier studies, the model has

been extensively validated regarding trait composition, living biomass, tree height and mortality (Sakschewski et al., 2015; Thonicke et al., 2020).

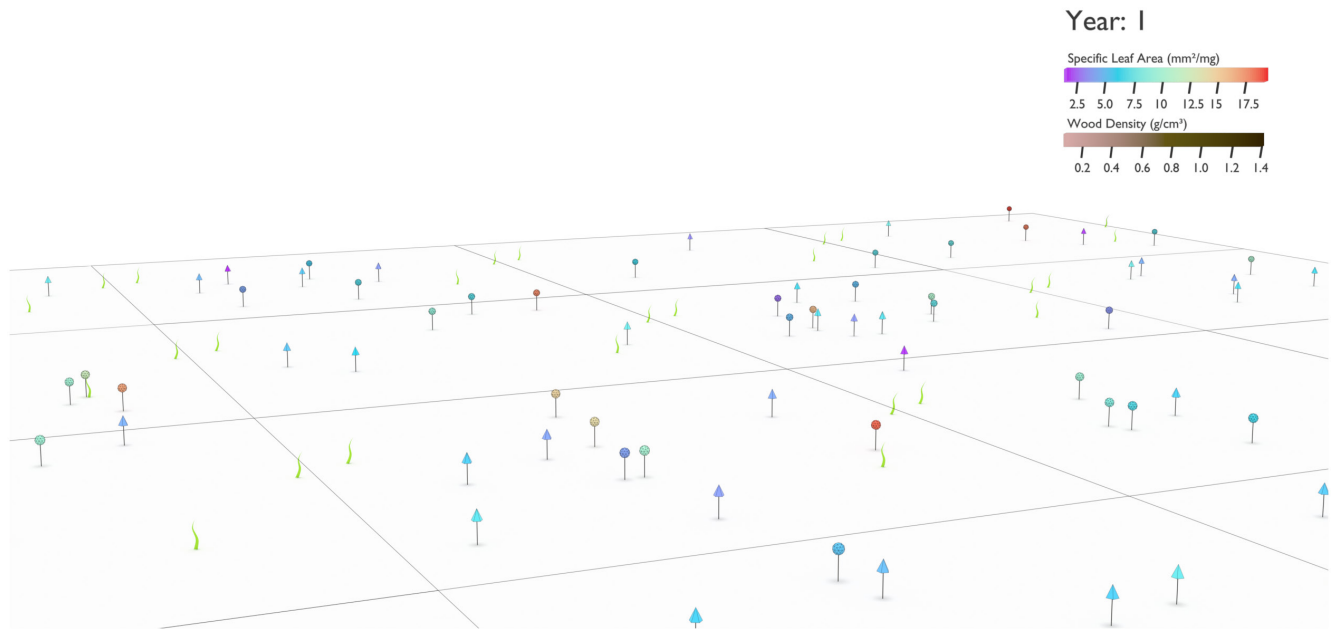
In the course of this study, the model has been adapted to reduce computation time and improve simulated forest biomass. Model changes since the publication of the original version for European natural forests (Thonicke et al., 2020) are further described in Methods S1A.

## 2.2 | Study regions

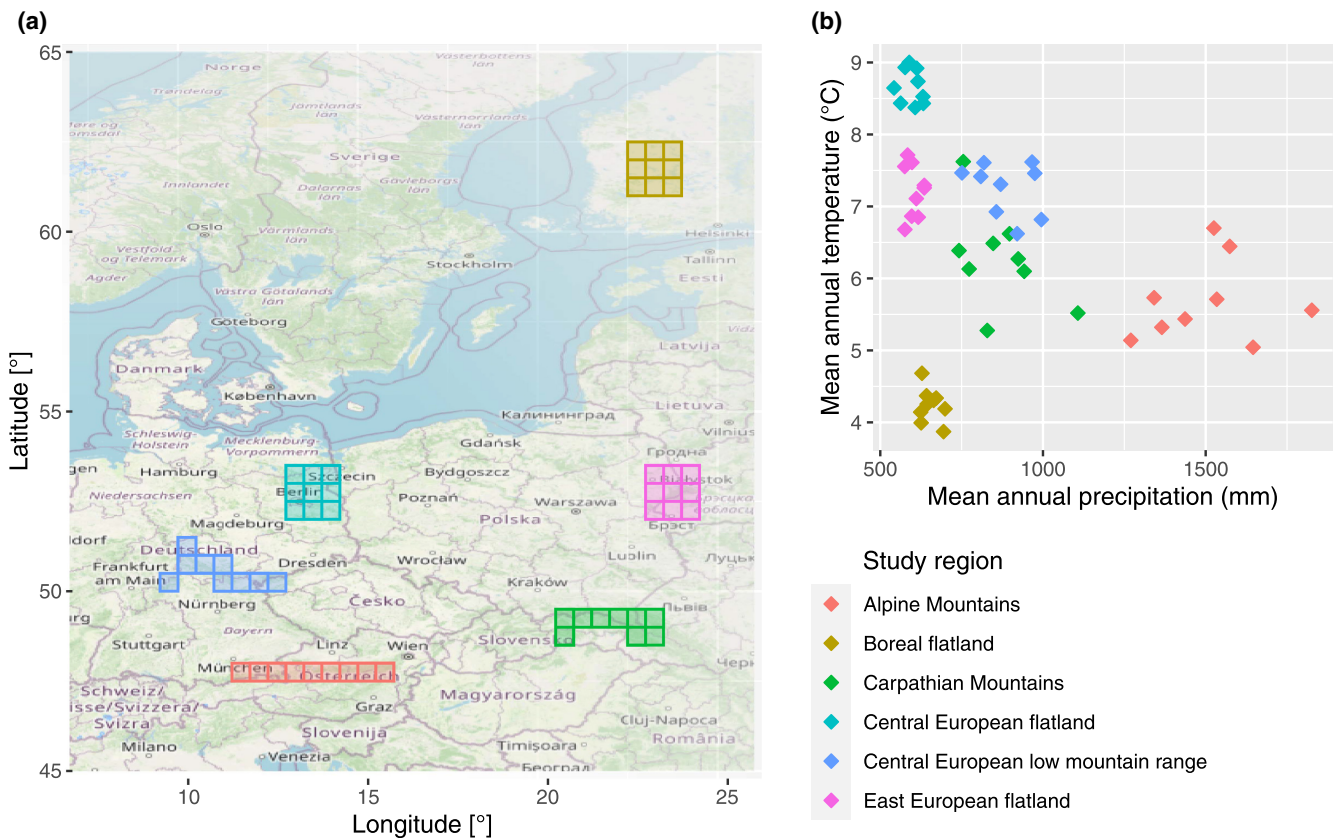
To cover a large environmental gradient, we applied the LPJmL-FIT model to six different regions across central and eastern Europe: Alpine Mountains, Boreal flatland, Carpathian Mountains, central European flatland, central European low mountain range and eastern European flatland (Figure 2a,b). Each region is represented by a manually chosen set of nine grid cells of 0.5° × 0.5° longitude and latitude in size.

## 2.3 | Experimental set-ups

Within this study, we investigated how four different experimental set-ups with varying degree of functional diversity affect forest adaptation under new climate normals in different study regions

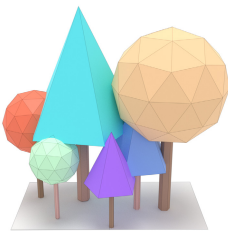
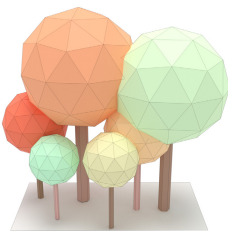
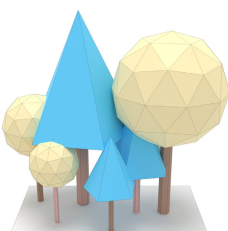
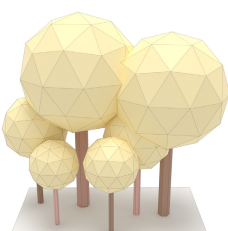


**VIDEO 1** Exemplary forest community assembly at a single site starting from bare ground. Trees compete for light and water on independent 10m × 10m forest patches. Every year new random sampled tree saplings join the community. Over time, best performing trees dominate the forest. Colour scales indicate specific leaf area (SLA) and wood density (WD) of individual trees. To view this video in the full-text HTML version of the article, please visit <https://onlinelibrary.wiley.com/doi/10.1111/gcb.17258>



**FIGURE 2** Illustration of the six study regions (panel a) and their mean annual temperature and mean annual precipitation (panel b) of each cell according to the spin-up climate data (from 1951 to 1980, see also simulation protocol). Map lines do not necessarily depict accepted national boundaries.

**TABLE 1** Overview of the four experimental set-ups in this study. Simulations differ in either leaf trait diversity (full leaf trait diversity [1,2] vs. best suitable leaf traits [3,4]) or diversity of plant functional types (all PFTs [1,3] vs. only broad-leaved summergreen PFT [2,4]).

	Experimental set-up	Description	Degree of functional diversity	Experimental condition for multilevel analysis	
				Full leaf trait diversity	Establish all PFTs
	1. High diverse mixed forest	All functional types, full leaf trait diversity	High	Yes	Yes
	2. High diverse broad-leaved forest	Only broad-leaved summergreen PFT, full leaf trait diversity	Medium	Yes	No
	3. Climate-adapted mixed forest	All functional types, best suitable leaf traits	Medium	No	Yes
	4. Climate-adapted broad-leaved forest	Only broad-leaved summergreen PFT, best suitable leaf traits	Low	No	No

(Table 1). Those set-ups specify the characteristics of newly established trees after the year 2020 in the model, which form the basis for future forest composition (see simulation protocol). Experimental set-ups can differ in two aspects (also denoted as experimental conditions in Table 1) to reach a varying degree of functional diversity:

1. Trees can either get randomly assigned to one of the four PFTs—or be set to the broad-leaved summergreen PFT, which was the most competitive PFT under any climate change simulation ('mixed forest' vs. 'broad-leaved forest').
2. Leaf traits can either be drawn out of the full leaf trait spectrum - or be constrained to the best-suited combination of specific leaf area and leaf longevity ('high diverse' vs. 'climate-adapted' leaf traits).

Here, best-suited leaf traits were defined as the mean specific leaf area and leaf longevity across all tree individuals for

each PFT and study region under transient climate conditions, called 'new climate normal' hereafter (repetitive years 2070–2099 for 500 years, see simulation protocol for details) if every plant strategy is allowed to establish. This assumes that the best-suited leaf traits belong to such individuals that are most productive and most successful therefore passing the environmental and competitive filtering under the new climate normal. In all experiments wood density, the other most important trait, is always randomly drawn from the PFT-specific trait range. Additional information on key functional traits in the model and best-suited leaf traits is found in Methods S1B. Combining the two experimental conditions described above ('mixed forest' vs. 'broad-leaved forest' and 'high diverse' vs. 'climate-adapted' leaf traits), results in four different experimental conditions with varying degree of climate suitable trees and functional diversity:

1. *High-diverse mixed forest*: Establishment of all PFTs and full leaf trait diversity within functional types.
2. *High-diverse broad-leaved forest*: Only broad-leaved summergreen trees, but full leaf trait diversity.
3. *Climate-adapted mixed forest*: Only trees with best-adapted leaf traits, but trees can belong to one of the four PFTs.
4. *Climate-adapted broad-leaved forest*: Only broad-leaved summergreen trees with the best-suited leaf traits.

## 2.4 | Simulation protocol and input data

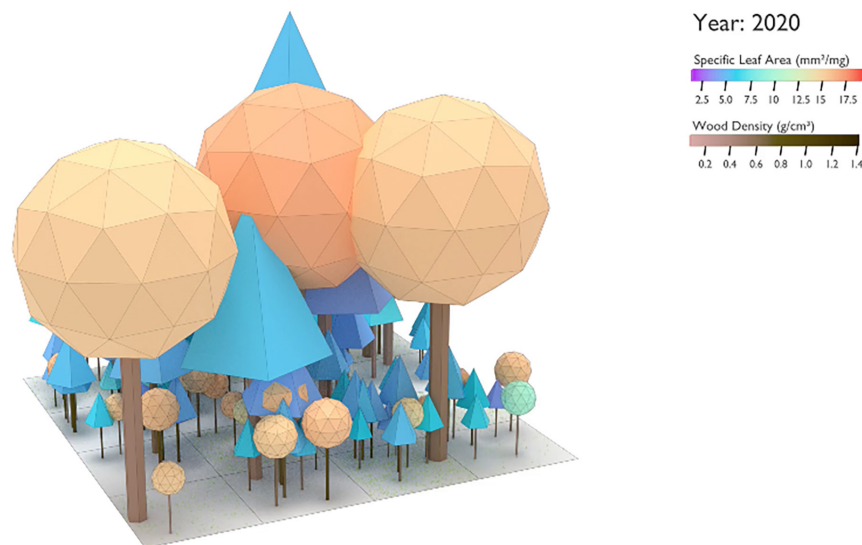
We forced our model using Hadgem2-ES (Collins et al., 2011) (bias-corrected with WATCH, Weedon et al., 2014) climate input data (temperature, precipitation and radiation) for three different RCPs (RCP2.6, RCP4.5, RCP8.5) on a  $0.5^\circ \times 0.5^\circ$  longitude-latitude grid. Soil texture was derived from the Harmonized World Soil Database version 1.2 (Nachtergaele et al., 2012) and soil depth was set to 2m for each grid cell. In order to avoid unrealistic strong  $\text{CO}_2$ -fertilization effects due to missing limitations in LPJmL-FIT, we held the atmospheric  $\text{CO}_2$  concentration over the whole simulation period. To keep our model runs comparable to the validated standard version of this model, we decided to leave the  $\text{CO}_2$  concentrations at the pre-industrial level of '296 ppm'. Minimizing  $\text{CO}_2$  fertilization aims to assess the impacts of environmental factors (e.g. climate change) on vegetation without  $\text{CO}_2$  fertilization's confounding effects (see also discussion of  $\text{CO}_2$  fertilization in Section 4.3).

For each grid cell, we started the simulation from bare ground allowing full leaf trait diversity and all PFTs to establish. A spin-up simulation recycling the climate input data 1951–1980 for 500 years was conducted to let carbon pools reach equilibrium, followed by the climate of 1980 to 2020. Model states in the year 2020 were taken as the starting points for all further simulations.

First, to obtain the best-suited traits required for simulation experiments, we continued to run the model allowing full leaf trait diversity and all PFTs to establish from 2020 to 2100 extending the simulation by 500 additional years by recycling end-of-century climate (2070–2099), that is, testing a new climate normal. From this model state, we extracted the mean specific leaf area and leaf longevity of all tree individuals for each PFT for the last 30 years of the simulation, which we further considered as best-suited leaf traits (Figure 1, circle 1). Best-suited leaf traits were extracted for each study region (Figure 2) separately.

Second, we split simulations into the four different experiments of this study (Table 1). In accordance with the simulation protocol to obtain the best-suited traits, we ran the model from 2020 to 2100 and extended the simulation from 500 years to year 2600 with the recycled end-of-century climate (2070–2099) for each experiment to investigate the transient behaviour of the model under a new climate normal (Figure 1, circle 2). The complete simulation protocol was conducted for each RCP scenario and study region separately (3 RCPs  $\times$  4 experiments = 12 simulations in each study region). A sample simulation experiment can be found in the video abstract (Video 2).

## Apply four experimental conditions



**VIDEO 2** Video visualization of a sample simulation experiment at a single grid cell: After model spin-up the 4 different simulation experiments were applied from year 2020 onwards leading to deviances in forest biomass over time. The high diversity experiment (high diverse mixed forest) lead to the highest biomass, whereas forest biomass is lowest if trees were constrained to the best performing leaf traits and plant functional type (climate adapted broad-leaved forest). To view this video in the full-text HTML version of the article, please visit <https://onlinelibrary.wiley.com/doi/10.1111/gcb.17258>

## 2.5 | Data analysis

The data generated according to the simulation protocol can be found under <https://doi.org/10.5880/pik.2024.001> (Billing et al. 2024). Data analysis conducted using R 3.6 (R Core Team, 2019). We evaluated the simulation experiments regarding their simulated biomass as a general indicator for resilience. Therefore, we calculated the relative change of biomass at the end of our simulation (post-impact biomass; i.e. arithmetic mean of the last 30 years of simulation) to the initial biomass (pre-impact biomass; i.e. arithmetic mean between years 2000 and 2029).

To investigate the overall effect of functional leaf trait diversity on forest biomass within our model simulations, we run a Bayesian multilevel regression. For that regression, we set the relative change of biomass in each simulation cell as a target variable and the functional diversity of the simulation experiments as a predictor. We fitted the Bayesian multilevel regression using the R package *brms* (Bürkner, 2017).

Bayesian multilevel regression is a statistical method that allows for the modelling data that has a nested or group structure (Gelman et al., 1995). Groups can represent different levels of hierarchy, such as students nested within classes and schools—or in our case simulation cells nested in different study regions. Bayesian multilevel regression is particularly advantageous when those groups only have a few observations (here: 9 cells per region  $\times$  3 climate scenarios  $\times$  4 experiments = 108 observations per study region) (Gelman et al., 1995). In addition, this multilevel approach is useful when dealing with data that can have group-specific effects: For instance, the performance of students belonging to different schools might not only depend on their individual background, but can be also explained via differences between schools (e.g. financial funding; effect on group level) (Goldstein et al., 1993). In the context of this study, we suspect that the effects of functional diversity can generally differ for each study region (study region = group level). Factors like seasonality, mean annual temperatures and initial PFT composition may lead to different forest dynamics among study regions and therefore effects of functional diversity could be different in each study region. The aim of this analysis is to estimate the effect for the relative change of post-impact biomass if: 1 = either all leaf traits are allowed to vary or 2 = all PFT can be established in our model simulations. For that we can split the four different experimental set-ups into two factors: full leaf trait diversity (yes or no) and establish all PFTs (yes or no) (Table 1). Therefore, those two experiment conditions (full leaf traits: yes/no; all PFTs: yes/no) were set as predictors for modelling the relative change of post-impact biomass in each grid cell.

We applied the following multilevel structure which aligns with the multilevel formula syntax as used in the *brms* package (Bürkner, 2017):

$$\text{biomass}_{\text{post-impact}} \sim (1 + \text{full\_leaf\_traits} + \text{all\_PFTs} + \text{full\_leaf\_traits} * \text{all\_PFTs} | \text{region}) (1) \\ + \text{full\_leaf\_traits} + \text{all\_PFTs} + \text{full\_leaf\_traits} \times \text{all\_PFTs}$$

where  $\text{biomass}_{\text{post-impact}}$  refers to the relative change in simulated above and belowground biomass in each grid cell. The independent variables `full_leaf_traits` and `all_PFTs` represent experimental conditions (1 or 0) for each experimental set-up as in Table 1, and `region` indicate the respective study region (Figure 2a).

According to Equation (1) the multilevel model comprises two levels: the study region level (terms in brackets; group level) and a level across all study regions (terms outside of brackets; population level). In the following, each of the predictors of Equation (1) is explained.

All terms in brackets in Equation (1) correspond to a study region-specific influences (study region level):

- '1 +' represents an intercept for each study region. This intercept recognizes that biomass change can be generally region-dependent. For instance, boreal forests might benefit more from climate warming compared to others.
- 'region' indicates that all predictors inside of the bracket can vary on the study site level (indication of the group level in the multilevel formula syntax).
- The term 'full\_leaf\_traits + all\_PFTs + full\_leaf\_traits  $\times$  all\_PFTs' specifies that the effect of allowing for all leaf traits to vary or to letting all PFT establish can vary depending study region (including their interaction term 'full\_leaf\_traits  $\times$  all\_PFTs').
- The term 'full\_leaf\_traits + all\_PFTs + full\_leaf\_traits  $\times$  all\_PFTs' represents the predictors across all study sites (i.e. the population level). The contributions of those terms in the regression are the same for all grid cells—regardless of which study region they belong to. They can be seen as overarching effects of allowing all leaf traits to vary or letting all PFT establish independently of the study region. They can contribute as single factors and as their interaction is similar to the study site level.

We conducted this Bayesian multilevel regression for each RCP separately with uninformative priors. To assess the model quality, we calculated  $R^2$  (Gelman et al., 2019) for each regression (Table S1, between 0.856 and 0.723). Finally, to investigate how—when allowing all leaf traits to vary—or—when letting all PFT establish—influence forest biomass we investigated the posterior distributions of the regression on the population level.

Posterior distributions can be interpreted as probability distributions for each of the coefficients in the regression. On the population level, posterior distributions show the general benefit of diversifying leaf traits or including all PFTs independently of the study site. Credible intervals (upper and lower 95%) of posterior distributions

were calculated to illustrate the range of uncertainty. All data generated and R-scripts are archived in a publicly accessible repository (Billing et al., 2024).

### 3 | RESULTS

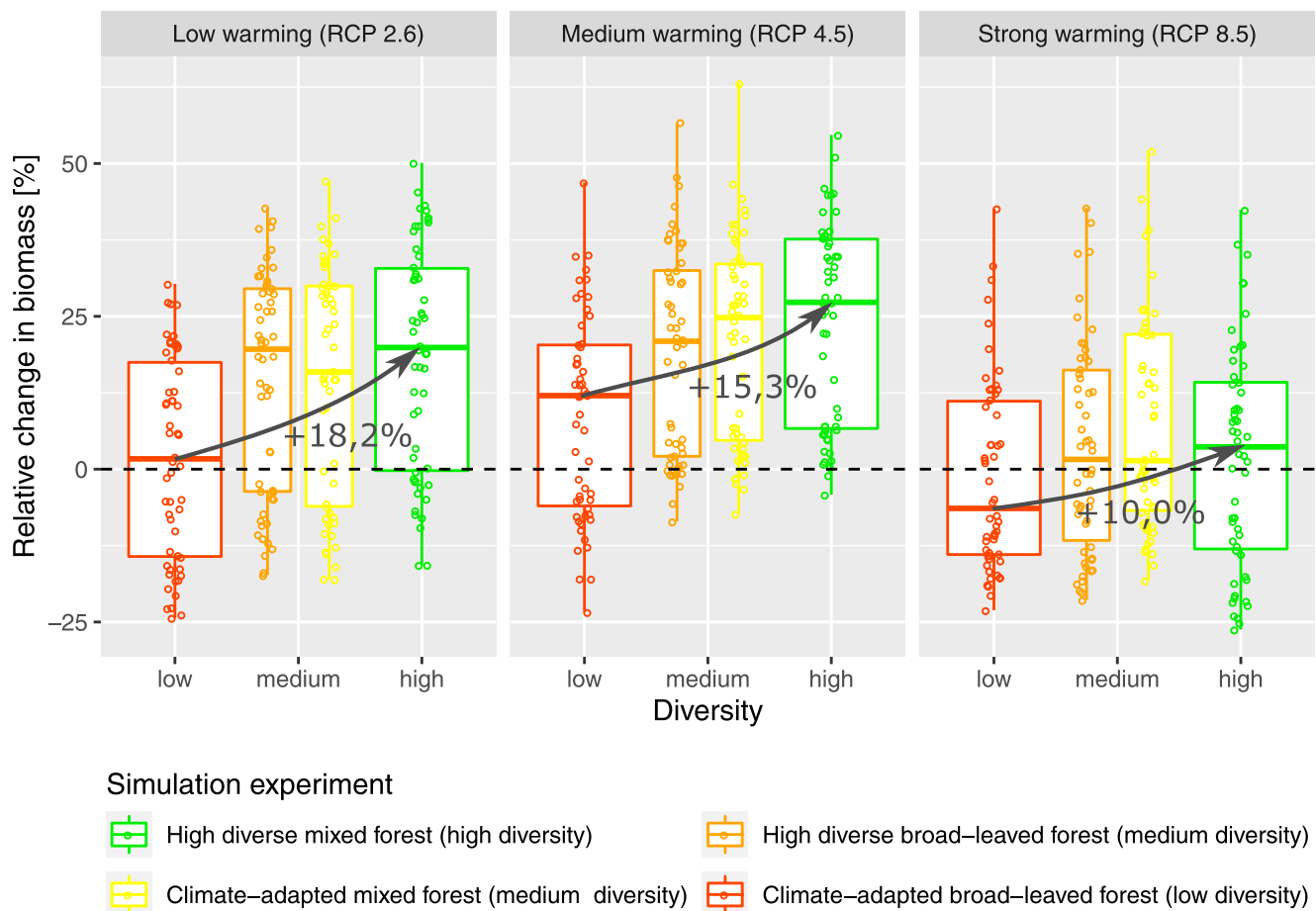
#### 3.1 | Functionally diverse forests lead to highest biomass

In this study, we conducted simulation experiments to investigate how forest adaptation strategies with varying degrees of functional diversity and the degree of best-suited functional traits cope with climate change. We find that simulations involving high functional diversity led to the highest long-term biomass (Figure 3). When future climate change was limited to 2°C of global warming, biomass increased by up to ~18.2% in the high-diversity simulation experiment compared to the low-diversity experiment (medians under RCP 2.6 in Figure 3). Apparently only allowing for tree individuals with the best performing leaf traits did not result in the highest biomass across all study regions (Figure S3). However, our model simulations

show that the benefits from functional leaf trait diversity become less with climate change intensity: While the positive effect of functional diversity reaches ~18.2% under the lowest warming scenario, it decreases down to ~10.0% under the strongest climate change scenario (Figure 3).

#### 3.2 | Positive effects of functional leaf trait diversity can depend on the facet of functional diversity

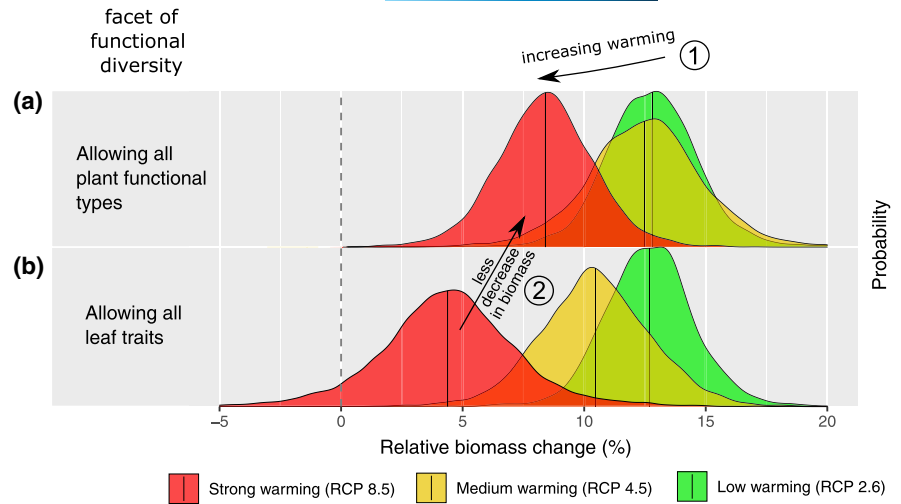
Furthermore, we conducted a Bayesian multilevel regression to test which facet of functional diversity might improve future biomass the most. Therefore, we estimated the overall effect of including full leaf trait diversity or allowing all PFTs to establish separately for each warming scenario (Figure 4, posterior distributions of factors described in Section 2). This analysis revealed that allowing leaf traits to vary increased forest biomass by the same amount as when including all PFTs in the simulation under the low-warming scenario. We found that either allowing full leaf trait diversity or all PFTs increased forest biomass by up to ~12%



**FIGURE 3** Relative mean post-impact biomass (years: 2570–2600) depending on climate scenarios (weak warming: RCP2.6; medium warming: RCP4.5; strong warming: RCP8.5) and simulation experiment. Each dot corresponds to one single simulation cell (nine cells per study region, all study regions shown per simulation experiment). High-diversity experiments generally lead to a higher increase in biomass, although the effect decreases with stronger climate warming.



**FIGURE 4** Posterior distributions of Bayesian multilevel regression on the population level which show the improvement in biomass after impact if forests are diversified (including either all PFTs, panel a, or flexible leaf traits, panel b) for each warming scenario. The effect of functional diversity decreases with climate change intensity (arrow 1). Allowing all PFTs in the simulation leads to generally higher biomass compared to allowing all leaf traits under strong warming scenario (arrow 2).



equally under the low warming scenario (RCP2.6) across all study regions (Figure 4, green density distributions). In line with trends in Figure 3, we also see that the positive effects of the individual facets of functional diversity also diminish with climate change intensity (Figure 4, arrow 1).

However, under stronger warming, we observe differences among the facets of functional diversity tested in this study. Allowing all PFTs in the simulation leads to generally higher biomass under strong warming by about ~4% compared to diversifying leaf traits (Figure 4, arrow 2). In addition, our analysis indicates that diversifying leaf traits can—in some instances—lead to a reduction in biomass under strong warming (Figure 4b, negative change in biomass).

## 4 | DISCUSSION

### 4.1 | Diversity and competition impact forest biomass

In this study, high functional diversity leads to the highest long-term biomass even higher than only allowing for the most performant phenotypes identified in this high functional diversity experiment. To explain and discuss these results and the underlying processes in detail, we here elaborate on the two experiments which showed the largest differences between each other namely the high diverse mixed forest (highest functional diversity) and the climate-adapted broad-leaved forest (lowest functional diversity).

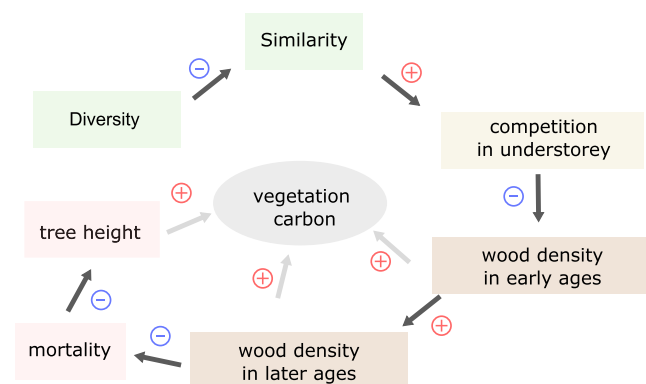
In our model, plant communities emerge from environmental and competitive filtering out of the standing tree community and newly established tree saplings. In the case of the high diverse mixed forest (highest functional diversity), we allow all PFTs and the full leaf trait spectrum to establish at any time so that future forest composition emerges from environmental and competitive filtering out of the complete plant spectrum. Through the large portfolio of plant strategies, environmental and competitive filtering selects a mixture of the most productive trait combinations and PFTs. For instance, although broad-leaved summergreen trees become the dominant

PFT in almost all simulations, the high diverse mixed forest option contains also shares of other PFTs such as boreal needle-leaved or broad-leaved evergreen trees (Figure S1). This indicates that this option allows ecological niches to be occupied better compared to all other simulation experiments, which partially explains the highest biomass.

Apart from niche occupation, beneficial effects from functional complementarity might improve individual tree performance and therefore biomass, which was observed in field studies (Díaz & Cabido, 2001; Madrigal-González et al., 2016; Ruiz-Benito et al., 2016) - and more specifically in the model used in this study (Billing et al., 2022). In this earlier study by Billing et al., functional complementarity was found to generally improve tree survival under climate change. In this study presented here, the discrepancies in forest biomass in the diversity experiments can be mainly explained via a mixture of complementarity, competition and filtering effects (Figure 5; details in Discussion S1A):

Analysis of wood density distribution across tree height classes in low- and high-diversity experiments (see Figure S7) reveals a notable trend: in low-diversity environments, high wood density trees are rare in the understorey (2–8 m in height). Reduced diversity increases tree trait similarity and therefore competition in the forest understorey. This homogeneity in the understorey intensifies competition (Figure S10), driving the need for faster initial height growth. Here, low-wood density trees have an advantage which shifts the wood-density distribution of the tree community. Consequently, also taller trees (>10 m) exhibit lower wood densities (Figure S8), which increases mortality rates and decreases maximum tree height (Methods S1B). This relationship persists over the whole simulation period (Figure S11) and is consistent across PFTs. The differences in wood density and tree height then explain disparities in forest biomass across diversity experiments (Figure 5).

In conclusion, we attribute the main cause for biomass discrepancies in our diversity experiments to a complex interplay of functional diversity, competition, growth and mortality. As the fundamental difference between simulation experiments lies in functional complementarity/similarity in leaf traits (Table 1, Figure 5), we argue



**FIGURE 5** General scheme of explaining effects that lead to biomass discrepancies in our simulation experiments which are underpinned by Figures S7–S12. Plus and minus signs indicate the nature of the source onto the target variable. For example: High diversity leads to lower similarity, lower similarity leads to lower competition in the understory (Figure S10), lower competition leads to higher wood density in early ages (Figure S7), which leads to higher wood density in later ages (Figure S8). High wood density decreases mortality and increases tree height (Figures S9, S11, and S12). High wood density and higher trees together increase vegetation carbon.

that functional complementarity could be seen as the main reason explaining biomass discrepancies among diversity experiments. We finally conclude that functional leaf complementarity can reduce competition in the forest understory.

The complementarity-competition effect we found indicates that forests, akin to natural forests with minimal management requirements and consisting of *only* well-adapted tree individuals bear the risk of stronger competitive interactions in the future. Therefore, we argue that tree-to-tree competition should be considered more strongly in the future, especially if forest management relies on climate-adapted, but less diverse forest compositions.

Across all our simulations, we observe that forest biomass is rather stable and biomass differences across simulations appear rather low. These findings might be over-optimistic due to several reasons. First, the available climate data used for our simulations still lack of representation of extreme drought events that can be caused by atmospheric blocking (Intergovernmental Panel on Climate Change [IPCC], 2023; Kautz et al., 2022), which might put additional pressure on simulated forests once included. Other studies have shown that functionally diverse ecosystems are more resilient to extreme events due to the portfolio and insurance effects (Messier et al., 2019; Oliver et al., 2015) because diverse ecosystems are more likely to contain species that can maintain the functioning of the ecosystem if other species fail (Loreau & de Mazancourt, 2013; Yachi & Loreau, 1999). Consequently, we expect that improving the presentation of extreme events in the climate data may lead to stronger disparities among the simulations so that forests with low functional diversity would perform worse. Second, all forests that we simulate are multi-aged forests dominated by natural regeneration.

In unfavourable years in which many trees die, younger trees can quickly take over their place which smooths the transient biomass response we observe. This generally increases forest resilience and can explain the relatively high biomasses across all simulations.

## 4.2 | The changing role of functional leaf trait diversity under stronger warming

The findings of this study indicate that the positive effects of functional diversity (FD) decline with high temperatures.

In general, the alpine and boreal forest sites considered in this study profit under increasing temperatures due to relatively cool and limiting initial temperatures, while both temperate lowland study regions appear to suffer from climate change (Figures S3 and S4, RCP8.5 in panels A and B vs. panels E and F). Here leaf traits become less decisive for forest development under very severe warming.

There is a general limitation of ecosystem productivity under very high warming (Huang et al., 2019). Very high local temperatures exceed the optimal range for ecosystem functioning as such so that higher functional diversity does not offer an alternative equally productive solution. A study by Huang et al. estimated the maximum optimal temperature threshold for needle- and broad-leaved forests to a mean annual temperature (MAT) of  $>18^{\circ}\text{C}$  (Huang et al., 2019). However, biodiversity effects in this study already start to be un-decisive from  $\text{MAT} >14^{\circ}\text{C}$  (Figure S5). Therefore, the decreasing importance of functional diversity might be likely not associated with maximum optimal temperature thresholds. Warming increasingly causes water stress to plants, so that other plant traits such as rooting depth or rooting shapes may be more important under higher temperatures, which have not been the subject of this study. Nonetheless, the temperature dependency observed in this study underscores the importance of considering both the direct effects of temperature and the modulating influence of biodiversity on ecosystem resilience and productivity. Overall, the lower importance of functional diversity under very strong warming, suggests that keeping global warming as low as possible remains essential to future forest adaptation.

The results of the Bayesian multilevel regression indicated that including all PFTs lead to generally higher biomass than diversifying leaf traits within functional groups (Figure 4). On the contrary, this may suggest that the presence of a mixture of different functional groups (e.g. summergreen and evergreen broad-leaved trees) is more important in supporting forest development under strong climate change than the diversity of traits within a functional group (e.g. broad-leaved summergreen trees). Especially under strong climate change, we observe that broad-leaved evergreen trees increasingly newly established aside from the present summergreen trees (Figure S1). Thus, by letting all PFTs establish, niches for broad-leaved evergreen trees may also be occupied, explaining the generally higher biomass. This suggests that under strongly expected changes in climatic conditions, previously absent functional plant groups may be considered for future forest adaptation.

Generally, the low importance of leaf trait variability under strong climate change may indicate that leaf traits might be less decisive under very strong warming compared to functional differences among functional groups or other functional traits. In the model, PFTs differ in water uptake and sensitivity to water/heat stress (Thonicke et al., 2020). Those differences might be more important under strong warming compared to the pure variation of leaf traits and could explain the lower importance of leaf trait variability under strong climate change.

### 4.3 | Limitations and further model development

In this study, we found that functional diversity can help forests to better adapt to new climate normals. However, the effects found in this study vary with the study region. For instance, alpine and boreal forests seem to profit from diversifying leaf traits under strong warming compared to the two lowland study regions (Figure S3). In our study, we explain those differences by initial temperature levels (see discussion above). Still, we must note that the relationship between leaf trait diversity and forest adaptation is ecosystem-dependent and should therefore be assessed case-specific.

There are several limitations to this study that should be taken into consideration when interpreting the results. In general, the findings of our study are to be seen within a certain context of the model concept. LPJmL-FIT classifies trees into PFTs rather than specific tree species, which means our results cannot be directly transferred to the species level. Interactions at the species level can be far more complex and require additional analysis, hence our findings rather provide a first general direction. Local conditions other than climate and soil texture constitute additional drivers that influence or modify the biomass benefits found here.

Additionally, the model is ecological in nature and does not consider certain human forest management measures such as thinning or fertilization. We rather tested in the model which advantage assisted tree planting would have on forest dynamics and its functional diversity in a setting close to natural forests demanding a minimum of forest management. Although different tree selections were tested in this study, providing precise management implications or species recommendations is out of scope of this study. Our experiments could be seen as a first test of management but rather serve for general ecological insight. Allowing more complex forest management in this model is currently tested, but still in an early development stage and therefore beyond scope.

In our model simulations, we kept the atmospheric CO<sub>2</sub> content constant at pre-industrial levels to keep the effects of further CO<sub>2</sub> fertilization at a minimum. CO<sub>2</sub> fertilization refers to increasing rates of photosynthesis in plants under higher atmospheric CO<sub>2</sub> levels. Current Dynamic Global Vegetation Models (DGVMs) tend to overestimate this effect due to missing constraints from nutrients like nitrogen and phosphorus (Hickler et al., 2015; Terrer et al., 2019) and investigating these mechanisms is a focus of ongoing research and

under debate (Smith et al., 2016). Test simulations of LPJmL-FIT suggest a substantial increase in vegetation carbon (Figure S6), yet we see these projections as unrealistically high. Given the uncertainty surrounding CO<sub>2</sub> fertilization and its unrealistic strong influence on the model, we conducted simulations without it (Knauer et al., 2023; Kovenock et al., 2021). This allows to assess the isolated effects of climate variables such as temperature and precipitation on vegetation without CO<sub>2</sub> fertilization's confounding effects. Thus, our findings should be interpreted in this context, with a further study needed to explore the potential effects of CO<sub>2</sub> fertilization (for further details see Discussion S1B).

Furthermore, the climate data used in the study may not adequately capture increasing climate variability and the potential impacts of climate extremes on forests, which could represent an additional threat to forest resilience and reduce the adaptation potential if considered. Moreover, other studies have shown that diverse forest better resist biotic and abiotic disturbances (Bauhus et al., 2017). Consequently, implementing disturbance agents such as bark beetle outbreaks or storm damages might further strengthen the importance of functional diversity.

Furthermore, diversifying more functional traits in LPJmL-FIT might help forests to better adapt to climate change. For instance, a diverse array of deep- and shallow-rooting plant, could help plant communities to access a wider range of water and nutrient resources to dampen potential future limitations thereof (Sakschewski et al., 2021). In addition, it was found that the diversity of hydraulic traits increases forest resilience (Anderegg et al., 2018) under drought. Therefore, diversifying root traits might further increase simulated forest biomass under climate change. Lastly, implementing leaf trait plasticity in the model might alter the importance of functional leaf traits observed in this study. However, implementing and investigating the effect of trait plasticity in dynamic flexible-trait vegetation models remains one of the most challenging objectives and is therefore a matter of future research (Berzaghi et al., 2020).

## 5 | CONCLUSION

We find that forests containing high levels of functional diversity have the highest biomass under the end-of-century new climate normals of several climate change scenarios. Even forest communities which are constrained to the best-performing leaf traits in low-diversity experiments did show a significant lower biomass than high-diversity communities. Therefore, our results challenge the notion that planting the most productive and best climate-suited trees *alone* automatically would lead to higher biomasses and the best carbon sequestration in the future. Instead, we argue that ensuring higher functional diversity leads to less similarity which decreases competition and hence enables for complementarity and a resilient and more productive forest.

We, therefore, recommend to increasingly consider competitive interactions if forest management aims for natural forest dynamics

while relying only on a small set of climate-adapted tree species. We conclude that aiming for high carbon sequestration with natural forest dynamics should go in hand with high functional diversity. This may involve fostering a mixture of tree species within different functional types, rather than focusing solely on highly productive trees allegedly best suited under climate change.

Nevertheless, outside a certain temperature range due to global warming functional leaf trait lose its ability to support forest biomass (MAT >14°C). Consequently, keeping global warming as low as possible remains essential to future forest development.

## AUTHOR CONTRIBUTIONS

**Maik Billing:** Conceptualization; formal analysis; investigation; methodology; visualization; writing – original draft; writing – review and editing. **Boris Sakschewski:** Conceptualization; visualization; writing – review and editing. **Werner von Bloh:** Investigation; software; writing – review and editing. **Johannes Vogel:** Visualization; writing – review and editing. **Kirsten Thonicke:** Conceptualization; supervision; writing – review and editing.

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## CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

## DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available through the GFZ Data Services at <https://doi.org/10.5880/pik.2024.001> (Billing et al., 2024).

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## SUPPORTING INFORMATION

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

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