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RESEARCH ARTICLE

Will forest dynamics continue to accelerate throughout the 21st century in the Northern Alps?

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Abstract

Observational evidence suggests that forests in the Northern Alps are changing at an increasing rate as a consequence of climate change. Yet, it remains unclear whether the acceleration of forest change will continue in the future, or whether downregulating feedbacks will eventually decouple forest dynamics from climate change. Here we studied future forest dynamics at Berchtesgaden National Park, Germany by means of a process-based forest landscape model, simulating an ensemble of 22 climate projections until the end of the 21st century. Our objectives were (i) to assess whether the observed acceleration of forest dynamics will continue in the future, (ii) to analyze how uncertainty in future climate translates to variation in future forest disturbance, structure, and composition, and (iii) to determine the main drivers of future forest dynamics. We found that forest dynamics continue to accelerate in the coming decades, with a trend towards denser, structurally more complex and more species rich forests. However, changes in forest structure leveled off in the second half of the 21st century regardless of climate scenario. In contrast, climate scenarios caused trajectories of tree species change to diverge in the second half of the 21st century, with stabilization under RCP 2.6 and RCP 4.5 scenarios and accelerated loss of conifers under RCP 8.5. Disturbance projections were 3 to 20 times more variable than future climate, whereas projected future forest structure and composition varied considerably less than climate. Indirect effects of climate change via alterations of the disturbance regime had a stronger impact on future forest dynamics than direct effects. Our findings suggest that dampening feedbacks within forest dynamics will decelerate forest change in the second half of the 21st century. However, warming beyond the levels projected under RCP 4.5 might profoundly alter future forest disturbance and composition, challenging conservation efforts and ecosystem service supply.

KEYWORDS
disturbance, forest change, forest development, forest structure, iLand, scenario uncertainty, tree species composition

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1 | INTRODUCTION

Forest ecosystem dynamics is increasingly altered by changes in climate and disturbance regimes (Duveneck et al., 2017; Hansen et al., 2001; Kruhlov et al., 2018). As different pathways of forest development can have strong implications for biodiversity and the provisioning of ecosystem services (Hilmers et al., 2018; Thom & Keeton, 2019) it is crucial to understand how forests might change in the future. Yet, the variation in climate change projections (Kalliokoski et al., 2018) makes future forest development highly uncertain. Warmer climate could, for instance, facilitate tree regeneration and growth in areas where trees have been cold-limited in the past (Lenoir et al., 2008). Warming in combination with drier conditions could, however, also limit tree regeneration because of increasing drought stress (Rammer et al., 2021; Vittoz et al., 2008). Climate also strongly alters tree mortality, with growing evidence that forest disturbance activity (e.g., driven by wind, bark beetles, and their interactions) will increase under future climate change (Millar & Stephenson, 2015; Seidl et al., 2017). As a consequence of the multitude of climate-sensitive processes, simulation studies suggest that forests will change profoundly and nonlinearly in the future.

Anticipating the future response of forest ecosystems to climate change is challenging because ecosystem processes interact to amplify or dampen climate sensitivity. The impact of changing disturbances on forest dynamics, for instance, can vary widely. More large, high severity disturbances may cause a homogenization of forests, amplifying future climate impacts and potentially leading to forest loss (Turner et al., 2021). Increases in the frequency of low to moderate severity disturbances (e.g., small-scale windthrow, or insect outbreaks in mixed forests), however, may enhance structural and compositional complexity (Čada et al., 2016; Halpin & Lorimer, 2016) and dampen the effect of future climate-mediated disturbances (Sommerfeld et al., 2021). More broadly, a development towards structurally and functionally complex forests (e.g., found in old-growth forests) is expected to buffer the effects of climate change compared with younger and/ or less complex forests (Bauhus et al., 2009; Thom et al., 2019). However, the net effect of the multiple, counteracting processes affected by climate remains widely uncertain.

Potential responses to climate change may be non-linear; thus, small differences in climate projections could potentially have large impacts on ecosystem dynamics. Conversely, ecosystem dynamics is driven by a number of complex feedbacks, which could dampen climate sensitivity. While there is unequivocal evidence that the earth will warm in the coming decades, the magnitude and rate of change remains uncertain (Giorgi, 2019; IPCC, 2021). Climate models have improved considerably over the past decades, reducing the uncertainties in future climate projections. Yet, downscaling the effects of global climate change, for instance, to mountain areas with highly complex topography, remains challenging (Giorgi, 2019; IPCC, 2021). Moreover, future anthropogenic emissions of greenhouse gases will depend on the decisions of policy makers and individuals (Hayhoe et al., 2017). As a consequence, future climate trajectories remain uncertain, with a 21st century warming between 0.3°C and 4.8°C projected at the global scale relative to 1986 – 2005 (Hayhoe et al., 2017). While a large variety of potential future climate trajectories is deemed plausible by the climate community, studies on future forest dynamics typically investigate only a few of these trajectories (Kruhlov et al., 2018; Manusch et al., 2014; Thom et al., 2017a). Yet, small differences in climate scenarios (e.g., different timing of drought events, different change rates between individual variables such as temperature and precipitation) could translate into large differences in ecological responses.

Here we investigate how future climate uncertainty translates into variation in future forest trajectories by studying a comprehensive ensemble of 22 downscaled climate change projections. We focus our analysis on future forest development in Berchtesgaden National Park (BGNP), situated in the German Alps. For this landscape previous analyses document a climate-driven acceleration of forest dynamics over past decades, with forests becoming structurally more complex, denser, and species rich, while the proportion of conifers has decreased (Thom & Seidl, 2021). The future of the forests of BGNP remains uncertain, as it is unclear whether the development observed in the past will continue, or whether dampening feedbacks will eventually stabilize forest structure and composition, decoupling it from climate change. Using a process-based landscape simulation model our specific objectives were (i) to analyze whether the past acceleration of forest dynamics is likely to continue in the future, (ii) to assess how uncertainty in future climate translates into variation in future forests, and (iii) to determine the main drivers of future forest dynamics. We hypothesized that forest dynamics continues to accelerate at BGNP, as climate change was found to be a major driver of past forest change (Thom & Seidl, 2021), and climate is likely to continue changing in the future. Besides direct effects of climate, we hypothesized that increases in natural disturbance are particularly important drivers of future forest change (Brice et al., 2020). Lastly, we expected the future variability in forests to be greater than the future variability in climate, with amplifying feedbacks between ecosystem processes outweighing dampening feedbacks on climate sensitivity.

2 | MATERIALS AND METHODS

2.1 | Study area

BGNP is located in the northern front range of the Alps in Germany (Figure 1). With an elevation range spanning from 603 m asl. (lake Königssee) to 2713 m asl. (Mt. Watzmann), the 20,808 ha BGNP landscape is characterized by highly complex topography. Across the landscape, Norway spruce (*Picea abies* [Karst.]) is the most abundant tree species. It occurs in mixed forests with silver fir (*Abies alba* [Mill.]) and European beech (*Fagus sylvatica* [L.]) in the montane elevation belt and naturally dominates in the subalpine vegetation belt, where it co-occurs with European Larch (*Larix decidua* [Mill.]) and Swiss stone pine (*Pinus cembra* [L.]). The upper subalpine vegetation

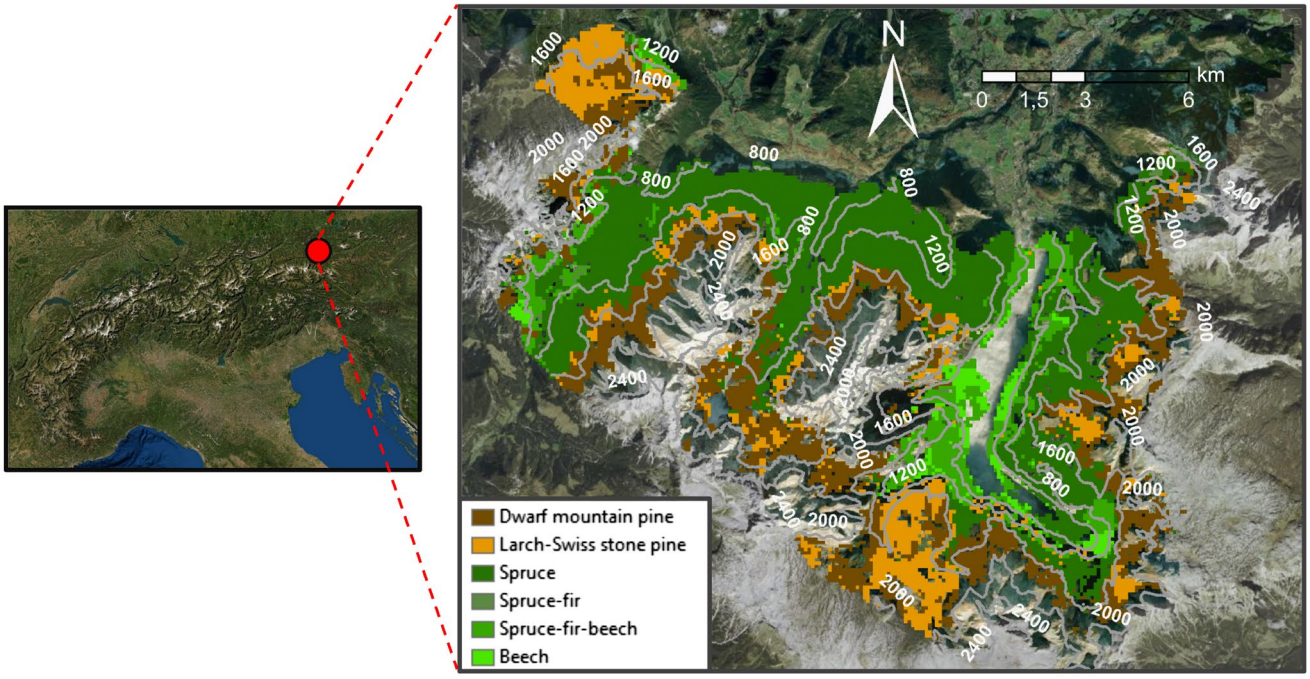

FIGURE 1 Current distribution of forest types across Berchtesgaden National Park (see section 1.2 in Supporting Information for details). The red dot shows the location of the landscape in the European Alps

belt is limited by a timber line at approximately 1,700 m asl., with the timber line ecotone characterized by a strong dominance of dwarf mountain pine (*Pinus mugo ssp. mugo* [Turra]). The study area has a long history of intensive forest management, focusing on timber production and fostering Norway spruce as the locally most important timber species. Hence, Norway spruce currently dominants large parts of the study area, including lower elevations that would be naturally dominated by European beech or silver fir (Figure 1). In 1978 the landscape became a national park under the IUCN category II. Management ceased entirely on 75% of the forest area, while the remaining forests are subject to restoration management, mainly enrichment plantings, to restore the potential natural vegetation (PNV) composition. Furthermore, sanitation logging is performed in a 500 m buffer strip along the national park border to prevent bark beetle dispersal into neighboring commercial forests.

2.2 | Simulation model

We used the individual-based forest landscape and disturbance model (iLand) to investigate future forest trajectories at BGNP. iLand is a high-resolution process-based model, designed to dynamically simulate feedbacks between climate (change), tree vegetation, and disturbance regimes over time (Seidl et al., 2012a, 2012b). The main entities of the simulation are individual trees, and the complete tree population on the landscape (i.e., frequently consisting of millions of trees) is modelled spatially explicitly. Simulated forest dynamics emerges from the interactions between trees and their environmental conditions. iLand incorporates processes in a hierarchical multiscale approach, that is, iLand considers processes at the individual tree, stand, and landscape level as well as interactions across these scales. Resource use efficiency is determined by temperature, radiation, soil water availability as well as vapor pressure deficit (VPD), calculated at daily time steps. Furthermore, atmospheric carbon dioxide (CO_2) concentration (annual resolution) and soil nutrient availability (time-invariant) are considered. Mortality of individual trees is determined by carbon starvation of individual trees, e.g., induced by stress from limited water, nutrient or light availability. Moreover, a wide range of disturbance agents can be simulated via process-based disturbance modules. Here we employed the modules for wind (Seidl et al., 2014) and bark beetles (Seidl & Rammer, 2017), which are currently the most important disturbance agents in Central Europe (Thom et al., 2013). Regeneration in iLand depends on the local availability of mature trees for seed production and dispersal via species-specific seed dispersal kernels. Establishment success is constrained by environmental filters (e.g., light availability, temperature, frost, drought) driving regeneration growth as well as density-dependent and density-independent mortality (Seidl et al., 2012a). The functional traits determining growth, survival and regeneration of trees in iLand are characterized via 61 species-specific model parameters, enabling the simulation of species-specific responses to environmental changes. iLand was previously parameterized, evaluated and applied for Central European ecosystems in general, and specifically for forests in the Northern Alps (Albrich et al., 2018, 2020; Thom et al., 2017b). Hence, we used model parameters as in these previous studies. A species of importance at BGNP, which was not yet parameterized in iLand is dwarf mountain pine, a shrub species often dominating vegetation at the timber

line ecotone (Wild & Winkler, 2008). To include this species in our simulations, we compiled species parameters for dwarf mountain pine from the literature and the TRY database (Kattge et al., 2020) and evaluated the resultant model performance (see section 1.2 in Supporting Information for parameterization details, and section 2.4 for model evaluation). iLand software and code are available under an open source license at http://iland-model.org.

2.3 | Model initialization

We initialized our simulations with the latest available information on vegetation and soils for BGNP. We derived information on soil depth and soil texture from forest site mapping data. We estimated plant available nitrogen and initial soil carbon stocks based on regional data for the Eastern Alps (Seidl et al., 2009). Simulations were run for the 8645 ha of BGNP covered with forest, determined from aerial photographs at 10 m spatial resolution. We merged spatial information from forest site mapping and forest type maps (indicating the PNV obtained from vegetation surveys) to derive 711 stand polygons (median size: 5.5 ha). We then used data from 3559 forest inventory plots (500 m^2), recorded in the period 2010–2012 (average 2011) on a regular grid of 100 m × 200 m, to derive information about species composition and structure for each stand polygon (Thom & Seidl, 2021). Specifically, we extracted species-specific information about diameter at breast height (DBH) and tree height distributions, stand density, and sapling numbers as well as standing and downed deadwood from inventory data to initialize current tree populations and aboveground carbon pools in iLand. To determine tree positions and consider canopy gaps appropriately in the initialized vegetation, we used airborne LiDAR data from 2009. To dynamically update the vegetation until the year 2020 (i.e., the initial year of our investigation) we simulated vegetation development from 2011 (i.e., the year represented by the available inventory data) to 2020, forcing disturbances as detected from remote sensing. When we initialized our simulations, disturbance data from remote sensing were available for the years until 2016 only (Senf et al., 2017); however, no major disturbance event occurred after this year (Senf & Seidl, 2021b). The thus derived state of the vegetation, deadwood and carbon pools in the year 2020 were used as the starting point for all simulations presented in this study. For more information on data and initialization procedures see Supporting Information S1.

2.4 | Model evaluation

iLand was previously evaluated in Central European forest ecosystems (Albrich et al., 2018, 2020; Honkaniemi et al., 2020; Silva Pedro et al., 2015; Thom et al., 2017b), yet this is the first application of the model at BGNP. Hence, we evaluated iLand's ability to reproduce expected forest dynamics at BGNP. We used a pattern-oriented modeling approach (Grimm et al., 2005), focusing on the ability to simulate the productivity of different tree species (as represented by the dominant height reached at a certain tree age), the PNV (an indicator for species interactions and their relative competitive strength), and natural disturbance impacts. In particular, we compared dominant tree heights (95th percentile) from 3452 forest inventory plots spanning a stand age from 50 to 892 years to iLand simulations. Overall, simulated dominant heights matched observations well for the most common tree species at BGNP (see Supporting Information S2). Furthermore, observed differences in dominant height across aspect and elevation were reproduced well by the model (see Supporting Information S2). A PNV estimate derived from local forest-type mapping based on vegetation analyses was compared against the end-point of a 2500-year simulation of natural forest development at BGNP (assuming stable historic climate conditions). PNV simulations were conducted from bare ground and resulted in a strong initial dominance of pioneer species (e.g., European larch and silver birch (*Betula pendula* [Roth]), followed by intermediate species (e.g., Norway spruce), and late seral species (e.g., European beech and silver fir). Both the temporal sequence of succession and the simulated spatial patterns of the PNV corresponded well to the expert assessments recorded in the field (Supporting Information S2). Dwarf mountain pine dominance was restricted to a reasonable elevation range (i.e., >1600 m asl.), being outcompeted by other species in lower elevations. Finally, we tested iLand's wind and bark beetle sub-modules against independent remote sensing data of past disturbance events (Senf et al., 2017). Specifically, we compared dynamically simulated versus observed disturbances for the period 1998–2016. The emergent wind and bark beetle disturbance simulated in iLand matched the observed total area disturbed satisfactorily. For additional information on the model evaluation exercises conducted see Supporting Information S2.

2.5 | Climate data

Obtaining high-resolution climate data as input for forest simulation modeling is a challenge in complex mountainous terrain (Giorgi, 2019; IPCC, 2021). We derived historic climate for BGNP for the period 1980–2009 from regional climate modeling (RCM), applying the Weather Research and Forecasting Model (WRF) at high spatial (5 km) and temporal resolution (1 h) (Warscher et al., 2019). WRF was driven by lateral boundary conditions from the ERA-Interim reanalysis data. As local-scale climate conditions are highly variable in BGNP, it was necessary to further refine RCM simulations (Smiatek & Kunstmann, 2019). Hence, we applied a bias correction based on quantile mapping (Laux et al., 2021) with observational time-series data of 35 meteorological stations (20 automatic and 15 mechanical stations) distributed across the watershed of the river Berchtesgadener Ache (Warscher et al., 2019). The results were then interpolated onto a 100 × 100 m grid corresponding to the spatial resolution at which environmental conditions are represented in iLand. Depending on the variables under consideration, different combinations of interpolation strategies were applied, consisting of elevation-dependent regression and inverse distance weighting.

Solar radiation was additionally corrected for topographic shading and cloud formation. All climate variables were aggregated to diurnal values to match iLand's temporal resolution. The set of climate variables used in iLand were minimum and maximum temperature, precipitation sum, solar radiation, and VPD. See Supporting Information S3 for more information on climate data.

A particular goal of our study was to investigate the variation arising from a broad array of potential future climate trajectories (Figure 2). To represent future climate we used an ensemble of regional climate change projections that were downscaled to 5 km resolution, compiled by the Bayerische Landesamt für Umwelt (LfU) (Zier et al., 2020). The LfU conducted a quality check of all climate change projections, for instance, by comparing regional and global projected patterns and by identifying outliers. In total, we obtained 22 climate change projections until the year 2100 from the LfU ensemble. Of those, seven were from the Representative Concentration Pathway (RCP) RCP 2.6, six were from RCP 4.5, and nine were from RCP 8.5. By calculating an offset for each climate variable relative to the locally refine historic climate data (baseline), we obtained high-resolution climate change projections as drivers for iLand. Comparing the baseline climate period 1980–2009 with the last 20 years of all climate change scenarios (2081–2100), minimum air temperature increased by on average 2.8°C (range: 0.6°C to 6.0°C), maximum air temperature by 2.9°C (range: 0.8°C to 5.7°C), annual precipitation by 50 mm (range: −157 mm to +214 mm), solar radiation decreased by 0.135 Mj m² day^{-1} (range: −0.414 Mj m² day^{-1} to +0.083 Mj m² day^{-1}), and VPD increased by 0.057 kPa (range: −0.012 kPa to +0.171 kPa). In addition, annual CO_2 values for each RCP scenario were obtained from the IIASA RCP database (http://tntcat.iiasa.ac.at/RcpDb). We also analyzed temporal changes in wind speeds (i.e., an important driver variable of wind disturbances in iLand) for the climate scenarios of the LfU ensemble. As we did not detect any trends over time, we assumed a continuation of the historic wind regime throughout the 21st century. For more information on climate change scenarios and data see Supporting Information S4.

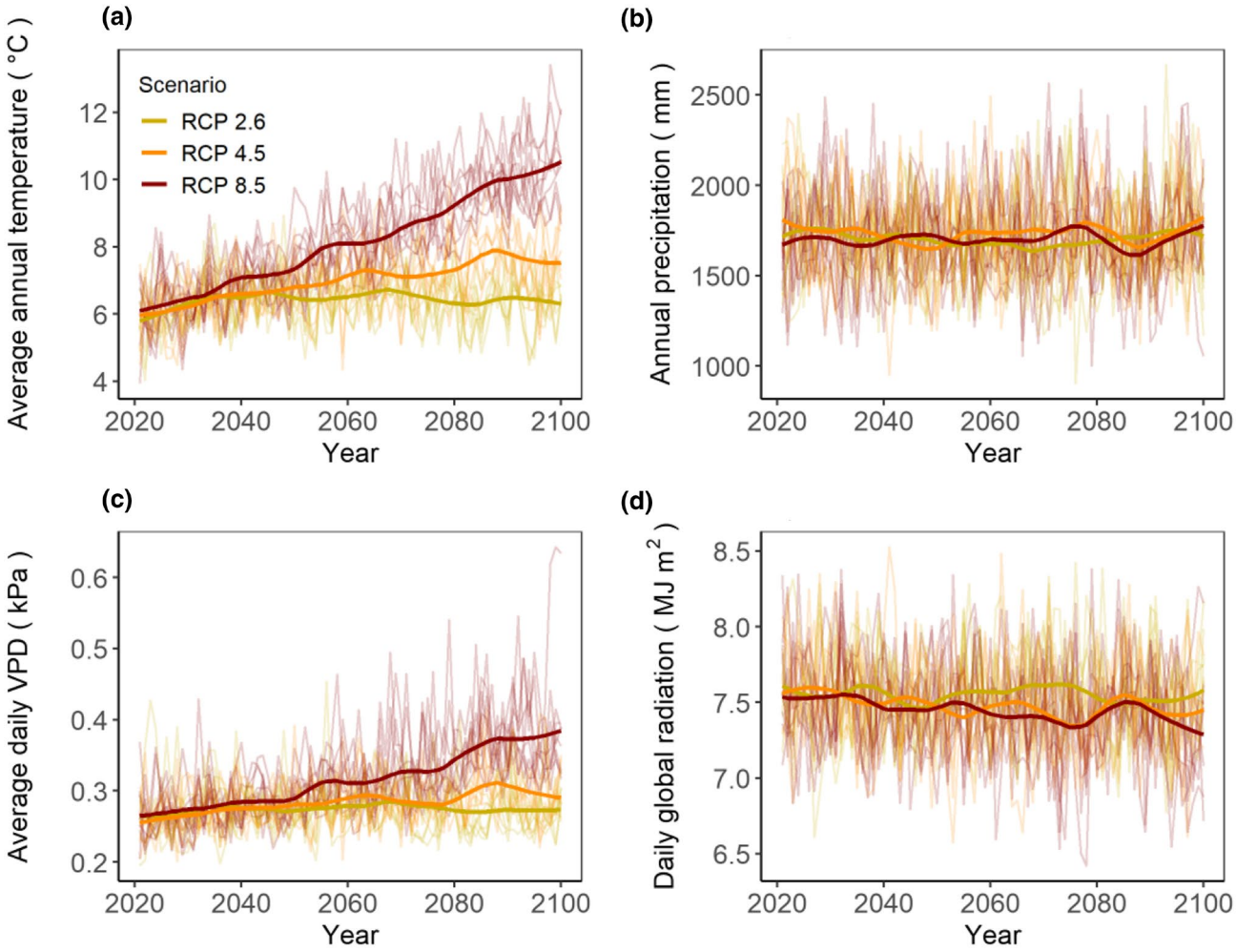

FIGURE 2 Future changes in the climate regime at Berchtesgaden National Park. Presented are 22 individual climate trajectories downscaled to the study area (fine lines) for (a) temperature, (b) precipitation, (c) vapor pressure deficit, and (d) global radiation change. Trend lines for the three RCP scenarios (i.e., RCP 2.6, RCP 4.5, and RCP 8.5) were smoothed by a loess function (bold lines)

2.6 | Simulations and analyses

Starting from the vegetation of BGNP in 2020, we simulated 80 years into the future, replicating each of the 22 climate change projections 20 times. In all simulations, unmanaged forest development was assumed for the entire BGNP landscape. Peak wind speeds were sampled from a Gumbel distribution fit to data from 14 local weather stations, and a different sequence of peak wind speeds was assumed for each of the 20 replicates.

From the simulated iLand output, we analyzed temporal and spatial variation in forest conditions as well as the emergent future forest disturbance regime. Output data were analyzed at a spatial grain of 100 m × 100 m. To investigate our first research question (i.e., whether forest dynamics continues to accelerate), we computed change rates for two indicators of forest structure and composition, respectively. We selected indicators that were found to be representative of past climate-induced acceleration by Thom and Seidl (2021), including DBH variation (i.e., the standard deviation in DBH), stand density (i.e., the number of trees with a height >4 m per hectare), conifer ratio (i.e., the share of conifer basal area on total basal area), and effective species number (ESN, i.e., the exponent of the Shannon Index based on basal area share, representing simulated tree species diversity). First, we computed absolute annual changes as landscape aggregates for each simulation run at ten-year intervals. Then we divided absolute annual changes by the value of the respective variable in 2020 and multiplied by 100 to express change rates relative to the initial state.

To address our second research question (i.e., how future climate uncertainty translates to variation in future forests) we first quantified the differences across scenarios, both in the drivers (climate) and in the responses (vegetation). We furthermore included disturbance (quantified as m^3 of growing stock disturbed by wind and bark beetles) as a process that strongly mediates between climate and vegetation. For this analysis we calculated the median and the median absolute deviation (MAD, i.e., a robust indicator of variation around the median that is insensitive to different sample sizes) for each indicator across climate change scenarios for the years 2080–2100. For the same period and variables, we derived the coefficient of dispersion based on the MAD across all simulation runs (%MAD, i.e., expressed here as percent of the median across all scenarios) (Ospina & Marmolejo-Ramos, 2019). %MAD is a robust indicator for comparing variation across variables that are measured on different scales. In addition, we computed %MAD for the period 2020–2040 to compare variation at the beginning and the end of the simulations. To further elucidate the spatial variation in future forest trajectories we contrasted the two most diverging simulation runs for each forest attribute. In particular, we calculated the difference between those runs at the level of 100 m × 100 m grid cells at the end of the simulation period.

Finally, addressing our third research question (i.e., what are the drivers of future forest dynamics), we analyzed the relationships among vegetation, disturbance, climate and elevation (as an indicator of site conditions) in a structural equation model (SEM). SEMs are increasingly used in ecological research to identify complex, causal relationships (Fan et al., 2016; Grace et al., 2015). One strength of SEMs is their ability to quantify reciprocal effects between variables. This is important in our context because, for example, changes in disturbance activity can alter vegetation structure, which in turn modulates future disturbances (Sommerfeld et al., 2021). We calculated changes in structural and compositional variables as well as in the amount of disturbance occurring within a 10-year period. As an indicator of climate change, we used the difference in temperature of each 10-year period compared with the average of RCP 2.6 projections for the period 2021–2030 (i.e., setting the baseline to the lower end of expected future temperature increase). Other climate variables were excluded from the model, either due to their high correlation with temperature or because of the lack of a temporal trend (Figure 2). We used lagged variables to explain changes of the following 10-year period based on values from the previous period. We randomly sampled 3333 observations at the level of 100 m × 100 m grid cells per RCP scenario across all replicates (i.e., 9999 in total) for the analysis. The data were used to fit a cross-lagged SEM based on a diagonally weighted least squares estimator. The initial SEM considered all potential covariates (i.e., elevation, temperature, DBH variation, stand density, conifer ratio, tree species diversity, and disturbance) for each response variable (i.e., DBH variation, stand density, conifer ratio, tree species diversity, and disturbance). Next, we omitted all non-significant ($\alpha = .05$) covariates and re-fitted the model until only significant variables remained. We evaluated the overall model fit using the chi-square statistic, comparative fit index (CFI), non-normed fit index (NNFI), root mean square error of approximation (RMSEA), and standardized root mean square residual (SRMS) (Bagozzi & Yi, 2012). The Chi-square statistic tests the null hypothesis that the predicted model and the observed data are equal. CFI indicates the relative non-centrality between a fitted model and a null model. NNFI is an indicator for model parsimony. RMSEA is the average amount of model misfit per degree of freedom, and SRMS is the square root of the average squared residual. A good model fit is obtained if the *p*-value of the Chi-square test is >0.05, CFI and NNFI ≥0.95, RMSEA ≤0.06, and SRMR ≤0.08 (Bagozzi & Yi, 2012).

All analysis were performed in the R language and environment for statistical computing (R Development Core Team, 2021). In particular, we used the packages tidyverse (Wickham, 2019a) and rgdal (Bivand et al., 2018) for data organization, lavaan (Rosseel et al., 2021) for SEMs, as well as ggplot2 (Wickham, 2019b), cowplot (Wilke, 2020), and raster (Hijmans et al., 2021) for visualizations.

3 | RESULTS

3.1 | Trajectories of future forest change

The trends in forest dynamics observed in the past also continued for the coming decades in our simulations. Until approximately mid-century BGNP continued to develop towards denser, structurally

more complex and more species rich forests (Figure 3, Figures S39 and S40). Change rates of forest structure were an order of magnitude higher than change rates in forest composition. In the first decades of the simulation, the divergence in trajectories of forest development between climate scenarios was small. Variation in forest attributes largely resulted from the variation between replicates, representing the stochastic nature of the natural disturbance regime (Figure 4). Change rates in DBH variation, stem density and tree species diversity continued to accelerate until 2040. In contrast, the loss of conifers decreased over time and leveled off around mid-century.

In the second half of the 21st century trajectories between forest attributes varied strongly, and the underlying climate scenario had a distinct influence on simulated forest development. While the share of conifers stabilized in the second half of the century in RCP 2.6 and RCP 4.5 scenarios, a strong and accelerating loss of

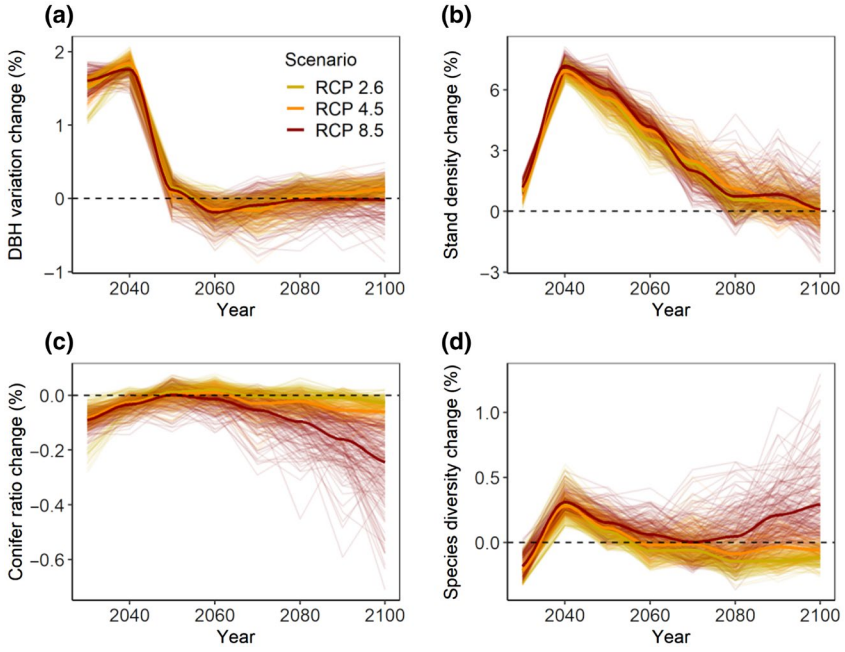

FIGURE 3 Future forest change at Berchtesgaden National Park. Presented are change rates in percent annual change relative to the state of the forest in 2020 for (a) diameter at breast height (DBH) variation (expressed as the SD of the DBH), (b) stand density, (c) conifer ratio and (d) tree species diversity (effective species number). Trend lines for the three RCP scenarios investigated (i.e., RCP 2.6, RCP 4.5, and RCP 8.5) were smoothed by a loess function (bold lines). Individual simulation trajectories are shown as fine lines at decadal time step. Note that x-axes always denote the last year of the respective 10-year change period (e.g., the value for 2030 represents the change in the simulation period 2021–2030). For absolute changes see Figure S40

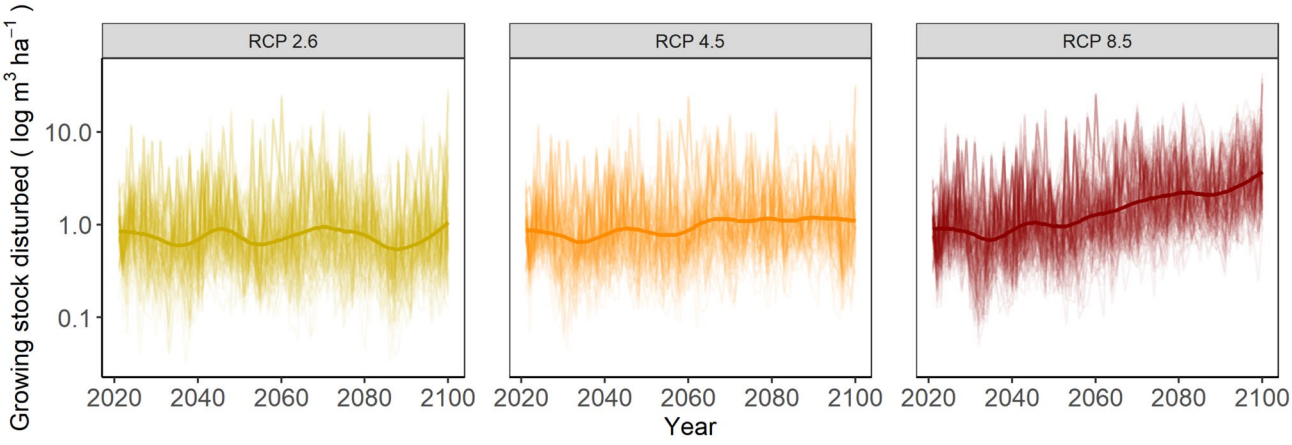

FIGURE 4 Trajectories of future forest disturbance at Berchtesgaden National Park by RCP scenario. Presented is the annual growing stock disturbed by wind and bark beetles on average per ha across the landscape. Trend lines (bold) for the three RCP scenarios investigated (i.e., RCP 2.6, RCP 4.5, and RCP 8.5) were smoothed by means of a loess function. Individual simulation runs are shown as fine lines. Note that the y-axis is log-transformed.

conifers occurred in RCP 8.5 projections. DBH variation stabilized after 2050 in all climate change scenarios. Change rates of stand density decreased in the second half of the 21st century, and stabilized at the end of the simulation period with no clear differences among climate change scenarios. Changes in tree species diversity stabilized at slightly negative rates in RCP 2.6 and RCP 4.5 scenarios after 2060. In contrast, tree species diversity continued to increase in RCP 8.5 scenarios throughout the second half of the 21st century.

3.2 | Uncertainty in future forest development

The representative concentration pathways represent a considerable range of uncertainty in terms of the climate in the last two decades of the 21st century (Table 1). The divergence in the median of annual average temperature between RCP 8.5 and RCP 2.6 projections was 3.4°C. Moreover, MAD increased with increasing atmospheric greenhouse gas concentration, signifying greater variability of temperature in high emission scenarios. The annual precipitation sum was, on average, 45 mm lower in RCP 8.5 compared with RCP 2.6. However, variation in precipitation was highest for RCP 2.6. We also observed considerable differences in VPD, being 0.09 kPa higher in RCP 8.5 than in RCP 2.6 projections with slightly higher variation in RCP 8.5. Global radiation was 0.1 MJ m^2 day^{-1} lower in RCP 8.5 compared with RCP 2.6 projections with comparable scenario uncertainty.

The uncertainty in climate was strongly reflected in the projected future disturbance regimes. Simulated disturbances differed strongly between climate change scenarios in 2080 – 2100 (Table 1, Figure S41). Compared with RCP 2.6, the amount of growing stock disturbed was almost doubled in RCP 4.5, and was four times higher in RCP 8.5 simulations. As with temperature variation, the uncertainty within a scenario family increased greatly with atmospheric greenhouse gas concentration. In RCP 8.5, MAD of growing stock disturbed was three times higher than in RCP 2.6. With increased climate forcing, also the agent dominating the disturbance regime changed, with bark beetle outbreaks increasingly dominating the disturbance regime (Figure S41). On average over all RCP 8.5 projections, bark beetle disturbance exceeded wind disturbances by a factor of four in the last two decades of the simulation. Regardless of scenario most disturbances occurred at low to mid elevations (Figures S42–S46). On average over all runs and years, the growing stock disturbed below 1400 m asl. (i.e., indicating the approximate location of the ecotone between the montane and subalpine elevation belts at BGNP) was 0.6 m^3 ha^{-1} yr^{-1} (52.1%) higher than above 1400 m asl. These elevational differences in disturbance were mostly driven by favorable conditions for bark beetle development at lower elevations (Figure S45).

The future uncertainty in climate and disturbance was only partly reflected in the simulated variation in forest structure and composition at the end of the 21st century (Table 1). Medians of DBH variation were similar across all scenarios, with a slight reduction in RCP 8.5 compared with other RCP scenarios. Median stand density was 66 trees and ESN was 0.2 species per ha higher in RCP 8.5 compared with RCP 2.6 projections, while the median conifer ratio was 2.8 percentage points lower. Differences between simulation runs were spatially heterogenous (Figure S47) and were generally higher at low elevations. For instance, below 1400 m asl. the divergences in scenario outcomes for DBH variation, stand density, conifer ratio, and tree species diversity were 2.9, 2.8, 10.1, and 2.7 times higher than above 1400 m asl.

TABLE 1 Climate, disturbance, forest structure, and composition at BGNP

				Climate change scenario 2080–2100		
Group	Variable	Unit	All scenarios 2020–2040	RCP 2.6	RCP 4.5	RCP 8.5
Climate	Temperature average	°C	6.3 (0.8)	6.5 (0.7)	7.7 (0.9)	9.9 (1.0)
	Precipitation sum	mm yr^{-1}	1700 (244)	1712 (279)	1720 (243)	1667 (211)
	Vapor pressure deficit	kPa	0.26 (0.03)	0.27 (0.03)	0.29 (0.03)	0.36 (0.04)
	Radiation	MJ m^2	7.5 (0.3)	7.5 (0.3)	7.5 (0.3)	7.4 (0.3)
Disturbance	Growing stock disturbed by wind and bark beetles	m^3 $ha^{-1}yr^{-1}$	0.7 (0.5)	0.6 (0.5)	1.1 (0.7)	2.4 (1.5)
Forest structure and composition	Diameter at breast height variation	cm	8.6 (1.8)	9.8 (0.4)	9.8 (0.3)	9.7 (0.4)
	Stand density	n ha^{-1}	436 (66)	1183 (48)	1236 (37)	1249 (50)
	Conifer ratio	%	87.8 (0.7)	87.6 (1.0)	86.6 (0.7)	84.8 (2.1)
	Tree species diversity (effective species number)	n ha^{-1}	1.9 (0.0)	1.8 (0.1)	1.9 (0.0)	2.0 (0.1)

Note: Presented are medians and the median absolute deviation (i.e., MAD, the absolute deviation from the median) across all replicates (in parentheses) of each climate scenario for the years 2080–2100. Moreover, medians and MADs are shown for the first two decades of the simulation (2020–2040) across all replicates and climate change scenarios.

Abbreviation: ESN, effective species number.

Future climate uncertainty resulted in a disproportionally greater uncertainty of future disturbances. Based on %MAD in the last two decades of the simulation, the scenario variation in simulated natural disturbance was 3.1, 6.1, 4.5, and 21.3 times greater than the variation in temperature, precipitation, VPD, and global radiation, respectively (Table 2). In contrast, the variation in forest structure and composition was considerably lower than the variation in climate, with %MAD being up to 14.8 times smaller compared with climate variables. Only variability in stand density and ESN exceeded variation in global radiation by a factor of 1.1 and 1.2, respectively. The variability of most variables increased over time. Comparing the period 2020–2040 with the period 2080–2100, %MAD of disturbance increased the most (+18.4% points), followed by temperature (+14.5% points), VPD (+7.3% points), ESN (+3.6% points), and conifer ratio (+1.0% points). In contrast, the variability in DBH variation (−16.5% points), stand density (−10.5% points), and radiation (−0.2% points) decreased over time.

3.3 | Drivers of forest dynamics

We identified both direct and indirect impacts of climate change on forest structure and composition (Figure 5; Table S1). Temperature was a direct driver of both structural and compositional change. In particular, temperature had a negative effect on DBH variation, stand density, and the share of conifers on the landscape. Furthermore, temperature was the strongest driver of natural disturbance, fueling disturbance activity. Disturbance, in turn, was the most influential driver of all forest attributes considered, resulting in indirect effects of climate change on these variables. Overall, the indirect impacts of climate change (i.e., mediated by disturbance change) on forest structure and composition were of higher importance than the direct impacts. We also found complex interactions among forest change and disturbance. While disturbance had a strong effect on all indicators of forest dynamics, the directionality varied. Stand density and tree species diversity increased with disturbance, whereas DBH variation and conifer ratio decreased. Effects of DBH variation, stand density, and conifer ratio on disturbance were of lower magnitude and of reversed sign. Tree species diversity did not have a significant impact on disturbance. Moreover, disturbance impacts were positively autocorrelated, indicating that past disturbances increased future disturbances (Table S1).

Variables of forest structure and composition also influenced each other, reflecting processes of forest dynamics, such as competition and succession (Table S1). The most important covariate was stand density which was strongly positively autocorrelated.

TABLE 2 Coefficient of dispersion across all simulation runs for the years 2020–2040 and 2080–2100 based on the median absolute deviation (%MAD). %MAD is the relative dispersion (in %) from the median (see Table 1)

Group	Variable	%MAD 2020–2040	%MAD 2080–2100
Climate	Temperature average	12.2	26.7
	Precipitation sum	14.3	14.3
	Vapor pressure deficit	11.5	18.8
	Radiation	4.2	4.0
Disturbance	Growing stock disturbed by wind and bark beetles	67.0	85.4
Forest structure and composition	Diameter at breast height variation	20.4	3.9
	Stand density	15.0	4.5
	Conifer ratio	0.8	1.8
	Tree species diversity (ESN)	1.1	4.7

Abbreviation: ESN, effective species number.

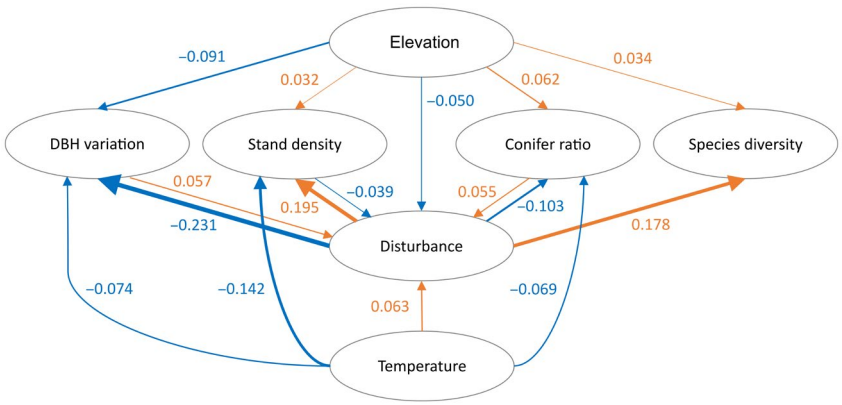

FIGURE 5 Cross-lagged path model on the drivers of future forest and disturbance dynamics. Cross-lags imply 10-year time lags in all relationships. The direction of influence is indicated by arrows. Presented are significant ($\alpha = .05$) standardized regression coefficients, with line width scaled by coefficient. For additional interactions among vegetation variables see Table S1

Furthermore, an increase in stand density was positively correlated with the share of conifers and negatively correlated with variation in DBH. Increasing DBH variation increased stand density and decreased species diversity. Moreover, an increasing proportion of conifers had a negative effect on stand density and tree species diversity. Lastly, tree species diversity increased DBH variation as well as stand density. All other interactions among forest indicators were not significant and were thus omitted from the final model. The SEM performed well for all goodness-of-fit indicators. The *p*-value of the Chi-square test was 0.117, and CFI, NNFI RMSEA, and SRMR were 1.000, 0.999, 0.008, and 0.004, respectively.

4 | DISCUSSION

4.1 | Future forest dynamics

Here we simulated the future dynamics of the mountain forests at BGNP. We found that the acceleration of forest dynamics observed in forest inventories since the mid-1980s (Thom & Seidl, 2021) is likely to continue for the coming decades, with increasing gains in stem density, structural complexity, and tree species diversity. In line with past observations our simulations suggest that compositional changes are an order of magnitude slower than structural changes. Overall, the finding of a continued increase in the tempo of forest change confirms our first hypothesis of continued acceleration of forest dynamics. Yet, the main driver of this acceleration appears not to be climate change, as forest trajectories differed only moderately between climate scenarios until 2050. This suggests that the forest trajectories of the coming decades are to a considerable degree determined by the current state of the vegetation, which is partly the result of past land-use. Before the landscape became a national park in 1978, homogenous Norway spruce and European larch plantations were promoted (Zierl, 2009) that are now transitioning towards more structurally and compositionally diverse forests (Thom & Seidl, 2021). This is in line with the development expected also for other landscapes of the Northern Alps, e.g., Kalkalpen National Park, where Thom et al., (2018) found that past land-use has a stronger impact on the 21st century carbon exchange than future climate change.

For the second half of the 21st century simulated trends in forest dynamics change considerably compared with the first half. For forest structure, change rates decreased and gravitated towards zero, indicating the emergence of a dynamic equilibrium of forest structures on the landscape. Although climate had little influence on this structural equilibrium, it did considerably influence the development of forest composition in the second half of the 21st century. Composition also stabilized at low change rates in RCP 2.6 and RCP 4.5 projections but showed accelerating change under RCP 8.5 simulations. The currently observed higher change rates in structure versus composition (Thom & Seidl, 2021) thus inversed towards the end of the simulation under RCP 8.5 scenarios. This suggests a non-linear response of forest composition to climate at BGNP. A previous study in the Inner Alps suggested that such a non-linear shift in vegetation composition might occur beyond warming levels of 2°C compared with historical climate (Albrich et al., 2020). Another study from the Inner Alps found that even an increase of 2°C might induce significant changes, with negative consequences for ecosystem services provisioning (Elkin et al., 2013). For BGNP, situated in the Northern Alps, it seems that such a turning point in future compositional trajectories might occur at somewhat higher warming levels (i.e., warming beyond RCP 4.5, that corresponds to a warming of >2.2°C compared with the period 1980–2009). This highlights that it is important to keep future emissions well below the levels assumed under RCP 8.5 to avoid considerable forest reorganization in the Northern Alps. The differences to previous findings from the Inner Alps might be explained by the considerably higher levels of precipitation in the Northern Alps (> +700 mm yr^{-1}), which could reduce climate sensitivity. However, further analyses are needed to better understand the causes and consequences of non-linear forest responses to climate change.

In line with our second hypotheses, we found natural disturbances to be a strong driver of future forest dynamics (Figure 5). Disturbances acted as the catalyst of climate impacts on forest dynamics, with indirect effects of climate change (via natural disturbances) being a stronger driver of both compositional and structural change than direct climate effects. Although disturbance has an immediate effect on tree species composition and structure, direct climate change effects on other processes (e.g., tree growth and establishment) only impact forest dynamics over longer time scales (Walker et al., 2012). The release of canopy space due to disturbance initiates the reorganization of forest vegetation, and thus accelerates adaptive cycles (Holling, 2001). Hence, disturbances can contribute to the autonomous adaptation of forest ecosystems to climate change (Dietz et al., 2020). While we here found dampening feedbacks between the emerging vegetation state (e.g., changes in the proportion of conifers) and the future disturbance regime (see also Sommerfeld et al., 2021; Thom et al., 2017a), disturbances still increased over the 21st century, particularly in RCP 8.5 scenarios. Bark beetles play a crucial role in future disturbance change (see also Temperli et al., 2013a). Strong warming could override past topographic buffers on bark beetle spread (Senf & Seidl, 2018) and result in large-scale disturbances particularly in low-elevation areas of BGNP. Future work should thus consider changes in the disturbance regime explicitly, given that indirect, disturbance-mediated impacts of climate change can be even more important than direct climate change effects.

4.2 | Scenario uncertainty

Our study is among the first to study a complete ensemble of climate change projections (n=22) by means of forest landscape simulation modeling (see also Snell et al., 2018). Addressing scenario uncertainty in simulation modeling can improve our understanding of future patterns in the trajectories of changes (Kalliokoski et al., 2018;

Petr et al., 2019). It furthermore allows the identification of potential non-linearities, such as the, on average, considerably different responses between RCP 8.5 scenarios and the other RCP scenarios regarding late century compositional changes. As expected, the uncertainty in simulated forest structure and composition increased over time and with increasing levels of atmospheric greenhouse gas concentration (Tables 1 and 2, Figure 3). Our findings suggest that short- to mid-term projections of landscape trajectories might be robust, as short-term forest dynamics is strongly driven by legacies, and climate projections only diverge considerably in the second half of the 21st century (see also Duveneck et al., 2017; Huber et al., 2021; Manusch et al., 2014). However, due to the stochastic nature of disturbances (Figure 4), ecosystems might embark on very different pathways locally, making accurate stand-level predictions difficult. As a result of elevated disturbance activity and increased variability, local forest dynamics becomes considerably more uncertain in an RCP 8.5 future (Tables 1 and 2, Figure 3).

Overall, we found that climate uncertainty translates nonlinearly to uncertainties in future forest trajectories. Future forest disturbance trajectories varied considerably more strongly than future climate trajectories (Table 2), suggesting that disturbances are particularly climate-sensitive processes in forest ecosystems (Forzieri et al., 2021; Marini et al., 2017). This is the result of concomitant increases in predisposing factors (such as warmer temperatures supporting more generations and higher activity of bark beetles, Wermelinger, 2004) and inciting factors (e.g., more frequent drought events reducing defense mechanisms against bark beetles, Netherer et al., 2015) of natural disturbances under climate change (Thom et al., 2013). Nonetheless, the variables of forest structure and composition investigated here had considerably lower levels of variation compared with climate, rejecting our third hypothesis. This is likely the result of dampening feedbacks within forest ecosystems, such as competition favoring shade-tolerant species and leading to density-dependent mortality (Franklin et al., 2002) or founder effects and local seed dispersal favoring self-replacement of trees (Grime, 1998). While disturbances have affected on average less than 1% of Europe's forest area per year (Senf & Seidl, 2021a), these self-regulating processes occur constantly throughout the forest landscape and modulate the climate responses of forest structure and composition.

4.3 | Caveats and consequences

A number of caveats need to be considered when interpreting our findings. First, we here rely on simulating modeling as one of the few scientific approaches available to study the impacts of potential future climate scenarios at the landscape scale. Consequently, our findings are contingent on the model being able to reproduce forest dynamics in our study system. In this regard, we conducted a suite of model evaluation exercises following a pattern-oriented modeling approach (Grimm et al., 2005), finding good agreement of simulations with expected patterns (see Supporting Information S2). Given the importance of legacy effects, a second crucial component in landscape modeling is the initialization of the forest vegetation (Temperli et al., 2013b). Here, we combined multiple sources of locally available data to faithfully reproduce the past legacies represented in the current vegetation at BGNP (Zierl, 2009). Nonetheless, we cannot fully rule out that the accelerating change in the first decades of the simulation is partly also an artifact of landscape initialization. However, we neither observed exceptionally high disturbance rates (Figure 4) nor a strong decrease in basal area in the first years of the simulation (Figure S39). As our simulated change rates also match observed change rates well (Thom & Seidl, 2021), we conclude that our initialization approach resulted in a robust starting point for scenario analysis. A further caveat of scenario analyses necessarily lies in the assumptions made in the scenarios. We here investigated a high number of different climate scenarios ($n = 22$) and did not prune the scenario ensemble based on *a priori* assumptions. However, extreme climatic events, such as the European drought of 2018 (Büntgen et al., 2021; Buras et al., 2020), which can be pivotal for future forest trajectories (Allen & Breshears, 1998) might still not be captured well in the available climate scenarios. While we considered the effects of wind, bark beetles, and drought as well as their interactions on forest dynamics in this study, we acknowledge that other disturbance agents will likely gain importance in Central Europe in the future. For instance, increasing fire activity or introduced pests and diseases might strongly alter forest structure and composition (Needham et al., 2016; Turner et al., 2021). As a result, we may underestimate tree mortality and its impact on forest dynamics in our study. However, climate change might also dampen some disturbance agents, such as ice and snow (Seidl et al., 2017). In addition, our study did not cover lowland forests, which might have a substantially different disturbance regime. Further investigations are needed to reduce the uncertainty of future disturbance regime projections. We furthermore disregarded the role of management in our analysis and simulated natural forest development without interference from humans. As restoration efforts in the management zone of BGNP (25% of the total park area) include enrichment planting with tree species such as European beech and silver fir that are better adapted to future climate conditions compared with Norway spruce, the 21st century tree species change might occur faster than in our simulations.

Our results have important consequences in the context of conservation biology as well as forest policy and management. An acceleration of compositional changes in forest ecosystems under severe climate change might challenge conservation efforts in the Alps (Dawson et al., 2011). As climate continues to change, forests and forest-dwelling species will have to migrate (Vittoz et al., 2013). Yet, the migration speed of tree species is limited. For instance, late successional European tree species migrate at rates of, on average, 15 m yr^{-1} in response to climate change (Meier et al., 2012). Subalpine forests are limited in their migration potential as edaphic conditions restrict their potential to move upwards in elevation (Henne et al., 2011). Changing climate conditions might thus increasingly pressure high-elevation forests in the future, if greenhouse

gas emissions remain high (Clavel et al., 2011). Moreover, differences between forest dwelling species in their ability to migrate (Bässler et al., 2013) can lead to novel species interactions, which might negatively affect biodiversity as well as ecosystem processes such as herbivory, pollination, or seed dispersal (Descombes et al., 2020). In the context of forest policy and management, at least two important conclusions can be drawn from our results: First, as projections of future forest development gain importance, for instance, in the context of global climate policy, it is crucial to consider scenario uncertainty explicitly. We here show that scenario uncertainty is particularly high in projections of future forest disturbance regimes, which—in turn—can have important implications in the context of climate change mitigation efforts (Bradford et al., 2013; Pugh et al., 2019). Second, considering only a small number of scenarios can mask potential non-linearities and turning points, such as the shift in compositional trajectories in RCP 8.5 scenarios documented here. The assessment and communication of scenario uncertainty is, thus, pivotal for the elaboration of robust policy and management recommendations (Petr et al., 2019). Our results, however, also indicate that strong dampening feedbacks exist that make future forest structure and composition considerably less variable than climate change scenarios. Although the currently observed acceleration of forest dynamics will continue in the coming decades, a downregulation in the second half of the century is likely. The importance of dampening feedbacks for robust future forest projections highlights the need for process-based models that explicitly consider both biogeochemical as well as demographic processes and their interactions.

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AUTHOR CONTRIBUTIONS

DT and RS conceptualized the study. RS and WR developed the iLand model. PL, GS, and HK applied the WRF model. DT and WR processed climate change data. DT curated all other data, conducted the analysis, visualized the results, and wrote the first draft of the manuscript. All authors commented and edited the manuscript.

DATA AVAILABILITY STATEMENT

The data supporting the findings of this study can be retrieved from https://www.datadryad.org/ at http://doi.org/10.5061/dryad.7wm37pvvw. Outputs from simulations are available from the corresponding author upon reasonable request.

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