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RESEARCH ARTICLE

Climate change accelerates ecosystem restoration in the mountain forests of Central Europe

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Abstract

1. Restoring degraded forest ecosystems is an important element in the ongoing challenge to sustain the integrity and functioning of the biosphere. However, the evaluation of restoration success is hampered by long lead times of management measures in forests. Moreover, forest change is accelerating also in the absence of management because of ongoing climate change. Yet, because a counterfactual is frequently missing, it remains unclear whether restoration measures are aided or impeded by climate change.
2. Here, we analysed the pace and success of forest restoration under climate change, combining field data and simulation modelling. We focused on the management zone of Berchtesgaden National Park (BGNP), Germany, where restoration aims to restore homogeneous Norway spruce (*Picea abies*) forests to structurally diverse mixed mountain forests. We evaluated three alternative restoration strategies: Two active strategies focused on planting the currently underrepresented silver fir (*Abies alba*) and European beech (*Fagus sylvatica*) but differing in the creation of gap-cuts, and a third passive restoration strategy without interventions. Strategies were simulated with the forest landscape model iLand from 2020 to 2100 under different climate scenarios (historic, RCP 2.6, 4.5, and 8.5).
3. The forests of BGNP developed into structurally diverse and mixed forests under all evaluated management strategies, and differences between active and passive restoration were generally small. While restoration goals for forest structure were largely met by 2100, forest composition remained far from target in all strategies. Climate change aided restoration by significantly increasing the prevalence of silver fir and European beech (+104.2% to +258.6%). Field data on short-term restoration effects were in line with simulated long-term trajectories.
4. *Synthesis and applications*: We here show that forest restoration efforts in Central European mountain forests will likely be accelerated by climate change. Nonetheless, the slow pace of restoration underscores the need for taking action. Our study highlights that active restoration measures such as tree planting can bring the system closer to restoration targets. However, it also demonstrates that passive restoration (no intervention) is a viable option for management,

highlighting the need to evaluate restoration measures against the counterfactual of a no intervention strategy.

KEYWORDS
active restoration, climate change impacts, disturbance ecology, forest management, passive restoration, protected areas, simulation modelling, tree planting

1 | INTRODUCTION

Climate change and the resulting changes in disturbance regimes render the future dynamics, functioning and distribution of ecosystems highly uncertain. Ongoing changes in the biosphere are already resulting in widespread biodiversity loss (Urban, 2015) and biotic homogenisation (Mori et al., 2018). The future of forests is particularly relevant as they are currently major carbon sinks (Harris et al., 2021) and harbour the majority of terrestrial biodiversity (FAO & UNEP, 2020).

Given the deteriorating state of the biosphere, ecosystem restoration is of prime importance. This decade has been declared the "Decade of Restoration" by the UN. Restoration management is the assisted recovery of degraded ecosystems and habitats in order to restore biodiversity, ecosystem functioning and the supply of ecosystem services (McDonald et al., 2016). Restoration efforts in forest ecosystems can, for example, help to restore carbon stocks (Domke et al., 2020) and mitigate climate change (Lewis et al., 2019), as well as reintroduce species that have been lost from the landscape (Tölgyesi et al., 2022). Forest restoration is particularly relevant in areas such as Central Europe, where forests are the dominating primary vegetation, but were heavily modified by centuries of human use (Roberts et al., 2018). Strategies to achieve restoration goals can be divided broadly into passive and active methods (Bradshaw, 2002). Passive restoration advocates for letting ecosystem dynamics proceed without human intervention, harnessing natural processes to achieve restoration goals. Conversely, active restoration considers targeted interventions such as planting desired and removing undesired species, often preceded by the removal of anthropogenic stressors like livestock grazing or timber extraction, to restore desired ecosystem states and trajectories. Active restoration typically requires more resources, but is often deemed necessary to achieve restoration goals within acceptable time frames (Holl & Aide, 2011).

Restoration management is faced with considerable challenges. The long-term effects of restoration are often hard to evaluate, particularly in ecosystems that develop over time scales from decades to centuries, such as forests. Furthermore, ecosystem dynamics could shift because of climate change, challenging restoration planning and management under drastically changing environmental conditions (Corlett, 2016). In forests, climate change can impact tree species abundance and composition, e.g. by reducing the competitiveness of some species over others, which could hamper restoration to historic conditions. At the same time climate change also increases disturbance frequency and severity (Seidl et al., 2017), which in turn accelerates forest dynamics (Thom et al., 2022) and creates opportunities for restoration (e.g. by post-disturbance tree planting). As a consequence of these competing influences the efficacy of restoration management under climate change remains highly uncertain to date.

Simulation modelling is a powerful tool to quantitatively assess potential future forest trajectories (Thrippleton et al., 2020). Process-based models that assess the impacts of climate change have matured considerably over the past decades (Bugmann & Seidl, 2022), and are increasingly applied also in the context of restoration management (Kobayashi et al., 2022; Shackelford et al., 2021). One advantage of simulation modelling is that it allows the evaluation of active restoration strategies against the alternative strategy of passive restoration, quantifying long-term trajectories of ecosystem development with and without restoration measures. As the effects of climate change can explicitly be considered in the form of scenarios, simulation models are potent tools for addressing future uncertainties in decision making on ecosystems (Petr et al., 2019).

Protected areas are often the main facilitators of restoration projects, given that intact ecosystems are a central aim of their management. In Germany, this is reflected by the fact that certain protected areas have a legal obligation for restoration management. Berchtesgaden National Park (BGNP), for instance, Germany's only national park in the Alps, is tasked by law makers to preserve and restore site-native forest ecosystems in its management zone (StMUV, 1978), as intensive timber production and use in previous centuries has resulted in large forest areas characterised by biotic homogenisation and reduced structural complexity. The national park administration has worked to restore these ecosystems since 1987, providing an example for one of the longest running and still ongoing forest restoration projects in the Alps. As similar forests with strong past human influence are widespread throughout the Alps, questions of restoration are increasingly relevant also outside of protected areas. Yet, how the increasing pace of change (Thom & Seidl, 2022) can be addressed in restoration – both inside and outside of protected areas – remains largely unclear.

Here, we used a process-based forest landscape model in combination with field data to investigate the effects of different restoration strategies at BGNP under climate change. Specifically, we analysed two alternative active restoration approaches (proactive and reactive management) with regard to their short-term effects (based on field data) as well as their outcomes over the 21st century under four different climate scenarios (simulation). In addition to the active treatments, which rely on tree plantings, we also ran simulations without active management interventions to test whether relying on natural dynamics alone (i.e. passive restoration) is sufficient to achieve the long-term restoration goal of BGNP. The goal, as defined in the national park law, is to preserve and restore site-native forest ecosystems to their natural composition and structure by promoting underrepresented tree species of mixed mountain forests, in particular silver fir, European beech, and Sycamore maple (StMUV, 1978). Specifically, we asked (i) "Can restoration goals be met within the 21st century?" and (ii), "How much better are active restoration strategies compared to passive restoration?". We hypothesised that despite the expected future acceleration of forest dynamics (Thom et al., 2022), neither restoration strategy will be able to meet the restoration targets during the 21st century, due to today's large deviation from target conditions. We, however, expected that active restoration will speed up the development towards restoration targets compared to passive restoration, and that this effect is already visible in the empirical data (e.g. ~15 years after restoration management strategy was carried out). Third, addressing the role of changing environmental conditions we asked (iii) "What is the effect of changing climate and disturbance regimes on restoration outcomes?". Here we hypothesised that an increase in disturbance frequency and severity under climate change will create more opportunities for underrepresented species to regenerate in disturbance-created gaps and hence facilitate restoration efforts.

2 | MATERIALS AND METHODS

2.1 | Berchtesgaden National Park (BGNP)

BGNP is the only German national park in the Alps (Figure 1a); it covers an area of 210 km^2, including a management zone (5250 ha, 25% of the park area, 600–1400 m a.s.l.) and a core zone (15,750 ha, 75% of the park area, 600–2713 m a.s.l.). In the core zone management was ceased upon the foundation of the park in 1978. Restoration activities focus on the forested parts of the management zone (3352 ha, 39% of the total forested area of the park), which also is the area under study here. Currently, the mean annual precipitation in the study area is 1630 mm (ranging from 1380 to 2020 mm and increasing with elevation) and the mean annual temperature is 6.2°C (ranging from 4.9 to 7.3°C and decreasing with elevation). Pollen archives show that the potential natural vegetation (PNV) is dominated by European beech (*Fagus sylvatica* L.), which dominates the submontane zone and also occurs in mixed mountain forests of the montane zone, alongside Norway spruce (*Picea abies* (L.) Karst.) and silver fir (*Abies alba* Mill.) (Mayer, 1966). The natural dominance of European beech is generally declining with elevation. The vegetation currently present in the management zone of BGNP deviates strongly from the PNV, and is dominated by Norway spruce (75.8% of the total basal area, Figure 1c). The prevailing Norway spruce stands are largely structurally homogeneous (Figure 1b), as they originate from clearcut forestry in past centuries, aimed to provide timber for local salt mining. European beech and silver fir are strongly underrepresented, and only make up 8.8% and 0.8% of the current basal area, respectively. In addition to foresters reducing the prevalence of these species based on considerations of timber productivity and forest operations, high historic game populations further limited their regeneration success.

2.2 | Study design

2.2.1 | Simulation model

We used the simulation model iLand (**i**ndividual-based forest **Land**scape and **d**isturbance model) to quantify the effects of different restoration strategies under scenarios of climate change. Simulated forest dynamics in iLand emerge from interactions between individual trees and their environment. A detailed descriptions of iLand can be found in Seidl et al. (2012); here, we focus on the two aspects that are of particular importance for the current study, that is disturbance and management modelling.

iLand features a number of detailed submodules simulating natural disturbances. In this study we simulated the two most important

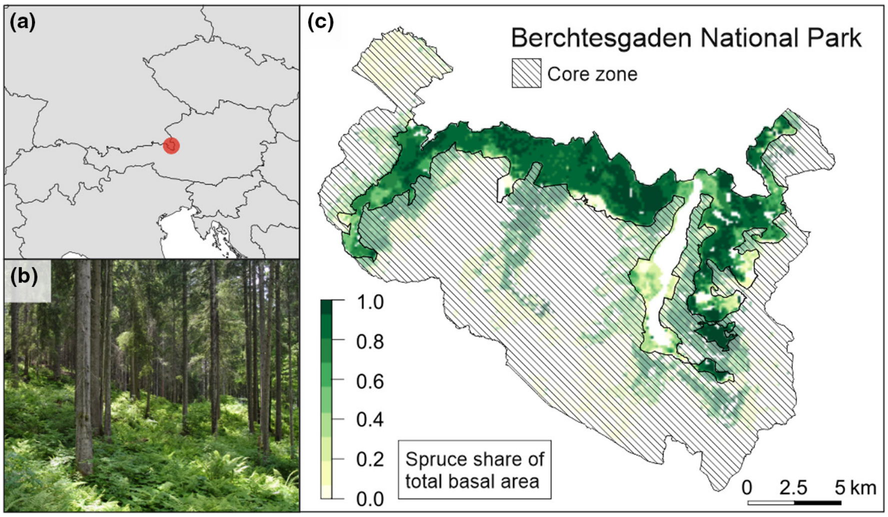

FIGURE 1 Berchtesgaden National Park (BGNP). (a) Location of BGNP in the South-Eastern corner of Germany. (b) Typical forest conditions in the management zone of BGNP, with the canopy layer dominated by even-aged Norway spruce and (c) map of BGNP with the management zone (i.e. the focal area of this study) showing the share of Norway spruce on total basal area (core zone of BGNP hatched).

disturbance agents in Central Europe, wind and bark beetles. The spatial pattern and impact of wind events are simulated as an emergent property by a process-based wind disturbance module that iteratively tracks the interactions between forest structure (tree stability, edge effect) and wind damage. Also, bark beetle disturbances are simulated dynamically and spatially explicit in iLand, capturing the interaction between the European spruce bark beetle *Ips typographus* (Curculionidae, Coleoptera) and its main host Norway spruce, and considering elements such as beetle dispersal, colonisation and population dynamics as well as host distribution and defence. Both wind and bark beetle submodules were successfully evaluated in previous studies in the Eastern Alps (Seidl & Rammer, 2017; Seidl, Rammer, & Blennow, 2014).

iLand is also able to mimic the complex silvicultural interventions implemented by managers in restoration management. Specifically, we used ABE, the module for **A**gent-**B**ased modelling of for**E**st management (Rammer & Seidl, 2015), to simulate different restoration strategies. Stand treatment programs specify the spatial scope, conditions, and timing of management activities under different restoration strategies. ABE accounts for the fact that management activities respond dynamically to disturbances, for example by scheduling tree planting in emerging disturbance gaps. The management activities considered here included felling of trees, planting of trees and harvesting of bark beetle-infested trees. Activities can be executed in different spatial patterns within a stand, such as planting trees in canopy gaps (rather than planting across the entire stand).

iLand was extensively evaluated at BGNP in a previous study, successfully testing the ability of the model to reproduce individual tree dimensions and natural forest dynamics (Thom et al., 2022). Here version 1.1 of iLand was used. More detailed information can be found on the model website (http://iland-model.org/), which also hosts the executable and full source code of the model. Appendix S1a gives a summary of how composition and structure of current vegetation at BGNP were initialised in the model.

2.2.2 | Climate scenarios

Historic climate data for BGNP (1980–2009) was obtained from weather station data in combination with dynamic simulation modelling, in particular using the Weather Research and Forecasting Model WRF at high spatial (5 km) and temporal (1 h) resolution (Warscher et al., 2019). Results were further downscaled to 100 m grid cells and bias-corrected using data from 35 meteorological stations distributed across the area (see Thom et al. (2022) for details). Future climate scenarios were derived from the "Bayern-Ensemble" (Zier et al., 2020), which is a curated ensemble of 22 regionalised climate scenarios for Bavaria. To represent a range of climate change pathways from moderate to severe change, we selected scenarios from the representative concentration pathways RCP 2.6, RCP 4.5 and RCP 8.5. We chose the global circulation model (GCM) ICHEC-EC-EARTH in combination with the regional climate model SMHI-RCA4 in the realisation r12i1p1, representing middle-of-the-road future climate trajectories within the respective RCP pathways. Under RCP 2.6 the temperature rises until 2050 and then stays at a level of 7.5°C (+1.3°C), while under RCP 4.5 temperature rises until 2080 and then remains at 9.1°C (+2.9°C). Under RCP 8.5 the temperature rises continuously until 2100, reaching 12.0°C (+5.8°C) at the end of the century. With regard to precipitation, differences between climate change scenarios are small; mean annual precipitation levels of all scenarios over the simulation period range between 1680 and 1690 mm. However, the interannual variation in precipitation is high, particularly under RCP 8.5. In addition to these three climate change scenarios we also simulated future forest development and restoration under a hypothetical scenario of historic climate, assuming stable climate conditions representing the period 1980–2009. This scenario was developed by resampling years with replacement from this period until 2100, with mean annual temperature remaining stable at ~6.2°C.

2.2.3 | Long-term restoration effect: Simulating restoration activities applied at BGNP

The restoration goal for the management zone of BGNP is to restore the mixed mountain forests of the management zone to their natural composition and structure, mainly by replanting currently underrepresented tree species. Restoration activities implemented to achieve this goal broadly fall into two strategies, proactive restoration and reactive restoration. Proactive restoration was practiced since 1987, and aimed at an accelerated transition towards the desired target conditions. Consequently, spruce-dominated stands were actively opened up by gap-cuts of 0.2 ha (approx. 50 × 40 m) and replanted with silver fir and European beech (total planting density of ~2000 saplings ha^{-1}). In addition, fir and beech were also planted in gaps created naturally by disturbances. In the light of increasing canopy openings from natural disturbances and with the aim to reduce the human impact also in the management zone of the national park, the restoration strategy was changed to only replant in disturbance gaps from 2017 onwards (reactive restoration). A third restoration strategy—passive restoration, which consists of ceasing all anthropogenic activity such as grazing and forest management—can be observed in the core zone of the national park, where vegetation development is solely influenced by natural drivers. Here, we mimicked these three restoration strategies applied in BGNP and simulated their restoration outcomes over the 21st century under different scenarios of climate change. Table 1 summarises the simulated strategies, and more details on their implementation can be found in Appendix S1b.

2.2.4 | Short-term restoration effect: Field data

To corroborate our simulation results on the long-term restoration success at BGNP we collected observational evidence for the short-term responses of forests to different restoration treatments. Specifically, we investigated two separate strata in a paired design: tree regeneration in windthrow patches with and without planting, and mature

TABLE 1 Overview of the three restoration strategies simulated for the management zone of Berchtesgaden National Park. Numbers indicate the areas of (natural and anthropogenic) canopy opening as well as planting, as simulated for the period 2020–2100 under reference climate. See Appendix S1b for additional details.

Drivers		Passive restoration	Reactive restoration	Proactive restoration
Natural disturbance openings	Wind	200.7 ha	203.7 ha	205.3 ha
	Bark beetles	299.8 ha	282.4 ha	283.7 ha
	Replanting	–	Fir and beech	Fir and beech
Management openings	Gap-cuts	–	–	580.4 ha
	Replanting	–	–	Fir and beech

Norway spruce stands treated with gap-cuts relative to those without intervention. The two strata thus represent both types of active restoration management (reactive: windthrow; proactive: gap-cuts) and contrast it to a corresponding control sample of passive restoration (i.e., no intervention). Stem density per species in the regeneration layer was measured on multiple plots (25 m^2) per site. Plot locations were determined by creating a 30 m grid around the center point of a patch in GIS, and randomly selecting locations from the resultant grid points. In the field, plots were located via a handheld GPS device, and only plots that were at least 50 m distant from the patch edge were considered. Regeneration was defined as trees with a height of more than 0.20 m and a diameter at breast height (DBH) <5 cm. All treatment and reference sites were located in close proximity, to control for differences in site condition (same elevation belt, similar soil conditions). The sampled sites were located in montane elevation zone of BGNP.

In areas affected by storm Kyrill (2007), control plots ($n=50$, distributed across four sites) consisted of windthrown areas where no clearing and planting had taken place. The corresponding reactive restoration plots ($n=50$, distributed across four sites) were disturbed by the same storm event, and had been subsequently cleared and planted with silver fir and European beech (total planting density of ~2000 saplings ha^{-1}). With regard to proactive restoration, control plots ($n=38$, distributed across 12 sites) consisted of mature Norway spruce forests with no known management history in the past decades and a stand age of >75 years. The corresponding proactive restoration plots ($n=38$, distributed across 12 sites) had been treated with gap-cuts (size ~0.2 ha) in the last 5–15 years and replanted with equal shares of silver fir and European beech. These 176 sample plots (total area of 4400 m^2 sampled) were used to quantify short-term management responses to active and passive restoration. All necessary permits for field work were obtained from the administration of BGNP.

2.3 | Analyses

We studied the three restoration strategies and four climate scenarios in a full factorial simulation experiment for the period 2020–2100 to evaluate the long-term effect of restoration. Both wind and bark beetle disturbance modules were active for all model runs, simulating natural disturbances as an emergent property of site, stand, and climate conditions. To account for the stochastic nature of disturbances, each combination of restoration strategy and climate change scenario was repeated 10 times, adding up to a total of $3\times4\times10=120$ individual simulation runs.

Species composition was quantified based on the species' importance value (IV), which was calculated as the sum of species proportions based on stem density and the species proportions based on basal area. Stem density and basal area react differently to different stimuli of restoration (cutting, planting), which is why we chose IV as a comprehensive and robust measure of species composition. IV values were rescaled between 0 and 1 (relative IV, abbreviated to rIV) to aid interpretability. In our analysis we put a specific focus on the target species of restoration at BGNP – silver fir and European beech – as they are also the key focus of managers at BGNP.

To analyse the development of homogeneous secondary forests back towards more diverse forest structures we focused on the coefficient of variation (CV) in the trees' DBH [cm] as the second analysis variable. It was calculated at the level of 1 ha stands and averaged over the study area. For both indicators, only trees with a height of ≥4 m were considered in the analysis of long-term restoration effects, accounting for the fact that many planted trees do not survive to maturity in harsh mountain environments. For the analysis of short-term effects based on field data we focused on analyses based on stem density, as trees were generally not tall enough to have a DBH, which precluded the calculation of rIV and CV of DBH. Data preparation as well as all analyses were done using the R project for statistical computing version 4.0.5 (R Core Team, 2021).

As the restoration goal stated in the relevant legal documents is vague ("restoring natural forest conditions") we derived target conditions for restoration from simulations with iLand. Forest development was simulated under historic climate for 2500 years, starting from bare ground and assuming seed input via a seed belt (i.e. assuming the forests adjacent to BGNP to be in a PNV state typical for their elevation, and providing the corresponding seed input to the simulated study area) containing all 29 species parameterised in the mode. Runs were replicated three times and the last 100 years were averaged to represent PNV conditions. Restoration targets with regard to forest composition and structure were then derived as the rIV and CV of DBH of the PNV.

3 | RESULTS

3.1 | Quantifying restoration targets

After 2500 years of simulation under historic climate, the equilibrium species composition of the BGNP management zone was dominated by European beech (rIV of 0.47 ± 0.01, mean ± standard deviation, Figure 2a). The second most common species was Norway spruce

(0.30 ± 0.01), followed by silver fir (0.12 ± 0.0) and European larch (0.09 ± 0.0). Other species made up 0.02 ± 0.0 of the rIV. Thus, the target species of restoration, silver fir and European beech, together dominate the PNV with a combined rIV of 0.59 ± 0.01. In contrast, their current rIV is 0.09 (silver fir: 0.01, European beech: 0.08). The simulated CV of DBH was 0.689 (range 0.679–0.696) under PNV conditions (Figure 2b), compared to 0.405 currently.

3.2 | Long-term effect of different restoration strategies in the absence of climate change

Forest composition changed in all simulations, regardless of restoration strategy. Compared to the initial state in 2020 we found an increase in the rIV of silver fir and European beech, and a decrease of Norway spruce in all simulated strategies (Figure 2a). These patterns were amplified by active restoration: While the rIV of silver fir more than doubled under passive restoration (+131%), it nearly quadrupled under reactive restoration (+268%) and increased more than sevenfold under proactive restoration (+647%). European beech responded less pronounced to management, doubling under passive (+104%) and reactive restoration (+114%) and increasing by 145% under proactive restoration. The rIV of Norway spruce decreased by 13% under passive restoration, by 14% under reactive and by 20% under proactive restoration. The rIV of the non-target species stayed fairly constant at ~0.18, with European larch increasing at the expense of sycamore maple in 2100 compared to 2020.

While composition moved significantly closer to the target state of restoration throughout the 21st century, restoration goals were not met by the end of the century. The combined rIV of silver fir and European beech was 0.18 under passive restoration, 0.19 under reactive restoration and 0.25 under proactive restoration in 2100. This means that even under the most intense restoration strategy the combined rIV of the target species fir and beech was

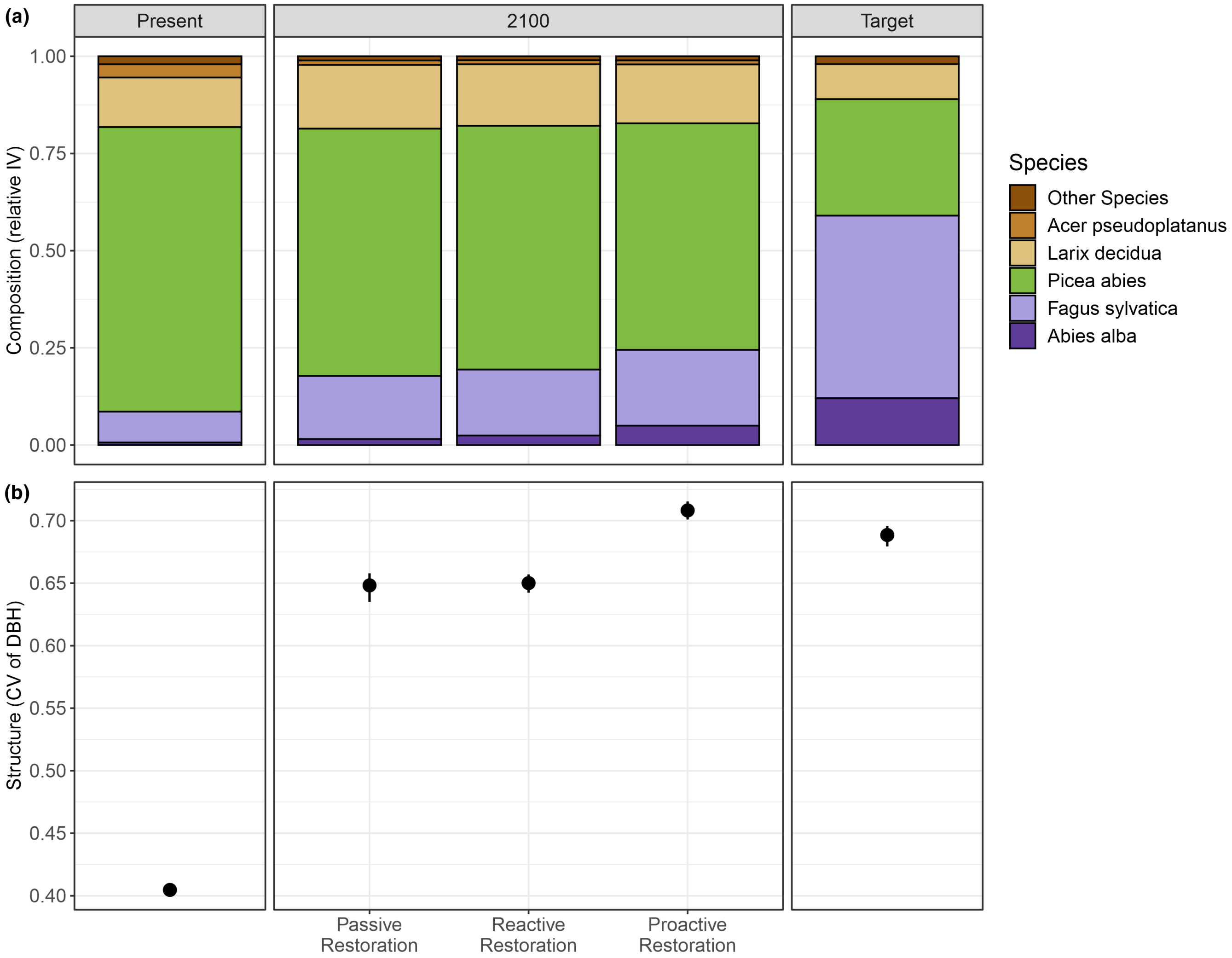

FIGURE 2 Forest composition and structure in the absence of climate change, shown for the initial state in 2020 ("Present"), the end point of simulations in 2100 for each restoration strategy, and the restoration target (based on simulated potential natural vegetation). (a) Relative importance values (rIVs) of the most common species. (b) Mean coefficient of variation (CV) of diameter at breast height (DBH) (dot) and range of values (whiskers).

still less than half of the target value (0.59). Relative to the target value the differences between the restoration strategies were moderate, with differences in rIV among species ranging between 0.02 and 0.11.

Structural diversity increased considerably from 2020 to 2100 in all simulations. The CV of DBH increased from 0.405 in 2020 to a mean of 0.649 under passive restoration (+60%), 0.650 under reactive restoration (+61%) and 0.708 under proactive restoration (+75%) in 2100 (Figure 2b). All strategies came close to the target state (0.689) by the end of the century, and the forest under proactive restoration was structurally even more diverse than the simulated target state. As for species composition, differences between management strategies were small to moderate also for stand structure.

3.3 | Short-term effect of different restoration strategies as observed in the field

Short-term restoration effects observed in the field were generally in line with long-term effects derived from simulations. Restoration had a positive effect on the prevalence of the target species silver fir and European beech in both empirically studied strata (i.e. mature spruce forests and windthrown areas, Table 2). This is in line with the management response observed in simulations (see Figure S2a in Appendix S2). In untreated, closed forests of mature Norway spruce (passive restoration) little regeneration was present. Gap-cuts implemented 5–15 years ago resulted in a nearly four-fold increase in overall stem density, and a pronounced dominance of Norway spruce in the regeneration layer. Also, in windthrown gaps, stem densities increased in response to active management; this effect was particularly strong for silver fir and European beech (i.e. a 24-fold and 79-fold increase, respectively). As in the simulations, regeneration density and composition were very similar across both active management strategies (gap-cuts and windthrows). Norway spruce continued to be the most common tree species also after restoration treatments, a pattern that is in line with Norway spruce remaining the dominant species in the simulations also at the end of the 21st century.

3.4 | Effects of climate change on restoration outcomes

Total area disturbed varied strongly over climate change scenarios, with bark beetle disturbances being especially climate-sensitive. Wind disturbance was lowest under historic climate (200.7 ha disturbed in the 8 years simulated) and increased by 19.1% under RCP 2.6, 21.6% under RCP 4.5 and by 42.4% under RCP 8.5 (passive restoration). Bark beetle disturbance decreased by 13.7% from its historic baseline (299.8 ha) under RCP 2.6, while increasing by 55.3% under RCP 4.5 and by 319.4% under RCP 8.5. Variation in area disturbed between different restoration strategies was small.

Climate change had a strong influence on trajectories of forest composition, while affecting forest structure only marginally. The prevalence of the target species of restoration, silver fir and European beech, generally increased with increasing severity of climate change (Figure 3a). The overall highest value of a combined fir-beech rIV (0.31) was reached under proactive restoration and climate scenario RCP 8.5. In contrast, the CV of DBH varied little with climate scenario (Figure 3b). The climate sensitivity of structure and composition varied with restoration strategy. Structure was most climate-sensitive under passive restoration (i.e. where structure is purely determined by climate-driven disturbances), while composition responded most strongly to climate under reactive restoration (where the increased amount of disturbances under RCP 8.5 also led to a distinct increase in the level of tree planting). The drivers of restoration success, particularly the important role of the area planted per year, are elucidated in more detail in Appendix S2b.

4 | DISCUSSION

4.1 | How long does it take to restore natural forests in Central Europe?

None of the assessed restoration management strategies was able to fully reach restoration goals within the 21st century. Even under the most intensive restoration strategy considered here, planting 978 ha of

TABLE 2 Observed stem densities (trees ha^{-1}) in the regeneration layer (height >0.2 m and DBH <5 cm), comparing active and passive restoration treatments for two strata: Mature Norway spruce forests proactively restored with gap-cuts and planting in the last 5–15 years, and areas windthrown by storm Kyrill in 2007 reactively restored by planting. Both active restoration strategies were compared to reference conditions of passive restoration (no intervention). n = number of 25 m^2 inventory plots investigated. Note that total stem densities also include other tree species, such as early-seral species not in the focus of restoration.

	Mature Norway spruce forest		Windthrow	
	Passive restoration (no intervention), n = 38	Proactive restoration, n = 38	Passive restoration (no intervention), n = 50	Reactive restoration, n = 50
Total stem density	3617 ± 3171	14,340 ± 11,313	8000 ± 7116	10,723 ± 8088
Silver fir	41 ± 120	1746 ± 1643	59 ± 208	1403 ± 1589
European beech	122 ± 285	1147 ± 1839	25 ± 101	1975 ± 3064
Norway spruce	61 ± 168	5320 ± 6641	2025 ± 2749	3067 ± 5522

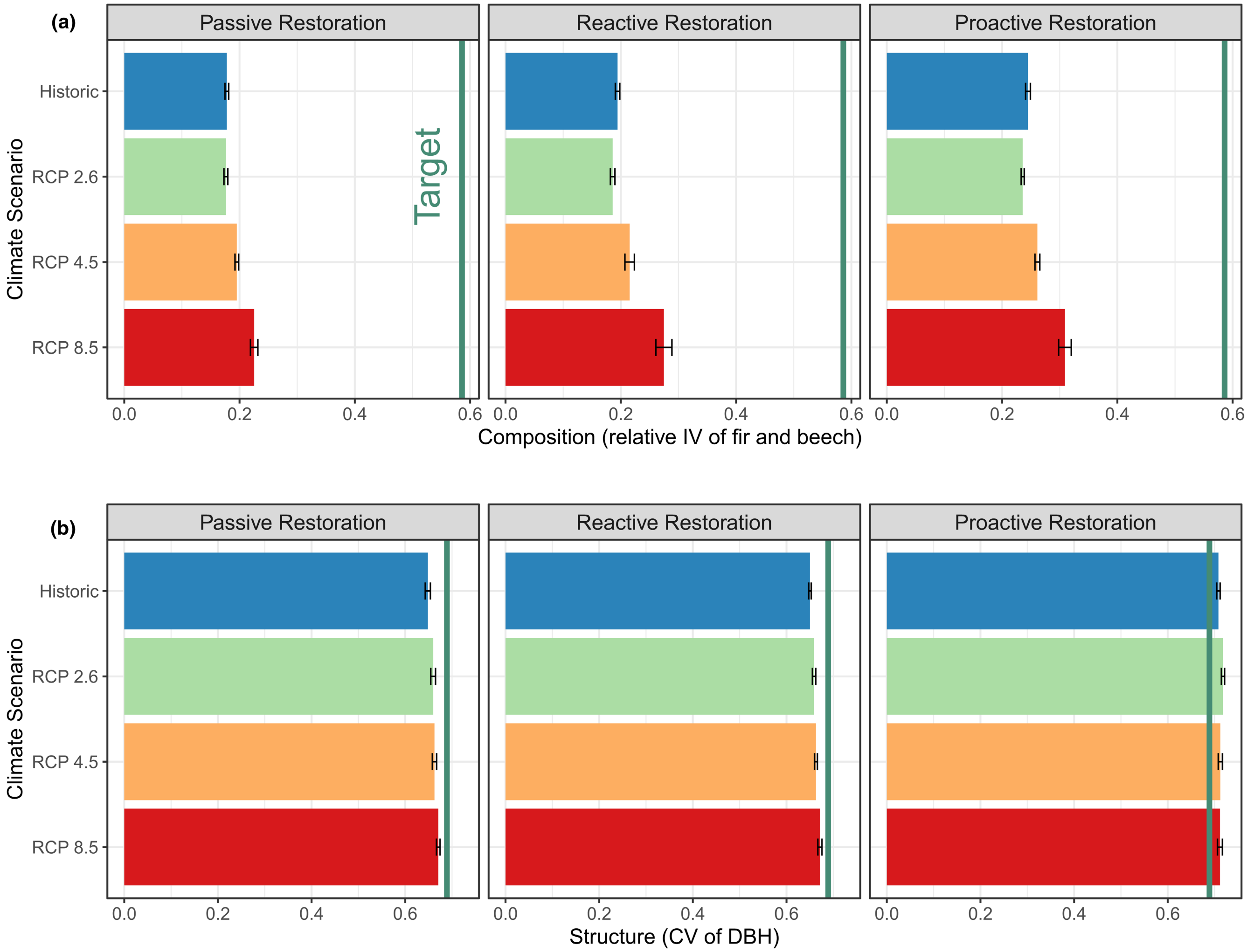

FIGURE 3 Simulated forest composition and structure under historic climate and different climate change scenarios in 2100. Bars show the mean and whiskers the 95% confidence interval over 10 replicated simulations. The target state for restoration is indicated by the bold green vertical line. (a) Forest composition. (b) Forest structure.

the 3352 ha study area with target species over the 81-year simulation period under reference conditions, the restoration goal was not reached with regard to species composition. The finding that forest composition only changes slowly is in line with previous findings for BGNP from both empirical and simulation studies (Thom et al., 2022; Thom & Seidl, 2022). High inertia in species composition were also reported from other naturally developing (Thom et al., 2017; Winter et al., 2015) and managed (Seidl et al., 2018) landscapes in the eastern Alps.

In contrast, forest structure converged with potential natural conditions by the end of the 21st century under all simulated management strategies. Our analyses thus suggest that the variation in tree diameter will return to natural conditions within the coming decades at BGNP. The finding that forest structure recovers significantly faster than forest composition is well in line with previous reports from forests of Europe (Thom et al., 2022) and North America (Seidl, Rammer, & Spies, 2014). However, Albrich et al. (2021) found that the variation in tree diameters had not yet recovered to old-growth conditions in a 220-year chronosequence of forest development after the cessation of management (passive restoration). Differences in structural development could, for example result from different disturbance regimes, given that disturbances can either diversify (at moderate disturbance rates) or homogenise (at very low or very high rates) forest structures (Senf et al., 2020).

4.2 | Which restoration strategy to take?

In all three restoration strategies studied here, the system was closer to the target state at the end of the 21st century than it is currently. Active restoration strategies performed better than passive restoration, but the differences between the strategies were moderate. This suggests that natural ecosystem processes played an important role in the simulated forest transformation. Active restoration measures helped to speed up the dynamics, especially with regard to tree species change, but did not fundamentally alter the trajectory of BGNP forests. The fact that natural development (passive restoration) and active restoration management were congruent suggests that homogeneous Norway spruce forests in Central Europe do not form a strong attractor of forest dynamics (characterised by stabilising feedbacks); hence restoration can work *with* the natural dynamics (Hartup et al., 2022), and the existing forests are not locked into their anthropogenically modified state (Staples et al., 2020). Ultimately, old-growth conditions will also re-emerge in Central Europe without the aid of active management measures (Albrich et al., 2021) but the required time frames might be considerable.

4.3 | Will climate change aid or impede restoration efforts?

Climate change accelerated restoration efforts at BGNP, particularly with regard to restoring natural tree species compositions. This positive effect was related to two simultaneous effects of climate change: First, warmer climate decreased the competitiveness of Norway spruce, because warmer and drier conditions increase its susceptibility to bark beetle attacks (Jakoby et al., 2019). Under RCP 8.5 the area disturbed by bark beetles was four times higher than under a continuation of historic climate. Second, warmer climate increased the competitiveness of European beech and silver fir, as both species have the center of their niche under higher temperatures than Norway spruce (San-Miguel-Ayanz et al., 2022). However, Norway spruce remained the dominant tree species under all climate scenarios. One factor contributing to the high resilience of Norway spruce is that droughts are largely absent from the simulated climate scenarios, as mean annual precipitation remained high during the whole simulation period in all scenarios (mean of 1680 mm year^{-1}). Due to the location of the study area at the northern front range of the Alps climate models see high precipitation in our study area also in the future, which is in stark contrast to other areas of Central Europe, which are already experiencing considerable drought-related mortality currently (Schuldt et al., 2020), and are expected to dry further in the future. We note, however, that due to the low water holding capacity of soils in our study area also shorter periods without precipitation can lead to water stress, particularly in tree regeneration (Simon et al., 2019). While other studies have found that climate change can impede restoration (Boulanger et al., 2019; Koch & Kaplan, 2022), we here provide an example in which restoration efforts will likely benefit from the expected changes in climatic conditions.

4.4 | Limitations

A number of important drivers of restoration success could not be considered in detail here. Browsing pressure can decrease regeneration success, as game inflict lasting damage on the growth and vitality of tree saplings (Kupferschmid et al., 2015). Browsing is a particularly relevant factor in the context of restoring silver fir and European beech, as these two species are preferred by browsers over Norway spruce, that is browsers select against our target species of restoration (Unkule et al., 2022). Browsing was not explicitly considered in this study, yet simulated regeneration responses were congruent with observations (see Figure S2a in Appendix S2), partly because active game reduction is an important part of the current forest restoration strategy at BGNP. A further factor that was not considered here are tending and thinning operations, i.e. silver fir and European beech were retained in the simulation only where they could outcompete Norway spruce (which regenerates widely throughout the landscape because of the ample seed source) without further active management interventions. Currently, managers at BGNP discuss whether tending activities favouring target species could further speed up restoration, but tending and thinning interventions have not been part of restoration management at BGNP in the past. We note that we here only simulated restoration strategies that either are or have been historically applied at BGNP. Strategies outside of this bracket that, for instance, more actively favour species change under climate change (e.g. assisted migration, Dumroese et al. (2015)) or favour more intensive restoration by treating larger areas, were not considered.

Another source of uncertainty relates to the way how restoration targets are defined. We here only focused on two response variables, representing forest structure and composition, focusing on dimensions that are intensively discussed by local managers. However, previous studies showed that the recovery speed of different indicators varies distinctly (Albrich et al., 2021), underlining that the choice of indicators for measuring restoration success will likely influence the obtained outcomes. Furthermore, as is currently common in restoration management, we here assumed a static restoration target defined against the background of historic climate. However, the effects of climate change and other anthropogenic pressures are creating novel forest ecosystems with pronounced dissimilarities to current ecosystems in their composition and structure (Hobbs et al., 2006; Radeloff et al., 2015). Consequently, conservation and restoration will need to increasingly formulate dynamic goals that acknowledge the inherently changing nature of social-ecological systems (Jackson, 2021). This could be acknowledged in future studies, for instance, by not only considering the effects of climate change on restoration outcomes but also on restoration targets (i.e. what is the “natural tree species composition” under the emerging environmental conditions).

5 | CONCLUSIONS

Restoration is an important element in ensuring the long-term integrity and functioning of ecosystems on our planet. However, restoration can have long lead times, particularly in forest ecosystems, where it may take centuries for certain ecosystem properties to realign with natural conditions. This underscores the urgency of taking action, not least because a resilience debt (Johnstone et al., 2016) can accumulate as environmental conditions continue to change. Active restoration is a powerful means for achieving restoration targets and for safeguarding ecosystem functions. Yet, our results indicate that in some cases passive restoration (no intervention) is also a viable option, highlighting the need to evaluate restoration measures against a no intervention strategy. For Central Europe our results show that near-natural forest structures emerged considerably faster than natural assemblages. We thus conclude that restoration efforts in the area should particularly focus on adapting and restoring diverse tree species compositions. Lastly, restoration management needs to explicitly consider climate change, as both effects of management measures and restoration targets can change considerably with a changing climate.

AUTHOR CONTRIBUTIONS

Christina Dollinger, Werner Rammer and Rupert Seidl conceptualised the study. Christina Dollinger curated all data, conducted the analysis, visualised the results and wrote the first draft of the manuscript. All authors commented and edited the manuscript.

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CONFLICT OF INTEREST STATEMENT

The authors have no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.v15dv422r (Dollinger et al., 2023).

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SUPPORTING INFORMATION

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

Appendix S1. Additional materials and methods.

Appendix S1a. Model initialization.

Appendix S1b. Simulation of restoration management.

Appendix S2. Additional results.

Appendix S2a. Evaluation of simulated restoration effects on regeneration.

Figure S2a. Management response in regeneration (difference between areas with active and passive restoration) for observed and simulated data in total stem density per ha (a) and stem density of the target species (b). Whiskers show the standard deviation.

Appendix S2b. Drivers of restoration success.

Figure S2b. Effect of mean area disturbed and mean area planted (per year, averaged of the 81-year simulation period) on forest composition and structure at the end of the 21st century across all simulation runs ($n=120$). Colors indicate different restoration strategies while symbols distinguish climate scenarios. (a) Forest composition. (b) Forest structure.

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