RESEARCH ARTICLE

The long way back: Development of Central European mountain forests towards old-growth conditions after cessation of management

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Abstract

Questions: Primary forests fulfil important roles in preserving biodiversity, storing carbon and increasing ecological understanding. Yet, they have become very rare in Europe. An important policy goal is thus to increase the share of naturally developing forests by creating protected areas in formerly managed forests. Here, we investigated: (a) if and how such forests return to conditions similar to old-growth; and (b) whether recently observed stand-replacing natural disturbances in combination with climate change set them onto an alternative developmental pathway.

Location: Dürrenstein Wilderness Area (IUCN Cat. Ib) in the Austrian Alps, containing the Rothwald, one of the last primary forest remnants of Central Europe.

Methods: We built a chronosequence of 87 plots, spanning 220 years of forest development after the cessation of management, and compared them to old-growth forests. We analysed the recovery of nine attributes of forest composition, structure and functioning. To evaluate stand-level development of these attributes after recent natural disturbance and climate change, we additionally used a process-based simulation model.

Results: Old-growth forests showed a wide range of variability across investigated attributes. Forests converged to old-growth conditions after management ceased, with seven out of the nine attributes falling within the range of old-growth at the end of our chronosequence. The variation in tree diameters and the downed amount of deadwood were, however, still significantly lower than in old-growth forests after 220 years of unmanaged stand development. Simulations did not indicate an alternative developmental pathway of recently disturbed stands.

Conclusions: While a full return to old-growth conditions can take centuries, a number of important forest attributes recover quickly, indicating that protecting formerly managed forests is a valuable strategy to enrich forest landscapes. Our results indicate that the mountain forests of Central Europe have high ecological resilience, developing towards old-growth conditions after both past management and current natural disturbance.

1 | INTRODUCTION

Pristine old-growth forests have become increasingly rare. In Europe, for example, only 2.2% of forests are considered "undisturbed by man" (FOREST EUROPE, 2020). While the existence of hitherto unidentified primary forest remnants is likely, known primary forests make up only 0.7% of Europe's remaining forest area (Sabatini et al., 2018). The absence of old-growth forests is of concern because they fulfil many important functions. Old-growth forests, which we here define as forests having developed under a natural disturbance regime with only minimal anthropogenic influence and showing characteristics such as high structural complexity (Spies, 2009; Nagel et al., 2013), are important hotspots of biodiversity. They provide refugia for species that have become rare in managed landscapes because of their structures (e.g., deadwood for saproxylic beetles) or because management narrowed the diversity of tree species (Nagel et al., 2013; Seibold et al., 2015; Dvořák et al., 2017). Furthermore, old-growth forests are also notable for their contribution to climate regulation through high carbon stocks and microclimatic buffering (Luyssaert et al., 2008; Frey et al., 2016). In addition, they are important reference systems for research aiming to understand forest dynamics, and serve as a reference for designing close-to-nature forest management approaches (Wirth et al., 2007; Nagel et al., 2013).

Recognizing both their importance and rarity, forest reserves have been established in Europe in the last decades aiming to increase the share of old forests in the landscape. However, previous research has indicated that management legacies can persist for decades to centuries after management ceases (Thom et al., 2018). The establishment of newly protected areas thus raises questions about their future development, particularly whether formerly managed forests are in fact able to return to old-growth conditions under changing environmental conditions, how long such a process may take, and how the old-growth forests of the future may differ from today's old-growth in terms of forests composition, structure and functioning. So far, research on these questions is sparse, particularly in Europe (Vandekerkhove et al., 2009; Paillet et al., 2015; Burrascano et al., 2018).

Answering such questions is often hampered by the limited availability of data on forest ecosystem dynamics covering more than a few decades. A common strategy to address this data scarcity is space-for-time (SFT) substitution. This method makes use of stands along a gradient of time since management/stand-replacing disturbance to construct a chronosequence, inferring the development of forest characteristics over time (Winter et al., 2015; Oliveras et al., 2018). Space-for-time substitution has become a common method in ecology, particularly when investigating secondary succession after disturbance (Pickett, 1989). The SFT assumption requires that the assessed stands developed under similar conditions, assuming stationary driving variables such as climate. However, ongoing climate change and recent amplifications in disturbance regimes raise questions about the validity of these assumptions. It remains unclear whether forest development in a changing world will still follow successional pathways derived from chronosequences, or if alternative pathways will emerge. In particular, are the environmental changes of the last decades (e.g., changes in climate, higher atmospheric CO_2 levels and changes in nutrient availability due to nitrogen deposition) severe enough that stands undergoing a reorganization phase after disturbance (Holling & Gunderson, 2002) are already on a different developmental pathway? Since these questions cannot be addressed by SFT, other approaches such as simulation modelling are important to complement chronosequence studies. Simulation allows us to assess whether non-stationary driving variables result in altered development trajectories, and can thus give indications of where SFT approaches reach their limits.

The Dürrenstein Wilderness Area (DWA, IUCN Category Ib) in the Austrian Alps provides an ideal setting to investigate natural forest development after the cessation of management, as some parts of the landscape have never been managed while others have a varied management history. At the heart of the DWA is the Rothwald forest, one of the few remaining old-growth forests in Central Europe. It frequently serves as reference condition for the assessment of natural population dynamics (Splechtna et al., 2005), and biogeochemical cycling (Pietsch & Hasenauer, 2006) in Central Europe, and was used as a blueprint for developing close-to-nature forest management strategies (Mayer, 1987). The protected area surrounding the Rothwald was enlarged in several waves, creating a wide gradient of time since the last management intervention, and providing a unique opportunity to study forest development in a SFT approach.

Using a combination of field-based observations along a chronosequence and process-based forest landscape model simulations we here address the questions: (a) do formerly managed forests recover towards current old-growth conditions and how does recovery differ among attributes of forest structure, composition and functioning; and (b) do recently observed disturbances in combination with climate change result in alternative vegetation developmental pathways?

2 | METHODS

2.1 | Study area

The Dürrenstein Wilderness Area (DWA) is located in eastern Austria (47°45'20" N, 15°02'10" E). At the onset of this study in 2017 it encompassed 3,449 ha of protected area and it extends from about

650 to 1,878 m a.s.l. (top of mount Dürrenstein, Figure 1). Embedded within the DWA is the Rothwald, a 460-ha old-growth forest. Due to a unique combination of topography (i.e., hampering logging and the transport of timber) and ownership history (after multiple ownership changes the area was purchased by Albert Rothschild in 1875, who kept the Rothwald unlogged and preserved it as a hunting reserve) it was never cut, unlike all the surrounding forests. Starting from this nucleus of old-growth, which was first formally protected in 1943 after having been taken from the Rothschild family by the National Socialists, the protected area was expanded in multiple steps, adding formerly managed forests under the stewardship of the Austrian Federal Forests as well as the Rothschild family (Pekny, 2012). In the early periods of management, these "formerly managed" and now protected forests were subject to selective cutting of conifers. Unlike species with heavier wood, these could be transported by flotation, the primary timber transportation strategy at the time. More recent forest management generally employed clear-cut systems, with rotation periods of between 100 and 160 years. In some areas, management intensity was relatively low due to high terrain ruggedness and limited accessibility (Pekny, 2012; Thom et al., 2018). The entire protected area was designated an IUCN Category Ib Protected Area in 2003, and was enlarged to the size of 3,449 ha in 2013 (Splechtna & Splechtna, 2016).

The DWA is located in the northern Limestone Alps with dolomite and limestone bedrock. Soils are dominated by Rendzinas and relictic loams (Rendzic Leptosols and Chromic Cambisols, Zukrigl et al., 1963). The most important tree species are European beech (*Fagus sylvatica*), Norway spruce (*Picea abies*) and silver fir (*Abies alba*; Splechtna et al., 2005). The area is characterized by a submaritime climate with long winters and short, relatively cool summers (Splechtna et al., 2005). Annual precipitation is high (up to 2,300 mm) and bimodally distributed, with peaks in summer and winter (Splechtna

et al., 2005), resulting in very high snow loads and ample water supply during the vegetation period.

2.2 | Data collection

In the summer of 2017, 87 sample plots were selected and recorded throughout the wilderness area. Stands were sampled across a gradient of time since the last clear-cut harvest (formerly managed stands), and also included completely unmanaged old-growth forest (reference conditions). We distributed our sampling evenly between two distinct site types, namely sheltered, relatively flat low to midelevation forests with higher shares of conifers ("valley plots") and forests on steep slopes at higher elevation and with higher shares of broad-leaved trees ("slope plots"; Mayer, 1987). We sampled both old-growth and formerly managed stands on both site types. We aimed for a roughly equal distribution between younger and older formerly managed stands as well as old-growth stands (Table 2). To establish a chronosequence, time since management was derived from historic and current forest management maps and auxiliary information from local managers. Stand age was confirmed via tree core sampling of a dominant tree at each plot.

Sample plots were established at randomly selected coordinates (marking the plot centre) within stands. For each plot we sampled a 50 m long and 4 m wide (200 m^2) transect oriented orthogonally to the slope direction (oriented north–south on flat areas) and separated into 50 4-m^2 subplots (Appendix S1). Only plots fully located within a stand were considered, otherwise the nearest alternative plot coordinates were chosen from a randomly created list of candidate plot locations. All live trees with a diameter at breast height (DBH) > 7 cm were recorded with DBH and species. For dead standing trees diameter, height and decay stage were recorded. In two

FIGURE 1 Study area and sample plot locations (points, colored by time since management). Photos show examples of conditions on sample plots for age classes: (a) <100 years since management (*n* = 20); (b) >100 years since management (*n* = 37, including beetle-disturbed plots); (c) primary forest (*n* = 30). (Photos by Rupert Seidl, Daniel Schraik.) The equidistance between contour lines is 150 m
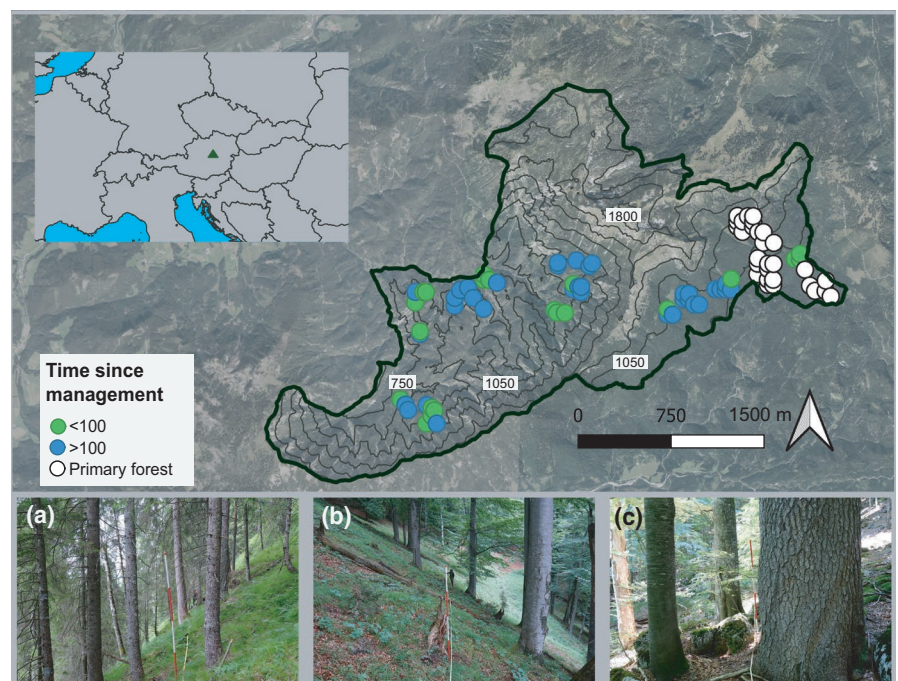
4-m^2 subplots (one at each end of the transect) the abundance of regeneration was recorded by counting all saplings above 10 cm in height. For each transect, four tree heights were measured, one randomly selected dominant tree each for conifers and broad-leaved trees as well as the tree closest to the centre of each regeneration subplot. Coarse woody debris was recorded in three 10-m transects originating from the plot centre and oriented at 120° from each other (following the protocol of the Swiss National Forest Inventory, Böhl & Brändli, 2007). Hemispheric photographs were taken at the plot centre as well as at the centre of the regeneration subplots by means of a Solariscope (Ing.-Büro Behling, 2015) to record light conditions.

Four plots were located in stands recently killed by bark beetles, making them distinctly different from all other plots, where recent natural disturbances had only affected a few individual trees at most. We were interested in whether these recently disturbed stands, which differ distinctly from other stands of similar time since management, might indicate the onset of an alternative stand development trajectory. We consequently treated this stratum separately in the analysis, despite the relatively small area affected by high-severity disturbance.

2.3 | Statistical analysis

From the data collected, a total of nine attributes were extracted, covering aspects of forest structure, composition, and functioning (Table 1). All data processing and analysis was performed using the R language and environment for statistical computing (R version 3.6.3; R Core Team, 2020). Forest structure was represented through the coefficient of variation in tree diameter, the median tree height, the Total Site Factor as an attribute of forest cover (i.e., the relative amount of total sunlight reaching the ground compared to open-field conditions; Anderson, 1964), and the number of saplings (stems with <4 m height) per ha. Forest composition was represented by the effective tree species number calculated as the exponent of the Shannon Index (Jost, 2006), with the Shannon Index calculated based on basal area shares using the *vegan* package (Oksanen et al., 2019), and the conifer share (basal area share of coniferous species, see Table 1). As attributes of forest functioning, in particular considering the climate regulation function, three above-ground carbon pools were calculated: live tree, snag (standing deadwood), and coarse woody debris (downed dead wood with a diameter of more than 7 cm) carbon. Carbon in live stem biomass was estimated using allometric functions that have been implemented and evaluated in a simulation model (Thom et al., 2017a), snag carbon was calculated using the approach presented by Ford and Keeton (2017), and for coarse woody debris we followed the method described in Böhl and Brändli (2007). For both deadwood pools, wood density reduction factors were applied for decay stages following Harmon et al. (2011). To calculate carbon content from biomass we used a uniform carbon fraction of 0.5 for all pools (Neumann et al., 2016).

TABLE 1 Attributes used and their definition, calculation and unit (where applicable).

Attribute	Definition and calculation	Unit
CV DBH	Coefficient of variation of tree diameters	cm
Median height	Median stand height	m
Total Site Factor	Relative amount of total surface sun light (direct and indirect) compared to open field conditions, averaged over three Solariscope measurements per plot	[0…1]
Sapling number	Stem number of regeneration (trees with height < 4m, per ha), summed across both regeneration subplots of each sample plot	*n*/ha
Effective species number (Shannon exponent)	Effective number of tree species (dbh >7cm) computed as the Shannon exponent weighted by basal area	*n*
Conifer share	Percent of coniferous species (*Abies alba*, *Larix decidua*, *Picea abies*, *Pinus sylvestris*, *Taxus baccata*) basal area on total basal area	%
Live tree carbon	Stem carbon in live trees, calculated using species-specific allometric functions (Thom et al., 2017)	t/ha
Snag carbon	Stem carbon of standing dead trees, calculated using the approach presented by Ford and Keeton (2017), with reduction factors for decay classes from Harmon et al. (2011).	t/ha
Coarse woody debris (CWD) carbon	Carbon of coarse woody debris, calculated following the method detailed in Böhl and Brändli (2007) with reduction factors for decay classes from Harmon et al. (2011)	t/ha

TABLE 2 Site conditions and attributes comparing stands with different time since management to old-growth conditions. Presented are group medians and 5th–95th percentiles (see also Appendix S1 for boxplots). Different superscript letters indicate significantly different groups (tested with the Kruskal–Wallis test and the post-hoc Dunn's test with Benjamini–Hochberg correction)

Attribute	Time since management		Old-growth
	<100 years	>100 years	
Number of plots	20	33	30
Site type (low/high elevation)	5/15	14/19	18/12
Mean elevation (m)	904 (773–1187)	1006 (813–1164)	1062 (971–1206)
Mean slope inclination (°)	23.4 (11.4–33.6)	23.2 (7.9–41.4)	17.5 (0–32.6)
Most frequent aspects	W (6), N (6)	E (11), S (9)	S (16), W (5)
CV DBH (cm)	0.412 (0.306–0.599)[a]	0.418 (0–0.683)[a]	0.597 (0.151–0.937)[b]
Median tree height (m)	20.6 (11.5–30.6)[a]	22.5 (3.1–34.4)[b]	20.0 (6.9–32.0)[ab]
Total Site Factor (0…1)	0.067 (0.036–0.271)[a]	0.087 (0.042–0.230)[a]	0.060 (0.036–0.271)[a]
Sapling number (n/ha)	0 (0–12,563)[a]	7,500 (0–60,750)[b]	7,500 (2,500–41,182)[b]
Effective species number (n)	1.79 (1–2.76)[a]	1.86 (1–3.74)[a]	1.77 (1–2.86)[a]
Conifer share (%)	96.7 (27.5–100)[a]	33.2 (0–100)[b]	34.2 (34.2–87.4)[b]
Live tree carbon (t/ha)	110 (30.1–169.0)[a]	152 (1.25–302)[a]	99.5 (27.9–375)[a]
Snag carbon (t/ha)	5.5 (0–14.4)[a]	0 (0–23.1)[b]	0.46 (0–42.6)[b]
CWD carbon (t/ha)	0.171 (0–0.861)[a]	0.570 (0–3.85)[b]	2.51 (0.378–8.18)[c]

As a first analysis step, plots were grouped into two formerly managed (<100 years, *n* = 20 and >100 years since last clear-cutting, *n* = 33) and one old-growth (primary forest, *n* = 30) categories. We chose 100 years as cut-off as we expected increasing disturbance activity and a stronger differentiation in forest structure for the second century of stand development, resulting in a diversification of forest attributes (Donato et al., 2012; Overbeck & Schmidt, 2012; Meigs et al., 2017). Furthermore, 100 years represents the approximate rotation period in surrounding managed forests, with the cut-off distinguishing between forests that have been unmanaged for shorter/longer periods than one rotation. The four plots that were recently disturbed by bark beetles were excluded from this analysis.

We analysed if the three groups differed significantly in their forest attributes. Non-metric multidimensional scaling (NMDS) using Gower's distance (Gower, 1971) was performed to visually explore the multidimensional variable space, employing the functions vegdist and metaMDS from the package *vegan* (Oksanen et al., 2019). We tested for significant differences at the level of individual attributes using a Kruskal–Wallis Rank Sum Test with a subsequent Dunn's test with Benjamini–Hochberg adjustment for multiple comparisons to investigate differences between groups.

In a subsequent step, we explored the continuous relationship between time since management and the development of the individual attributes using generalized linear models with a Poisson error distribution and log-link for count data (sapling number). For continuous variables we used a gamma error distribution and identity link (CV DBH, Shannon exponent, conifer share, carbon pools) or log-link (median height, Total Site Factor). We calculated the percentage of plots that were within the variability of old-growth forests (mean

plus/minus standard deviation) in order to determine how strongly stands recovering from management deviate from unmanaged reference conditions.

2.4 | Simulations

We used a simulation approach to analyse the influence of recent environmental changes on development trajectories of stands affected by high-severity bark beetle disturbance. Specifically, we tested if the changes in climate and nutrient deposition of the recent past are already sufficient to set forest development off on an alternative development trajectory. By focusing on stand development under the climatic conditions prevailing in recent years we amend the insights gained from the chronosequence analysis, which represents stand development under past climate.

We employed the simulation model iLand (Seidl et al., 2012a, 2012b) in a stand-level simulation experiment. iLand is an individual-based forest model which can be used to simulate forest dynamics from stand to landscape scales. It is a process-based model in which forest dynamics emerge from demographic as well as biogeochemical processes. Trees compete for resources based on ecological field theory and primary production is modelled using a light use efficiency approach. Tree mortality can occur through ageing, carbon starvation, disturbance (here we simulate wind and bark beetle disturbance, which are the two primary disturbance agents in our study system) and management (Seidl et al., 2012a, 2012b, 2014a, 2014b; Rammer & Seidl, 2015; Seidl & Rammer, 2017). Regeneration is simulated spatially explicitly at a grain of 2 m × 2 m and depends on the abiotic environment as well as the seed input of adult trees,

with the possibility of simulating additional seed input from outside the simulated area (Seidl et al., 2012a, 2012b). The model has been thoroughly tested and parametrized for simulations in the study region (Thom et al., 2017a, 2017b) as well as across a wide range of different forest landscape conditions (Seidl et al., 2012a, 2012b; Honkaniemi et al., 2020; Petter et al., 2020). No site-specific calibration of species parameters was performed for this study.

As detailed information on climate and soils were not available for the disturbed stands studied via simulation modelling (n = 4), we imputed data from sites with similar environmental conditions from nearby Kalkalpen National Park (located 45 km to the west of the DWA) to obtain required model drivers. Kalkalpen National Park is part of the same geological region and is comparable to the study area with regard to edaphic and climatic conditions as well as forest types. Furthermore, iLand has been intensively tested for the forests of Kalkalpen National Park using the same driver data as used here, lending confidence to our model simulations (Thom et al., 2017, 2017b, but see below for additional model tests specifically conducted for this study). Soil and climate data were selected based on elevation, aspect and slope. Time series of historical climate data (temperature, precipitation, radiation, vapour pressure deficit) as well as plant-available nitrogen (based on nitrogen deposition data) reaching back to 1905 were developed previously (Thom et al., 2018). We extended this time series to 1900, the beginning of our simulations for this study, using the approach described in Thom et al. (2018). In addition, time-invariant soil variables (texture and depth) were also extracted from corresponding sites at Kalkalpen National Park. Each sample plot was represented by a one-hectare simulation area.

To evaluate the performance of iLand in the DWA, we ran experiments assessing the ability of the model to reproduce observed patterns of forest dynamics following a pattern-oriented approach (Grimm et al., 2005). Specifically, we simulated natural forest development for 1,000 years under past climate conditions (reference climate period: 1900–2010) and compared results to the empirical old-growth data collected for Rothwald forest. Considering the potential differences between the two site types, this test scrutinized the ability of iLand to reproduce forest dynamics at the DWA in general, and to faithfully quantify the nine attributes under study here. The model was well able to reproduce the observed central tendency and variation in most attributes investigated. The species composition emerging from the simulations also corresponded satisfactorily to expectations for each site type (Appendix S1).

After successfully evaluating iLand for the DWA, we used the model to assess whether recently disturbed forests will develop towards a state similar to the one observed for old-growth forests, or if the environmental changes of the recent past will drive the system towards a new state. To that end, we simulated 2,000 replicated one-hectare stands to account for the stochasticity in the simulation (500 replicates per stand). We recreated stand history by initializing the stands in the year 1900 (the approximate year of the last management intervention) with individual spruce saplings, mimicking the common historic practice of planting spruce after clear-felling (Thom et al., 2018). We then simulated the stands for 115 years under historic climate conditions and under dynamically simulated bark beetle and wind disturbances (with wind data from nearby Kalkalpen National Park). The present condition (post high-severity disturbance by bark beetle) was subsequently generated by forcing a stand-replacing disturbance, killing all mature trees and leaving deadwood on site. From this state (representing a recovery trajectory from management that was interrupted by a natural disturbance), the stands were simulated under current environmental conditions (climate resampled from the years 2010–2020) for 700 years. This represents a temperature increase of 1.26°C, an increase in CO_2 concentration of 105 ppm and an increase of 10 kg ha^{-1} year^{-1} in available nitrogen compared to the initiation of previous stand development after management in the year 1900 (Appendix S1). iLand's dynamic modules for bark beetle and wind disturbances were employed throughout the full simulation period.

To test whether recently disturbed stands develop towards reference old-growth conditions in our simulations we extracted the same nine attributes from the model which we also used in the analysis of the field data. We compared simulated forest attributes to data from old-growth stands of the corresponding site type (higher elevations and steeper slopes, 12 plots). We also calculated the share of simulated replicate stands that fell within the range of old-growth conditions (defined as one standard deviation above and below the mean of conditions observed at Rothwald forest) for each forest attribute in two distinct periods: First, we investigated simulated forests 85–185 years post disturbance, i.e. the age bracket corresponding to the formerly managed stands observed empirically. Second, we analysed results for the last 100 years of the simulation, testing the convergence simulations to old-growth conditions after more than 500 years of simulated stand development (Thom et al., 2017).

3 | RESULTS

3.1 | Forest stand development after management

After the cessation of management, forests developed towards old-growth conditions as they aged. Forests that were last cut <100 years ago were still significantly different from old-growth forests for several attributes. Differences decreased for forests that were last cut >100 years ago. Using NMDS (Figure 2) and the assessment of stress (value representing the difference between distance in reduced dimension space compared to the complete multidimensional space) vs dimensionality we found two dimensions to be a suitable level of complexity for analysis (stress < 0.2). Old-growth and forests that were unmanaged for more than 100 years overlapped strongly in the NMDS. Forests for which management was ceased less than 100 years ago differed more strongly from old-growth and also occupied less two-dimensional space in the NMDS, indicating a generally lower variation in forest
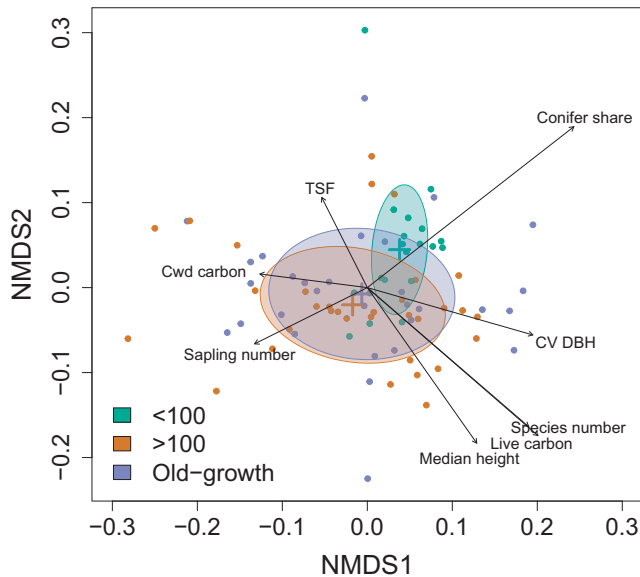
FIGURE 2 Non-metric multidimensional scaling (NMDS) of the nine attributes of forest structure, composition, and functioning. Shown are the first two axes for three groups of stands (cessation of management <100 years ago [n = 20], cessation of management more than 100 years ago [n = 33] ago and old-growth [n = 30]). Crosses indicate the centroids of the three groups in NMDS space. The ellipses indicate the standard deviation around the centroid for each group. Attributes with a significant impact (α = 0.05) are identified with arrows. The length of the arrow is proportional to the strength of the influence. Colored points represent the underlying raw data, colored by groups

conditions. A major driver in the separation of groups in the NMDS was conifer share.

For five out of nine attributes, forests <100 years after the cessation of management differed significantly from old-growth forests. The variation in tree diameters was significantly lower in formerly managed stands compared to old-growth stands ($p = 0.009$, with the median value 31% lower in the former compared to the latter). Stands that were harvested <100 years ago were also significantly different from old-growth stands regarding sapling density ($p < 0.001$, 100% lower median value), and had a considerably higher share of conifers ($p = 0.001$, 180% higher median value). While live tree carbon did not differ between the two groups, carbon in snags ($p = 0.035$) and downed coarse woody debris ($p < 0.001$) was significantly different in younger formerly managed stands compared to old-growth forests. Snag carbon was 10 times higher in young formerly managed stands, with older managed stands and unmanaged stands often having no snags at all. In contrast, downed coarse woody debris was 93% lower in younger formerly managed stands compared to old-growth stands. The deviation between old-growth forests and forests developing after management decreased for stands >100 years after the last clear-cutting. Specifically, only two forest attributes still differed significantly between these two groups, namely the variation in tree diameters ($p < 0.001$, 30% lower in older formerly managed stands compared to old-growth) and the

carbon stored in downed woody debris ($p < 0.001$, 77% lower in formerly managed stands).

Subsequently, we analysed development trajectories relative to old-growth conditions across the chronosequence of plots to elucidate temporal patterns of stand development in more detail (Figure 3). Tree diameter variation declined with stand age and was outside of the range of variability of old-growth forests at the end of our chronosequence (age 221). Median tree height and Total Site Factor both fell within the range of variability observed for old-growth forests for almost the entire age range covered by our chronosequence (from age 30 to age 221). For median height, 84% of all chronosequence stands were within the range of old-growth variation (Total Site Factor: 91%). Sapling density strongly increased with stand age, with 81% of all chronosequence stands falling within the range of variation of old-growth forests. Tree species diversity increased in forests >150 years old, and 54% of the chronosequence stands were within the range of variability of old-growth forests. Conifer share decreased sharply with stand age, falling below 25% in the oldest stands recorded. Among the chronosequence stands, 45% had conifer shares that fell within the range of variation of old-growth forests, which covered a wide range of between 4% and 71% of conifers on total basal area. The variation of carbon stocks in old-growth forests was also large, and chronosequence plots were largely within this range throughout the entire chronosequence investigated. Carbon in downed coarse woody debris was generally lower in chronosequence stands recovering from management compared to old-growth stands, but 47% of the chronosequence stands were still within old-growth variability. For live and snag carbon this share was 79% and 94% respectively. Because of the importance of deadwood, we also report deadwood volume in Appendix S1. Overall, differences between old-growth forests and stands forming a chronosequence of forest development after the cessation of management were less pronounced than expected, due to a very high variation in old-growth conditions. In general, most forest attributes developed towards old-growth over time. Deviations from this pattern were displayed by the variation in tree diameters, sapling numbers and the share of conifers, for which the trajectories move away from the central tendency of old-growth conditions during our 220-year chronosequence.

3.2 | The role of recent bark beetle disturbance

We used simulation modelling to investigate how recent bark beetle disturbance may alter the trajectories of stands recovering from management. Recent bark beetle disturbance slowed the development towards old-growth conditions, but six out of the nine attributes returned to the range of current old-growth forests in the simulations. This indicates that the changed environmental conditions under which the recent disturbances occurred (climate, CO_2, nitrogen deposition) are unlikely to result in trajectories towards fundamentally different system states. However, post-disturbance development differed strongly between forest attributes (Figure 4).
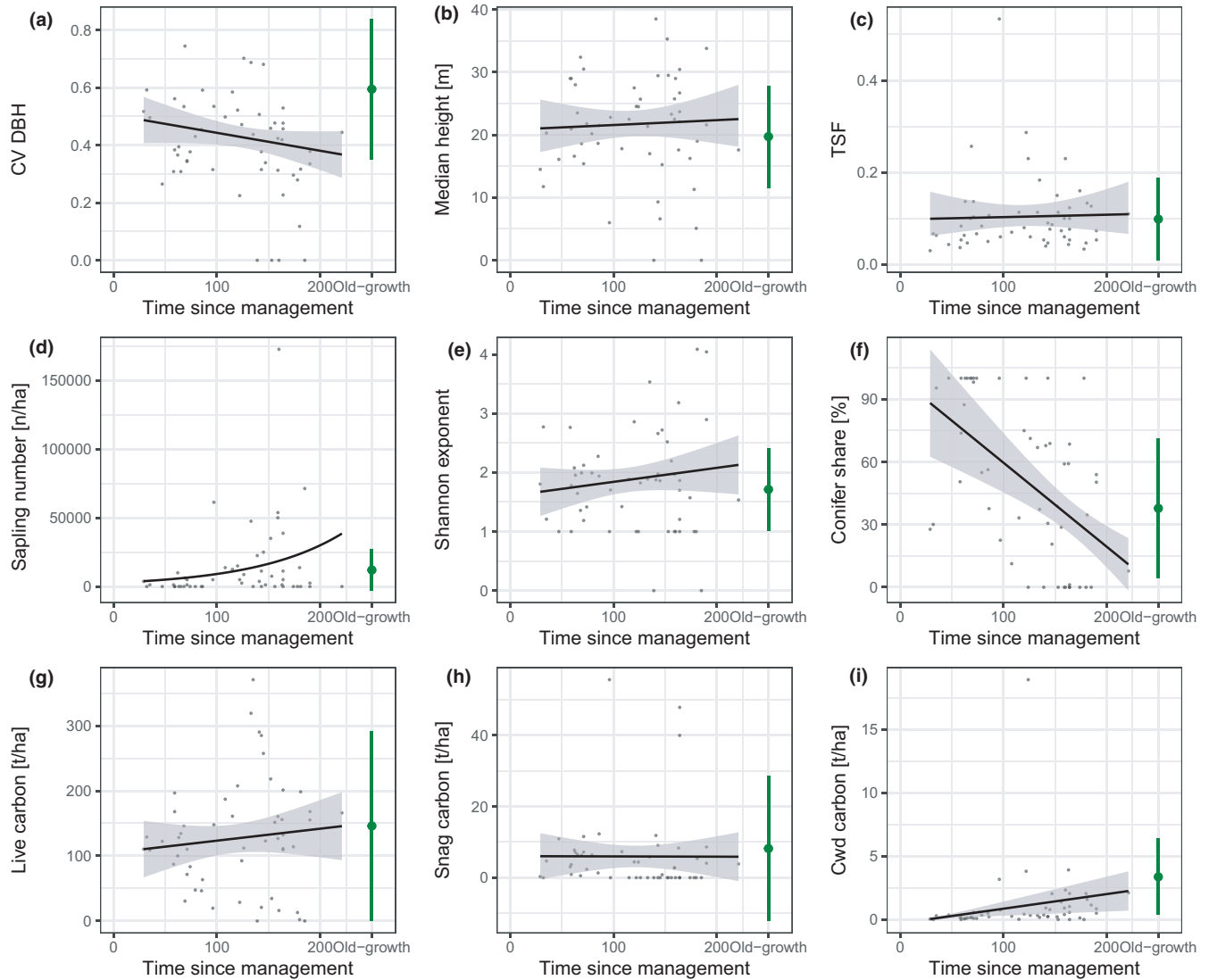
FIGURE 3 Forest development across age, derived as a chronosequence of time since last clear-cutting management. The black line shows the mean with the gray area indicating the variation (standard error). Gray dots are the individual chronosequence plots (n = 33). Green dots and lines show the mean and variation (plus/minus one standard deviation) of old-growth stands (n = 30). Confidence intervals for sapling numbers are too narrow to be visible in the plot

While some attributes returned to the range of variability of old-growth forests within a few decades after disturbance, others took centuries to recover.

Tree diameter variation recovered within 200 years after the simulated bark beetle disturbance. Median tree height, however, only slowly approached old-growth conditions and was still outside of the range of old-growth variation after 700 years under current environmental conditions. Total Site Factor recovered quickly, with 80% of plots reaching old-growth conditions in the first 100 years. Sapling numbers were higher than the observed old-growth values (only 24% of simulated stands were within the range of old-growth conditions by the end of the simulation). Species diversity increased with time since disturbance, and was within the observed range of conditions of old-growth forests. Conifer shares declined over the simulation but remained higher than the conifer shares observed for old-growth forests. Carbon

pools were within the range observed for old-growth conditions already early in the simulations. For 80% of stands live carbon was already within the range of old-growth values in the first 100 years of the simulation. The trajectories of snag carbon and carbon in downed coarse woody debris followed a similar pattern.

4 | DISCUSSION

Primary forests untouched by human land use are becoming increasingly rare. One possible action to counter this loss and ensure that the important roles fulfilled by old-growth forests are sustained (e.g., biodiversity refuge, climate regulation, source of ecological understanding) is to protect formerly managed forests and let them once more develop naturally or actively guide them towards old-growth conditions through restoration efforts (Sabatini et al., 2020).
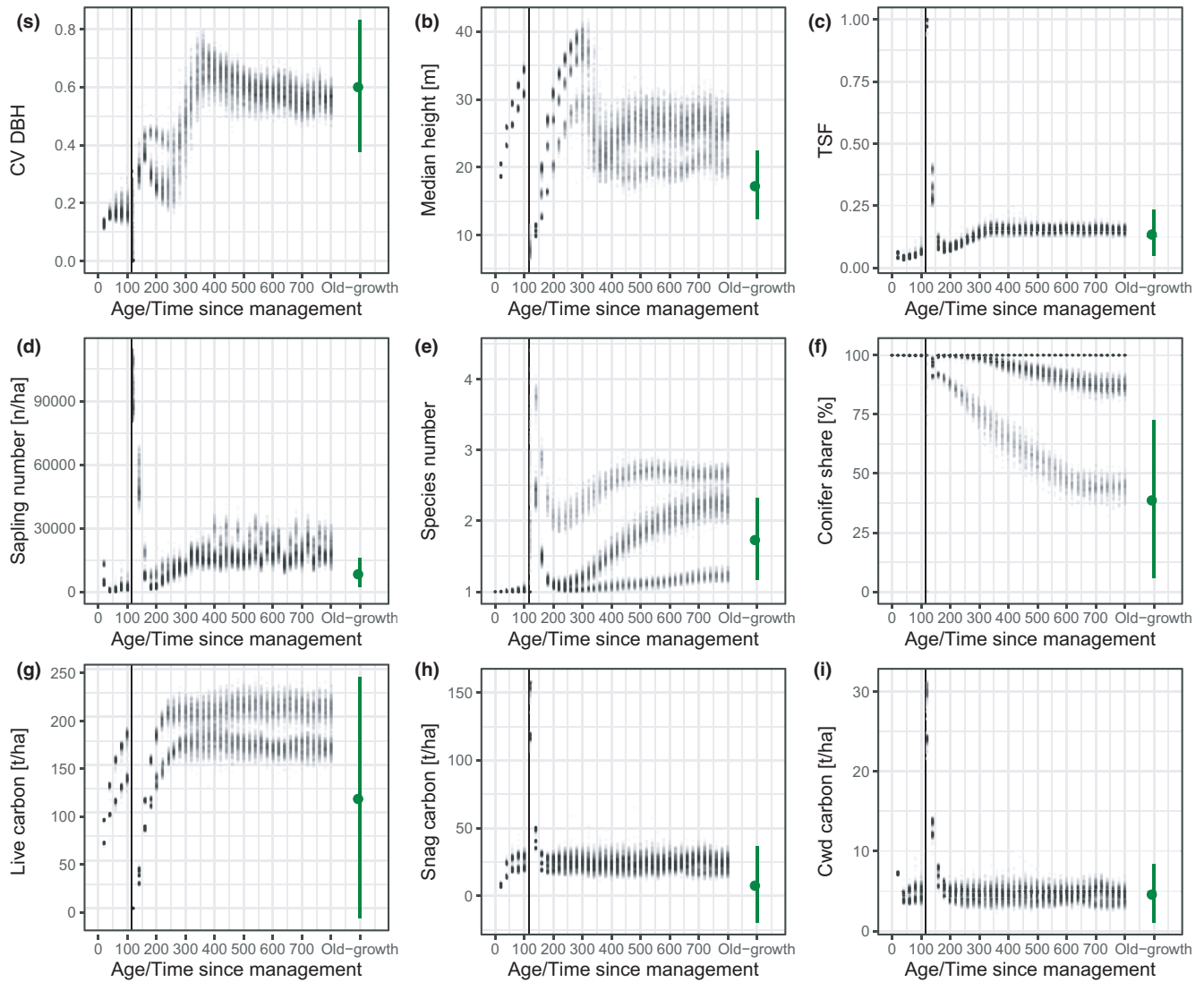
FIGURE 4 The influence of recent bark beetle disturbance on the stand development trajectory after the cessation of management, simulated with the forest landscape model iLand. Vertical line indicates the occurrence of a stand-replacing bark beetle disturbance (as observed for ~5% of the chronosequence plots). Gray dots indicate individual simulated plots (*n* = 2,000). The green dots and lines show the mean and variation of observed old-growth plots of the site type corresponding to the simulated plots (slope plots, *n* = 12)

The speed of reconvergence to old-growth conditions remains unclear, however, and is also contingent on management legacies (Thom et al., 2018). Here we combined field observations across old-growth forests and formerly managed stands with simulation modelling to understand the development of forests after the cessation of management. We further analysed if recent disturbances may set forests onto an alternative development trajectory.

4.1 | Legacies of management on forest development

Our analysis indicates that formerly managed stands return to old-growth conditions in the eastern Alps, but that the recovery is highly variable across forest ecosystem attributes. A key aspect

of analysing the return to a reference state is the definition of the reference conditions used for comparison. We here show that old-growth conditions at DWA are highly variable, constituting a very broad reference range for formerly managed forests (Figure 3, Table 2). This broad range — particularly distinct for attributes of forest functioning — meant that some focal attributes returned quickly to within the range of variability of old-growth forests after the cessation of management. A number of ecosystem attributes even conformed to old-growth conditions throughout the entire chronosequence because of the high variation inherent in old-growth forests. Policies targeting old-growth in conservation thus need to acknowledge that a broad variety of developmental stages exist in old-growth forests.

Beyond the observation that old-growth forests can be very diverse, our study indicates that forests can already be structurally

and compositionally complex and exhibit some characteristics of old-growth at relatively young ages (Donato et al., 2012). Various factors can contribute to structural and compositional complexity arising already in young stands. These can range from high variation in environmental and site factors (Sesnie et al., 2009), to variation in population dynamics, seed availability and dispersal (Barbeito et al., 2009) as well as competition from both trees and other plants (Donato et al., 2012). In addition to variation existing already at early stages, variability can be introduced during stand development. Important factors promoting diverse stand developmental pathways are natural disturbances which can create gaps, promote variety in stand structures and lead to higher levels of deadwood stocks (Meigs et al., 2017; Senf et al., 2020).

Empirical studies investigating the development of formerly managed stands towards old-growth forest conditions are rare, in particular for European forests and for stands where management ceased relatively long ago, like in our case (Paillet et al., 2015). Those studies that do exist are often focussed on the development of deadwood stocks after the cessation of management, and generally report a relatively fast recovery (von Oheimb et al., 2005; Meyer & Schmidt, 2011). Observations for other forest attributes are even rarer: Paillet et al. (2015), for instance, compared French forest reserves with different management histories, and found that forest structure and composition recovered slower than deadwood pools after management.

We note that important old-growth features not assessed here, such as the number of very large trees and the abundance of tree microhabitats such as cavities (Remm & Lõhmus, 2011), may take an extensive time span to recover (Rademacher et al., 2001; Bütler et al., 2013). However, even if the recovery of the full spectrum of old-growth features may take centuries (Rademacher et al., 2001), our study indicates that attributes of value for conservation can emerge already relatively soon after management has ceased. This suggests that an increase in the protected forest area could contribute to tackling the global loss in biodiversity (European Commission, 2020).

We used a chronosequence approach to analyse the long-term development of forest ecosystems, an approach that is commonly applied in ecology but also comes with pitfalls (Pickett, 1989). In using this approach, certain steps must be taken to ensure that the chronosequence is suitable to draw conclusions about the temporal development of ecosystems. A key aspect is to ensure the comparability of the differently aged stands regarding environmental drivers. We here ensured this comparability by choosing stands in close spatial proximity to each other, and stratifying by environmental conditions (elevation, slope, aspect, site type). Frequently, old-growth stands are not entirely comparable with formerly managed stands regarding their environmental drivers, resulting e.g., in differences in productivity, which are often part of the explanation of why old-growth stands remained untouched by humans (Pickett, 1989). This can reduce the inferential potential of a chronosequence considerably. We addressed this problem by distinguishing two distinct site types, and sampling across them in both the old-growth forest (Rothwald) and the formerly managed stands.

Another challenge of applying a chronosequence approach is related to the origin and development of formerly managed stands. While we know the approximate time since the last clear-cutting (the predominant historical management method in the area) from current and historic stand maps (corroborated with our own tree cores), regeneration method and potential stand treatments at younger ages are poorly documented. We excluded all stands that showed visible signs of silvicultural interventions (e.g., cut stumps from tending or thinning operations) to exclude effects from more recent, non-stand-replacing interventions. However, we cannot completely rule out the occurrence of low-intensity management interventions.

4.2 | Resilience of stand development trajectories to recent disturbances and climate change

Another major source of uncertainty regarding the chronosequence is rooted in the implicit assumption that environmental drivers remain constant during the period covered by the chronosequence. This assumption is, however, problematic given the historic changes in climate, CO_2 levels and nitrogen availability (Eastaugh et al., 2011; Dirnböck et al., 2014). To address this particular uncertainty, we used a simulation model to test whether disturbances occurring under current conditions (warmer temperatures, higher CO_2 levels, elevated nitrogen deposition) lead to alternative pathways of stand development. In our simulations, stands disturbed today largely recovered to reference old-growth conditions within a few hundred years under current climate. This recovery towards a reference state that is the result of historical environmental conditions suggests that the forest ecosystems assessed here are resilient to the recent changes in environmental drivers. However, much stronger changes in climate than those observed already are expected for the coming decades. These changes might result in drastically altered forest development and even lead to tipping points in forest structure and composition (Albrich et al., 2020).

An important factor that affects many managed and unmanaged forests in Europe is a high ungulate density promoted by humans (Reimoser et al., 1999). In fact, many forests untouched by management (e.g., the Rothwald forest, serving as a reference for old-growth conditions in this study) have a long history of being used as hunting grounds and therefore often carry legacies of high ungulate densities (Mayer, 1987; von Oheimb et al., 2005). We did not include ungulate browsing in our simulations, which may partially explain the higher sapling density in simulations compared to observations. Also, while a tree species diversity comparable to old-growth forests was already present in young stands in both field data (Figure 3) and simulations (Figure 4), certain species (such as silver fir) can be strongly suppressed through browsing. Ungulates can therefore cause strong alterations in forest composition in the long-term (Didion et al., 2009). While we here focussed on tree species diversity, we did not analyse particular species or species groups (such as late-seral species), which could have been suppressed through browsing, resulting in a potentially protracted return to old-growth conditions (e.g., Seidl et al., 2014a).

4.3 | Outlook and implications

Here we show that old-growth forests can be highly variable in their structure, composition and functioning, and that conditions that are within the range of this variability can already emerge relatively early after the cessation of management (cf. Donato et al., 2012). Regarding some features, in particular carbon stocks, forests recovering from management are already similar to old-growth forests after only a few decades of stand development in our study area. This finding suggests that the protection of forests helps to restore important features of old-growth in landscapes where they have gone largely missing, such as in Central Europe. Restoration of old-growth may also greatly support forest biodiversity (Vandekerkhove et al., 2011; Seibold et al., 2015). Consequently, the protection of forests, alongside integrative forest management strategies (Kraus & Krumm, 2013; Krumm et al., 2020), is an important approach to halt biodiversity loss (European Commission, 2020). We note, however, that quantification of the biodiversity implications of the early convergence of stand development trajectories was beyond the scope of the current study and requires further in-depth analysis (Hilmers et al., 2018).

While many forest attributes returned to old-growth conditions fairly rapidly after the cessation of management, some did not converge over the 220-year chronosequence studied here. The variation in tree diameter and the amount of C in downed deadwood still differed considerably from old-growth forests even after more than two centuries of stand development. This suggests that they could be central indicators for gauging how similar or different to old-growth a forest is (Spies, 2004). The potential (and limitations) of such indicators that can be easily applied by managers deserves additional research in the future. The fact that these attributes can also be actively influenced by management (e.g., deadwood enrichment, structural enhancement thinning; Keeton, 2006; Bauhus et al., 2009) underlines that the emergence of old-growth conditions could also be accelerated by targeted silvicultural measures in managed forests.

Finally, we find that Central European mountain forests are resilient to the ongoing wave of natural disturbances. The changes in environmental conditions observed over the last century have not yet set these forests onto alternative developmental pathways, and they are still likely to converge to conditions represented by current old-growth stands. Continued warming could, however, result in tipping points being crossed (Albrich et al., 2020), which underlines that resilience itself is a moving target for management.

AUTHOR CONTRIBUTIONS

KA and RS developed the study design. KA conducted the field work with assistance from RS and DT. DT and WR helped setting up and conducting the simulations. KA analysed the data and wrote the manuscript with input from all co-authors.

DATA AVAILABILITY STATEMENT

Data supporting the findings of this study are available at https://doi.org/10.6084/m9.figshare.14797803.

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SUPPORTING INFORMATION

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

Appendix S1. Additional results and model evaluation