Universität für Bodenkultur Wien
University of Natural Resources
and Life Sciences, Vienna

Department of Forest and Soil Sciences
Institute of Silviculture
Supervisor: Prof. Dr. Rupert Seidl

Investigating the resilience of forest ecosystems to changing climate and disturbance regimes

Dissertation
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Katharina Albrich

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What we are doing to the forests of the world is but a mirror reflection of what we are doing to ourselves and to one another.

Chris Maser

Preface

The main body of this thesis consists of three papers, two of which have undergone peer review and are published and one which has been submitted and is undergoing peer review at the time of the submission of this thesis. The full papers can be found in the Appendix of this thesis (Section 9, Appendix A-C). In the synthesis sections (Sections 1-6), I aim to frame the three papers and discuss the overarching topics of forest resilience and the use of forest simulation models in forest resilience research. While I give a brief overview of the methods and result of the individual papers within these sections, please refer to the Appendices for the full methodology and results of each study.

For each of these three studies I was the main author and contributor. On each paper, all co-authors contributed throughout the process, particularly through advising on study design and data analysis as well as contributing to the writing and revision of the manuscript but I did the majority of work for each paper in each stage. For the first study ("Simulating forest resilience: A review", Appendix A), I co-designed the study design, did the bulk of the literature review, did the full analysis and wrote the manuscript. For the second paper ("The long way back: Development of Central European mountain forests towards old-growth conditions after the cessation of management", Appendix B), I also co-designed the study, organized and led the field campaign, set up the simulation part of the study, analyzed the data and wrote the manuscript. Finally, for the third paper ("Climate change causes critical transitions and irreversible alterations of mountain forests.", Appendix C), I also co-designed the study, set up the landscape in the model as well as the simulation scenarios, analyzed the data and wrote the manuscript.

The work and time that has gone into this thesis has been substantial and I learned a lot, both on the scientific and personal level. I hope that this thesis in its entirety contributes to the understanding of forest resilience and that the reader will find it interesting and potentially useful and inspiring for their own research.

When referring to this thesis, please either cite the respective papers:

Albrich, K., Rammer, W., Turner, M.G., Ratajczak, Z., Braziunas, K.H., Hansen, W.D., & Seidl, R. 2020. Simulating forest resilience: A review. *Global Ecology and Biogeography* 29: 2082–2096.

Albrich, K., Thom, D., Rammer, W., & Seidl R. (submitted). The long way back: Development of Central European mountain forests towards old-growth conditions after the cessation of management

Albrich, K., Rammer, W., & Seidl, R. 2020. Climate change causes critical transitions and irreversible alterations of mountain forests. Global Change Biology 26: 4013–4027.

Or the thesis in its entirety.

Albrich, K (2021) Modelling the resilience of forest ecosystems in Central Europe to changing climate and disturbance regimes. Dissertation, University of Natural Resources and Life Sciences (BOKU), Vienna p. 147

Abstract

Forests are very important to human wellbeing and global ecosystem functioning. They provide a multitude of ecosystem services and harbor high levels of biodiversity. However, these important roles of forests are under increasing pressure from climate and land use change. To deal with the mounting uncertainty from these changes, we need suitable concepts to guide forest research and management. Resilience can be such a concept to investigate the impacts of future changes on forests. However, resilience is a very broad concept and using it in forest science comes with conceptual and methodological challenges. In this thesis, I contribute to the forest resilience discussion by (1) reviewing the use of forest simulation models for forest resilience, and (2) using field data and a simulation model to investigate the recovery and resilience of Central European mountain forests.

I used several methodical approaches to explore forest resilience in this thesis. In a literature review of studies investigating forest resilience with simulation models, I catalogued the types of drivers and responses of forest resilience addressed as well as which processes seen as important for resilience were included in the models used. Subsequently, I applied a forest simulation model in combination with field data to investigate the recovery of forests after management and disturbances under past climate. Finally, again using a simulation model, I looked at the impact of climate change on species composition and forest structure in a mountain forest landscape.

I found diverse applications of simulation models to forest resilience. The resilience of forest cover to fire was most frequently investigated. The level of process detail varied widely and I identified a clear need for further model development. In the second study, I found that forests in the study landscape were generally able to recover from past management and stand-replacing bark beetle disturbance under past and current climate. However, in the third study, I found strong and irreversible changes in forest structure and composition under climate change, leading to a substantially different forest state.

While forests are often very resilient systems, future changes in environmental conditions may substantially challenge their resilience. Simulation models are a highly useful tool to address the challenges forests are facing and we need to further invest into model development to aid in understanding and supporting forest resilience.

Keywords: forest resilience, forest recovery, disturbances, protected areas, simulation model, iLand, landscape model, climate change, forest management, ecosystem functioning

Kurzfassung

Wälder spielen eine wichtige Rolle für das menschliche Wohlergehen und das Funktionieren von Ökosystemen weltweit. Sie stellen zahlreiche Ökosystemleistungen bereit und beherbergen eine Vielfalt an Arten. Diese Leistungen von Wäldern geraten jedoch durch Klima- und Landnutzungswandel zunehmend unter Druck. Um mit den durch diese Änderungen entstehenden Unsicherheiten und Herausforderungen umzugehen, sind sinnvolle Rahmenkonzepte für die Waldbewirtschaftung und -forschung nötig. Resilienz ist ein vielversprechendes Konzept hierfür. Jedoch ist die Resilienzforschung ein sehr breites Feld und die Anwendung des Resilienzkonzepts bringt einige methodologische Herausforderungen mit sich. In dieser Dissertation trage ich zur Waldresilienzforschung bei, indem ich (1) die Anwendung von Simulationsmodellen für Resilienzfragen analysiere und (2) ein Simulationsmodel anwende, um die Erholungsfähigkeit und Resilienz von zentraleuropäischen Wäldern zu untersuchen.

Ich verwendete in dieser Dissertation mehrere methodische Ansätze um Waldresilienz zu untersuchen. Zuerst führte ich eine Literaturstudie durch und erfasste, welche Treiber und Reaktionen von Ökosysteme untersucht wurden. Des Weiteren erhob ich, welche der Prozesse, die in der Literatur als wichtig für Waldresilienz gesehen werden, in Modellen implementiert sind. In der Folge wendete ich selbst ein Simulationsmodell in Verbindung mit einer Chronosequenz aus Felddaten an, um die Erholung von Waldbeständen nach Bewirtschaftung und natürlichen Störungen unter vergangenem und derzeitigem Klima zu untersuchen. Schließlich untersuchte ich die Auswirkungen von Klimawandel auf Artendiversität und Waldstruktur in einer weiteren Simulationsstudie.

Ich fand vielfältige Anwendungen von Simulationsmodellen in der Waldresilienzforschung. Am häufigsten wurde die Resilienz von Waldbedeckung gegenüber Feuer untersucht. Die Implementierung von Prozessen in Modellen variierte stark und ich identifizierte den Bedarf für weitere Modellentwicklung. In der zweiten Studie stellte ich fest, dass sich die untersuchten Bestände unter historischem und zukünftigem Klima meist von früherer Bewirtschaftung und Borkenkäfer erholen konnten. Im Klimawandel änderten sich in der simulierten Waldlandschaft jedoch sowohl Baumartendiversität als auch Waldstruktur substanziell.

Wälder sind meist grundsätzlich resiliente Ökosystem und können sich von Störungen erholen. Jedoch stellen die zukünftigen Umweltänderungen eine große Herausforderung für die Resilienz von Wäldern dar. Simulationsmodelle sind ein wichtiges Werkzeug um diese Änderungen zu untersuchen und weitere Modellentwicklung ist nötig, um Waldresilienz zu verstehen und zu fördern.

Stichwörter: Waldresilienz, Walderholung, Störungen, Klimawandel, Simulationsmodell, iLand, Landschaftsmodell, Waldbewirtschaftung, Schutzgebiete, Ökosystemfunktionen

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1 Introduction

The world's forests are facing unprecedented challenges due to climate and land use change. Within the last century, forests have been increasingly exposed to climate extremes, changing disturbance regimes with both a general increase in disturbances and the introduction of novel disturbance agents, and increasing land demands for potentially conflicting land uses (Lambin & Meyfroidt, 2011; Ramsfield *et al.*, 2016; Seidl *et al.*, 2017).

Forests are important hotspots of biodiversity (Parrotta *et al.*, 2012; Rahbek *et al.*, 2019) and are crucial for human well-being because they provide and support ecosystem services such as, among others, fuel, food, clean water, medicinal plants and recreation (MEA, 2005). Additionally, forests play an important role in climate change mitigation and adaptation through sequestering and storing carbon (Fahey *et al.*, 2010; Vass & Elofsson, 2016), dampening local climate extremes (De Frenne *et al.*, 2019) and providing biomass to replace fossil fuel products (Gustavsson *et al.*, 2006). Given these diverse and important roles of forests in the biosphere, the future of forests under changing conditions is of high interest.

We largely lack historical equivalents for the conditions forests are facing under climate change, particularly in conjunction with human influence (Hobbs *et al.*, 2006; García-López & Allué, 2013). Additionally, considering the uncertainty involved in rapidly evolving climate and social change, we need to understand and prepare for the future of forests under a wide array of scenarios (Millar *et al.*, 2007). Under conditions which are outside the historical range of variability of a system, the likelihood of abrupt changes in system behavior increases (Seidl *et al.*, 2016). This may come with lengthy recovery times after disturbances or even novel ecosystem states with substantial changes in forest structure, composition and functioning. These uncertain future conditions for forests and forest-based ecosystem services challenge researchers and practitioners and call for methodological frameworks which aid the investigation and discussion of these developments and their uncertainties. One way of conceptualizing these system reactions is the theory of resilience. Resilience is a term used in many disciplines, from engineering to psychology and, of particular interest for this thesis, ecology (Thorén, 2014). Within the discipline of ecology, resilience was pioneered by Holling (1973) and has evolved continuously, spawning a multitude of definitions and sub-definitions (Grimm & Wissel, 1997). It has also become a popular "buzzword" in policy documents and discussions, however often lacks clear and actionable definitions in this context (Carpenter *et al.*, 2001; Standish *et al.*, 2014).

Frequently used definitions in ecological research are engineering resilience, ecological resilience and socio-ecological resilience. Engineering resilience centers on the time needed to recover from a disturbance, assuming the presence of a single equilibrium state that a system can return to after a disturbance (Pimm, 1984). Ecological resilience (Holling, 1973; Holling & Gunderson, 2002) focuses on the ability of a system to maintain its functions, structures and feedbacks in the face of disturbance. It acknowledges the presence of multiple equilibrium states including the possibility that a system may not return to its state prior to disturbance but rather shift to an alternative state. Socio-ecological resilience focuses on coupled human and natural systems and their ability to stay within a desirable state-space (i.e., maintain their structures, functions, and services as desired by society) under disturbance (Walker *et al.*, 2004). It highlights the role of adaptation in particular. Within this thesis, I generally use a definition falling under "ecological resilience".

While resilience can be a helpful concept for dealing with uncertainty and large variations in environmental drivers, applying it in forest research poses challenges. Trees, the main defining organisms of forests, have long life-cycles and are stationary, prolonging the system's response times. This means that the impact of changes in environmental drivers may become apparent only years to decades later. Even though abrupt changes in forest state variables are possible, for example through forest disturbances, assessing the resilience of the system to these disturbances requires long observation times due to the long timeframe of processes of recovery and adaptation.

These specific challenges of investigating the resilience of forests to varying drivers profoundly affect the methods that can be used. Experimental manipulation, for example, a common practice in other systems such as lakes, is hard to implement in forests. Similarly, it is difficult to observe these changes in an empirical manner, as observation times would need to be very long. While both experimental and observational research in young forest stages after disturbances can be insightful and produce important knowledge about the resilience of forest ecosystems (Hansen *et al.*, 2018; Turner *et al.*, 2019; Hoecker *et al.*, 2020), it only covers a small part of the life-cycle of trees and is limited in its spatial extent. In many cases old-growth stages are of particular interest given not only their important role in relation to biodiversity and ecosystem services (Luyssaert *et al.*, 2008; Nagel *et al.*, 2013) but also their role in understanding natural forest development and guiding the development of close-to-nature forest management approaches (Wirth *et al.*, 2007; Martin *et al.*, 2021).

In many such cases, other classical ecological methods such as chronosequences (space-for-time substitution) can be informative by using forest stands along an age gradient to understand long-term recovery after natural disturbance or management interventions (Pickett, 1989). Such approaches however are challenged by the underlying assumption of stationarity in regards to environmental drivers (such as e.g. climate or nutrient availability). Without this stationarity, the equivalence between stands of different ages cannot be assumed. However, even in recent historical climate this stationarity is no longer a given and in regards to future climate and disturbance regimes cannot be assumed.

Therefore, models play an important role in addressing future challenges to forests. They allow for simulating the response of forest ecosystems over large temporal and spatial extents. Another, equally important advantage of models is that multiple, interacting drivers in various combinations can be simulated. When researching forest resilience, where we often encounter many interacting drivers acting upon a forest ecosystem at the same time (e.g. climate change and human land use, wind and bark beetles), this is an important objective in many research endeavors.

Many forest simulation models or models applied to forests exist. Each model is built with a certain set of assumptions and presumed use cases in mind. This inevitably has an impact on model design, and eventually, on which questions can be answered confidently with a certain model. Using models in ways they were not built for increases the risk of results being less robust than expected. Model choice should be driven primarily by suitability for the question at hand, meaning that the most complex model is not always necessarily the best model.

At the same time, model development is ever ongoing and increasingly complex models are being developed. As resilience is being discussed more frequently also outside science, namely in forest policy and management (Bone *et al.*, 2016; Newton, 2016; Stephens *et al.*, 2016; Sotirov & Storch, 2018) research of resilience and resilience modelling efforts arise also from communities other than the traditional resilience field, emphasizing the need to properly ground this research in ecological theory. This means that a greater variety of models are becoming available to use for resilience questions. This increasing diversity in modelling approaches strengthens resilience research. However, it requires a lot of diligence in selecting models and judging the suitability and robustness of modelling approaches to properly address the increasing challenges forests are facing at present and in the future.

2 Objectives

This thesis seeks to contribute to the forest resilience discourse by adding to the knowledge about simulation modelling as a tool to understand the resilience of forest ecosystems to the changes in environmental and anthropogenic drivers. Additionally, it applies simulation modelling to understand the response of Central European mountain forests to climate change and anthropogenic impacts in particular. The thesis consists of three chapters addressing these objectives from different angles:

(1) It highlights new avenues for model development and application to improve the understanding of forest resilience by providing a literature review about the use of simulation models in investigating forest resilience.

(2) In a coupled approach using space-for-time substitution and a forest landscape model, it investigates the legacies of human impacts and disturbances on protected, formerly managed forests.

(3) Finally, looking to the future in a fully model-based study, it tests the influences of climate change and the buffering effects of topography in a mountain forest landscape on forest composition and structure.

3 Materials and methods

The three papers making up this dissertation are thematically and methodically connected and build upon each other. Paper I (Appendix A) is a literature review of the use of forest simulation models in investigating forests resilience. Paper II (Appendix B) and Paper III (Appendix C) present model applications. Paper II uses a combined approach of a chronosequence of field data and a simulation model to investigate the recovery from management and disturbance. Paper III is a simulation study with multiple topography scenarios to investigate the impact of climate change on forests structure and species composition.

3.1 Study landscapes

The field work and simulation sections of this thesis focuses on two landscapes in the Austrian Alps, the Dürrenstein Wilderness Area in Lower Austria (Figure 1, green panels) and the Stubai Valley in Tyrol (Figure 1, blue Panels).

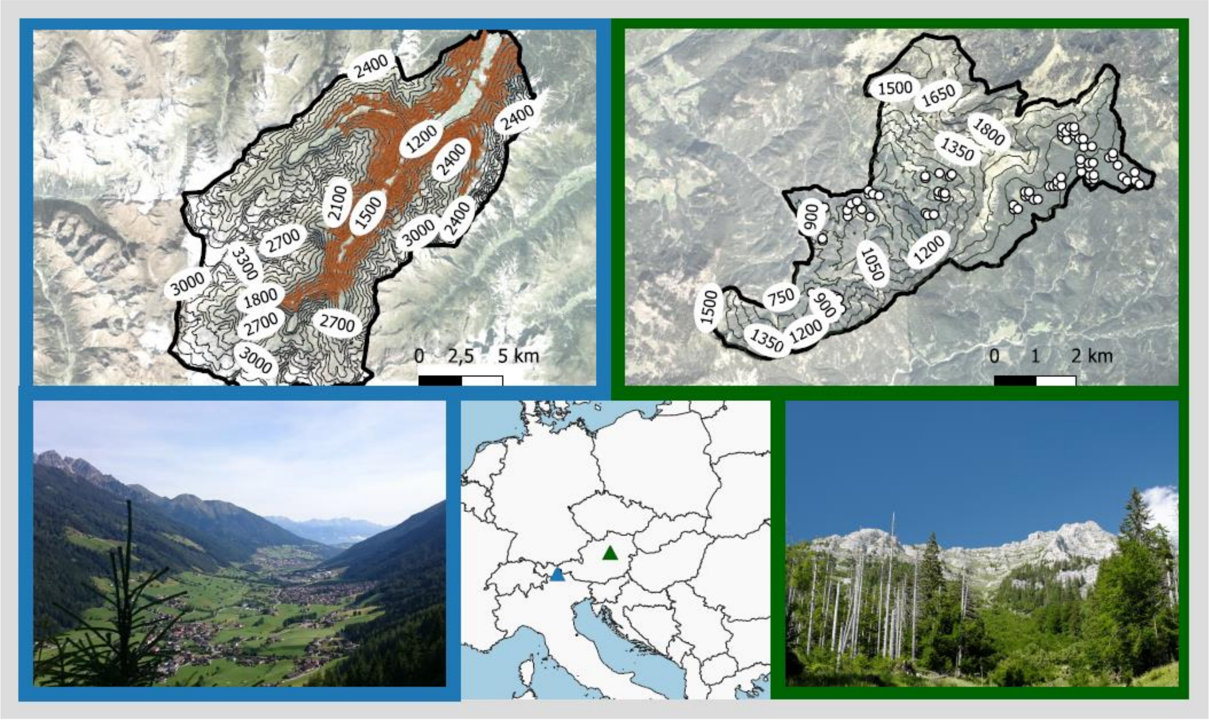

Figure 1: Overview map of study areas presented in this thesis: green panels show the Dürrenstein Wilderness area (dots in top green panel are sample plots used in the study), the blue panels show the Stubai Valley (brown area is the simulated forest area). Photos by Katharina Albrich (left), Rupert Seidl (right)

3.1.1 Dürrenstein Wilderness Area, Lower Austria

The Dürrenstein Wilderness Area (DWA) is located in the Northern Limestone Alps in Eastern Austria, in the province of Lower Austria (47.10°N, 11.29°E). It's elevation ranges from around 650 m a.s.l. to 1878 m a.s.l. (peak of mount Dürrenstein) and it is an IUCN Category Ib protected area. It's origins as a protected area lie in the history of the primary forest remnant "Rothwald", located in the eastern part of the current protected area. This forest was spared even when large-scale harvesting was going on in the neighboring forests (Pekny, 2012). This is due to a combination of ownership disputes, difficulties in wood extraction and a forest owner (Albert Rothschild) who recognized it as an area of natural beauty as well as a promising hunting area and thus kept it from being logged. The area was first formally protected under the Nazi regime (in 1943) after it was taken from the Rothschild family. After the Second World War, ownership was returned to the Rothschild family but the Rothwald remained under protection and the protected area was progressively enlarged through contributions of formerly managed forests under ownership of both the Rothschild family and the Austrian Federal Forests. It was declared an IUCN Category Ib protected area in 2003 and was extended to its current size of 3.449 ha in 2013 (Pekny, 2012; Splechtna & Splechtna, 2016). The area has a rich history of forest research, going as far back as 1910 when a first sample plot was established during a visit of the Austrian Foresters' Association (Mayer, 1987).

The forests in the DWA are dominated by European beech (*Fagus sylvatica* L.), Norway spruce (*Picea abies* (L.) Karst.) and Silver fir (*Abies alba MILL.*). The lower elevations generally have higher conifer shares with beech shares increasing in higher elevations (Splechtna *et al.*, 2005). More recently managed stands have higher shares of Norway spruce (Appendix B). The climate is submaritime, characterized by long winters and relatively cool summers. Precipitation follows a bimodal distribution, with peaks in summer and winter (Splechtna *et al.*, 2005). While no continuous climate timeseries is available for within the Wilderness Area, mean annual temperature for a nearby weather station (Lunz am See, 608 m a.s.l) is 7.27 °C and mean annual precipitation sum is 1676 mm (average 1988-2017, Schönemann, 2019). The region's geology is characterized by dolomite and limestone and soils are primarily Rendzinas and relictic loams (Splechtna & Gratzer, 2005).

3.1.2 Stubaital, Tyrol

The Stubaital (ST) is a mountain valley in the province of Tyrol in western Austria (47.10°N, 11.29°E). Due to the mountainous topography, it exhibits a large elevation gradient, from the valley bottom at 900 m a.s.l to the highest peaks at above 3,500 m a.s.l. The forests are dominated by Norway spruce at lower elevations with gradually increasing shares of European larch (*Larix decidua* MILL.) at higher elevations. The timberline is formed by Swiss Stone Pine (*Pinus cembra* L.) with admixed larch. For the period 1961-2014, the mean annual temperature was 4.1°C (decreasing from 7.2°C to 0.6°C with increasing elevation) and the mean annual precipitation sum was 998 mm (increasing with elevation from 826 to 1,163 yr^{-1}). The geology of the ST is dominated by metarmophic materials (Orthogneiss and Paragneiss) with localized occurrences of limestone. The ST exhibits a complex land-use mosaic of forestry, grassland management (including cattle-grazing on high elevation pastures) and tourism as well as permanent settlements (Tappeiner et al., 2008). Here, I focus on the forested area of the valley, around 4800 hectares of forest in total.

3.2 Methods

3.2.1 Literature review

I conducted the literature review using online literature databases (Scopus and Google scholar) with a variety of keywords surround resilience topics (see Appendix A for details). After preliminary vetting, 119 studies were included in the review. The analysis focused on the types of resilience questions that were addressed in these studies, particularly the drivers and responses (to what and of what, *sensu* Carpenter *et al.*, 2001) and which groups of models were used for these studies. The core of the review is a catalogue of processes compiled from literature which are deemed important for resilience. For each model application, I assessed whether the model included that process or not. A detailed description of the literature review can be found in Appendix A.

3.2.2 Field survey

3.2.2.1 Survey design and data collection

I chose a chronosequence approach for which I visited 87 sample plots within the DWA with a field team in the summer of 2017, across both the primary forest and formerly managed stands. The sampling plot locations were determined by a combination of targeted selection and a sample grid. We chose mature stands using historical and current forest maps provided by the DWA administration. The chronosequence (or space-for-time) approach is a common method in ecology, particularly when working in long-lived systems such as forests, where direct long-term observations are difficult to implement. A few considerations need to be taken into account to ensure the chronosequence is methodically solid, in particular in choosing the reference end-point of the sequence (Pickett, 1989) which here is represented by the primary forest Rothwald. To construct a meaningful chronosequence, we were careful to sample across the age strata as well as two elevation strata (more sheltered, lower elevation stands with a higher share of conifers and higher elevation stands in rougher terrain with a higher share of beech) both within the primary forest and in the formerly managed stands. Four of the plots were excluded from the main chronosequence as they experienced a recent stand-replacing bark beetle disturbance. They were, however, used for the simulation part of the study (see below). Within the stands, the precise location of the sample plots was determined using a sample-grid (100 m distance between points) to avoid bias in selecting the sample location while in the field.

The sample plots were set up as transects which followed the horizontal contour lines. The transect was 50 meters long and 4 meters wide (200 m^2 total plot area) and subdivided into 50 subplots of 2x2 meters. On the plot, the field teams recorded the DBH (diameter at breast height) of all trees with a diameter larger than 7 cm. On each plot, four tree heights were measured. Standing snags were recorded with their height, diameter and decay stage. Coarse woody debris was recorded on three 10-meter-long transects, radiating out from the center of the plot. On each piece of deadwood (>7 cm diameter) that intersected the transects the diameter and its angle were measured as well as the decay stage. Two of the subplots (one at each end of the plot) were designated as regeneration plots, where stems up to 4 m height were counted by size class. At the center of each transect and at the two regeneration plots, a light measurement (based on a hemispheric photo) was taken with a Solariscope (Ing.-Büro Behling, 2015).

3.2.2.2 Data analysis

After data collection, I calculated nine indicators across the categories forest composition, forest structure and forest functioning (see Table 1 and Appendix B for details) on the plot level. As a first step the plots were separated into three groups, young formerly managed stands (last clear-cut less than 100 years ago), old managed stands (last clear-cut more than 100 years ago) and unmanaged stands. For this groups, the indicators were analyzed using a non-metric multidimensional Scaling approach (NMDS) to graphically depict the differences between formerly managed and unmanaged stands. I tested for differences between the groups using PERMANOVA. Group differences for individual indicators were tested using a Kruskal-Wallis Rank Sum Test with a subsequent Dunn's test (with Benjamini-Hochberg adjustment for multiple comparisons).

To visualize the development across the chronosequence, I used polynomial (second degree) functions for the indicators over the age spectrum. I visually assessed whether the ranges (mean plus/minus standard deviations) of the oldest formerly managed stands overlapped with the range of the old-growth forest. I also calculated the proportion of stands that fell within the old-growth range. A more detailed description of the analysis can be found in Appendix B.

Table 1: Indicators calculated from field data. DBH stands for diameter at breast height.

Indicator	Calculated from	Additional information
Coefficient of variation of DBH	Measured tree diameters	
Median height [m]	Measured heights	
Total site factor [0…1]	Measured (Solariscope)	Direct and diffuse light intensity relative to open areas (Ing.-Büro Behling, 2015)
Number of regeneration individuals [n/ha]	Number of saplings > 4 m counted on regeneration	
Effective number of species (Shannon exponent) [n]	Species shares of basal area (calculated from measured DBH)	Exponent of the Shannon index
Conifer Share [%]	Basal area shares of conifer	Species: *Picea abies*, *Abies alba*, *Larix decidua*, *Pinus sylvestris*, *Taxus bacchata*
Life biomass carbon [t/ha]	Measured tree diameters	Allometries implemented in iLand (Thom *et al.*, 2017a)
Snag carbon [t/ha]	Tree volume (measured diameters, heights from height curves), reduction factors based on decay stage	Approach from Ford & Keeton (2017), with decay class reduction factors from Harmon *et al.* (2011)
Coarse woody debris carbon	Measured diameters from transects	Volume calculation from Böhl & Brändli (2007), decay class reduction factors from Harmon *et al.* (2011)

3.2.3 Simulation modelling

3.2.3.1 The model – iLand

iLand is a spatially explicit, process-based forest landscape model. It simulates forest dynamics on the landscape scale as an emergent property of demographic processes on the level of individual trees. Detailed descriptions of iLand can be found in Seidl *et al.*, (2012a) and Thom *et al.* (2017b). The model source code and executable as well as an in-depth Wiki can be found at iland-model.org. I briefly describe the core processes and modules of iLand in the following.

- Basic demographic processes

iLand is based on ecological field theory and simulates trees as individual agents. Each tree is defined by its neighborhood field of influence, specifying its competitive status. A continuous light influence field is simulated across the whole landscape and trees compete for light.

Tree growth is modeled using a Light Use Efficiency approach (Landsberg & Waring, 1997). The amount of utilizable photosynthetically active radiation (uAPAR) is determined on the stand level by environmental drivers (air temperature, vapor pressure deficit, water availability). GPP is calculated from uAPAR modified by nutrient availability and CO_2 fertilization effect. NPP is calculated as a constant fraction of GPP and assigned to each individual tree based on its share of uAPAR. Age effects on growth are applied at this point and carbohydrates are allocated to tree carbon pools hierarchically (roots, foliage, reserve and finally stem growth). Stem growth is dynamically adapting to competitive status of the tree with variable allocation between height and diameter growth (Seidl *et al.*, 2012a).

Mortality is simulated probabilistically by combining an intrinsic mortality effect (based on tree age) and a stress mortality effect (based on the carbohydrate reserves pool). If a tree cannot meet the carbohydrate requirements to replace the basic structural turnover (root and foliage), it is considered stressed. Mortality happens if a tree's combined mortality probability (intrinsic+stress) exceeds a random number between 0 and 1 (Seidl *et al.*, 2012a).

Regeneration processes include spatially explicit dispersal of seeds, establishment and sapling growth and competition (Seidl *et al.*, 2012b). Fecundity is modulated by the occurrence of seed years. In addition to seed availability, seedling establishment is influenced by environmental variables, namely temperature limitations, water availability and light availability (competition). Sapling growth is modelled using a mean tree approach with sapling growth again determined by environmental factors and light availability. Trees move from the regeneration simulation module to the individual based modelling structure at the height of 4 m.

- Natural Disturbance

In iLand, several natural disturbance agents can be simulated dynamically: wind (Seidl *et al.*, 2014a), bark beetle (Seidl & Rammer, 2017), and fire (Seidl *et al.*, 2014b). The **wind** module simulates wind damages based on wind event characteristics (speed, duration, wind direction), topography and stand characteristics (tree species characteristics, height, and stand edges). Depending on species and soil characteristics (frozen or unfrozen soil) trees can be broken or uprooted. The **bark beetle** module is primarily driven by climate, bark beetle phenology and vegetation characteristics (tree species, age, stress, and tree defense mechanisms). Bark beetle dispersal is simulated spatially explicitly and bark beetle populations react to the availability of host trees from e.g. wind disturbance (Seidl & Rammer, 2017). The **fire** module (not used in this thesis) models wildfire based on weather and vegetation characteristics (Seidl *et al.*, 2014b). Beyond bark beetles, a general simulation module for **biotic agents** is available which allows for the simulation of various kinds of biotic agents including newly emerging pests and diseases (Honkaniemi *et al.*, 2021).

- Management

iLand has multiple avenues to simulate management. A basic management interface and an Agent Based Management Engine (ABE), allowing for dynamic simulation of management with multiple agent and in response to changing environmental conditions (Rammer & Seidl, 2015).

3.2.3.2 Set-up of simulation and simulation design

- Dürrenstein Wilderness Area

For the DWA, rather than setting up a full landscape of the entire area, I used a plot-level/generic landscape approach focusing on the plots disturbed by bark beetle. Sample plots were represented by one-hectare cells (resource units). I replicated each of the four plots which were affected by stand-replacing bark beetle disturbance 500 times to cover model stochasticity and arranged them into a rectangular landscape. Environmental drivers (soil and climate) were derived via a matching approach (based on elevation, aspect and slope angle) from the database of the Kalkalpen Nationalpark (Thom *et al.*, 2017b), which is located nearby and features very similar environmental conditions. The suitability of this matching approach was evaluated by comparing the vegetation occurring under these conditions to the data measured in the field. For the simulations, I recreated the vegetation development from the last management intervention around 1900 with a historic climate, CO_2 and plant-available nitrogen time series reaching to 2017. From then on forward, the climate was held constant (with climate sampled from the period 2010-2020) to the end of the full 700-year simulation period. A detailed explanation of this set-up can be found in Appendix B.

- Stubaital

A detailed description of the preparation of model inputs for this study landscape can be found in Seidl *et al.* (2019). For this study, I prepared a specifically designed climate scenario that allows for assessing the impact of a strong climate change signal over long time spans. Briefly, the scenario is based on the GCM-RCM combination of HadGEM2-ES and CLMcom-CCLM4-8-17 driven by RCP 8.5 (Seidl *et al.*, 2019) and I produced a climate timeline with a stepwise change (1°C change on each step, 1000 years equilibration time at each temperature step) by sampling from periods within the original scenario that matched the temperature step. Temperature increases up to +6°C (relative to historical climate) through these steps and then returns to +0°C again in a stepwise manner, resulting in 13000 total simulated years per run. Precipitation stays at a stable level throughout the simulation but varies between simulated years, focusing on precipitation reduction, with 4 different levels (historical mean annual precipitation and -10%/-20%/-30% relative to historical MAP). While different climate scenarios and models predict widely varying precipitation scenarios, the reductions in this simulation study are within the range of precipitation change forecast by the scenario and climate model combination used here.

I also designed a specialized set-up to investigate the effect of topography on forest resilience to climate change. I created three topography scenarios: a complex scenario that represents the actual natural landforms of the landscape; an intermediate scenario, which is a simplified landscape created by averaging and binning the climate and soil variables and an uniform scenario, where the entire landscape runs under uniform environmental drivers. This allowed me to analyze how topographic variability contributes to resilience by buffering climate change impacts. The topography scenarios came with two different versions of seed dispersal. In addition to the seeds from mature trees growing on the landscape, additional seeds can enter the landscape from its borders. In the complex topography scenario, only a small area representing the valley entrance acted as seed source, mimicking the natural conditions, where the rest of the valley is surrounded by high (currently partially glaciated) mountains, not allowing for seed input from these sides. In the uniform scenario, the entire surroundings of the landscape acted as a seed source, as could be the case in a flatter, less limited landscape. The intermediate scenario was run both with the small and the large seed area. All combinations of precipitation scenarios and topography scenarios were simulated 10 times to account for stochastic processes in the model. In the analysis, I compared the species composition and diameter distribution at each temperature step to analyze the difference between the warming and cooling trajectory for each topography and precipitation scenario. A more detailed description of the entire set-up and analysis can be found in Appendix C.

4 Results

4.1 Use of simulation models in forest resilience research

We found a diverse array of simulation models being used to investigate forest resilience. They range from simple frameworks of differential equations to complex forest landscape simulators or Dynamic Global Vegetation Models. While the simpler models are often custom-built for the research question at hand, more complex models have usually been developed for other applications and subsequently applied to resilience questions. The spatial and temporal extent of model applications varied widely, from plot-level to global and from a few years to several millennia. Geographically, resilience modelling studies were unevenly distributed, with hotspots in Europe and the Americas. The temperate and tropical forest biomes were particularly well represented. The full results of the study can be found in Appendix A, in the following I briefly present the two main results, focusing on the type of questions being investigated and the representation of important resilience processes in models.

4.1.1 Drivers and responses of resilience investigated with forest simulation models

I grouped all studies by the drivers (resilience to what) and ecosystem responses (resilience of what) investigated, which allowed me to more easily compare studies operating under different definitions of resilience. The most frequently modelled drivers were fire, climate change and land use, while the most frequent responses were forest cover, forest structure, forest functioning, and forest composition. The most frequent driver-response combinations were resilience of forest cover to fire and resilience of forest functioning to climate change. While a variety of models was used for each combination of drivers and responses, there were a few patterns of model applications, particularly in relation to forest responses (of what): forest composition, structure and functioning were most frequently modelled with forest landscape models, while forest cover was most frequently simulated with simpler analytical models. In regards to drivers, fire was most often simulated with forest landscape models, climate change with landscape models and Dynamic Global Vegetation Models and land use was simulated with a large variety of model types.

4.1.2 Representation of resilience processes in forest simulation models

I grouped the processes into three groups: regeneration, legacies and soil. Naturally, not all models included all processes. Here, I highlight a selected few processes and model components. The full set of processes can be found in Appendix A.

Only 41 % of studies included any regeneration processes. Generally, regeneration was simulated as one single process rather than as an emergent property of multiple processes (such as dispersal, establishment, seedling growth and survival). Among influences on regeneration success, light availability and reproductive maturity (need for trees to reach a certain age to be able to produce propagules) were most frequently considered. Other influences, such as herbivory and competition from non-tree vegetation were only rarely considered. Legacy processes were infrequently simulated in the studies we found (33 % of model applications). The most frequent type of legacy we found were life trees remaining after disturbance. Other legacy types, such as seed banks were infrequently considered despite their large importance in certain systems. Soil processes were the most frequently implemented group of processes (46 % of model applications). Water availability was the most frequent and often only included soil process. Nutrient cycles (mainly nitrogen) were simulated in around 20% of model applications. Other soil processes, such as erosion, were included only very infrequently. The most detailed representation of soil was found in the models used to address resilience to climate change.

4.2. Recovery of mountain forests after management

4.2.1. Development of newly protected, formerly managed stands

In the empirical part of the study, I created a chronosequence from 83 plots (located in formerly managed stands as well as stands without any management history) to investigate the development after the end of management for nine indicators. The old-growth stands were extremely diverse and covered a wide range of indicator values. Formerly managed stands were generally able to return to within the old-growth range during the observed chronosequence, with the exceptions of the coefficient of variation of diameters (dbh) and conifer share. I also calculated the share of plots that fell within the range (mean plus/minus standard deviation) of old-growth forest. This share was over half for all indicators except for conifer share, where only 45% of plots were within the old-growth variation. Overall, the formerly managed stands developed to be within the (wide) old-growth range over the chronosequence.

4.2.2. Recovery of forests after stand-replacing disturbance

In the simulation of the stands affected by stand-replacing disturbance, I found that most of the indicators were also recovering to within the old-growth range under current climate over the multi-century simulation duration with the exception of the regeneration stem number, median height and conifer share, which were all higher than in the observed data. So, while a majority of indicators recovered to within old-growth range, there was still some difference from the old-growth state even after several hundred years of natural forest development under current climate. The full results can be found in Appendix B.

4.3 Resilience of mountain forests to climate change

Climate change had a strong impact on the studied forests landscape, fundamentally changing structure and species composition. Here I present the two key results of the study, the response of forest composition and structure to changes in temperature and precipitation and the buffering ability of topographical complexity. The full study can be found in Appendix C.

4.3.1 Response of forest composition and structure to climate change

Both species composition and size structure reacted strongly to climate change. Species composition changed from a typical mountain forest composed mainly of Norway spruce to a system dominated by European beech and, at even higher temperatures, to a warm-adapted system of oaks and Scots Pine (*Pinus Sylvestris L.*). The diameter distribution shifted from a landscape dominated by few large trees under historic climate conditions to many smaller trees. With decreasing precipitation, this shift came at lower temperatures compared to higher precipitation availability. After reversal of the climate change signal ("cooling down"), the landscape recovered but needed to get to relatively lower temperatures related to the warming trajectory in order to reach similar species composition and size structure, showing hysteresis between the two system states (large trees, mainly spruce vs. small trees, mainly oaks).

4.3.2 Buffering effect of topographic complexity under climate change

I compared three topography scenarios (uniform, intermediate and complex) to investigate the buffering capacity of topographic complexity. There was a clear effect of topography on the development of both forest species composition and size structure. Under uniform topography (entire landscape under the same environmental drivers), the shift between the two system states was abrupt and occurred at lower temperatures on the warming trajectory compared to the intermediate and complex topography scenarios. Recovery also happened earlier with the buffering effect of topography in the more topographically complex scenarios. However, particularly in the intermediate scenario with limited seed input, there was larger stochasticity in the development pathways of the landscape.

5 Discussion

5.1. Forest resilience simulation opportunities and development needs

A big challenge in researching resilience in general, and in understanding its most important processes with models, is the frequently vague use of the resilience concept which doesn't necessarily fit within any particular definition. This makes it hard to identify general trends and needs in resilience research. In my review of model applications in resilience, I used a framework based on work by Carpenter *et al.* (2001), classifying the studies with respect to the driver and response variables investigated and assessing a catalogue of possible model processes relevant to resilience. Such a catalogue of processes relevant to understanding forest resilience, while solidly rooted in previous research on resilience processes (Frelich & Reich, 1999; Johnstone *et al.*, 2016; Martínez-Vilalta & Lloret, 2016), remains necessarily incomplete as we are still far from sufficiently understanding all processes that contribute to forest resilience. In addition to processes identified in my review which warrant further attention and inclusion, there certainly are many other processes which we are only beginning to understand and which have therefore not yet made it into models at all. Consequently, further research into processes supporting forest resilience is crucial also for model development. Ideally, research and model development can benefit from each other directly through a bidirectional exchange. Process-understanding gained from empirical and experimental research feeds into model development, testing and improvement. But model applications can also act as guides to identify areas in which further research is needed and can help in formulating new research questions and directions, even in designing experiments specifically to address processes relevant for resilience which then feed back into model development (Dietze *et al.*, 2018).

Increased attention should be directed at including intra-species variations in models. Few models feature genetic variation and adaptation at this level, meaning that models are often not able to depict the full response diversity of forests, potentially underestimating resilience in some cases. (Billings *et al.*, 2015; Longo *et al.*, 2018). Another area which warrants further model development is the inclusion of feedbacks in models, for example in relation to nutrient cycles or climate regulating services of forests (Bond-Lamberty *et al.*, 2015; Frey *et al.*, 2016). These feedbacks can act both as a stabilizer or as a driver that may further push a system towards a threshold, making them crucial parts of modelling resilience. In order to better understand the level of process-complexity needed in models to investigate forest resilience, targeted model comparisons with different models and implementations of processes can be a powerful tool. Comparing the outcomes of simulations at different levels of mechanistic detail and different theoretical formulations of the same process can guide model development and further research into various processes of forest resilience (Bugmann *et al.*, 2019; Petter *et al.*, 2020).

5.2. Long-term legacies of management in mountain forests

Most forest attributes investigated were able to recover to within the broad range of old-growth variation over the multi-century observation period, both in the chronosequence and the simulation part of the study. The recovery of forests from any disturbance is a complex process and so is the development of formerly managed forests after management has ceased. Some categories of forest attributes recovered more quickly than others. This has also been observed in other studies (Paillet *et al.*, 2015; Rappaport *et al.*, 2018). In particular, forest functioning (carbon pools) seems to recover faster than forest structure, which in turn recovers quicker than forest composition (Slik *et al.*, 2008; Chua *et al.*, 2013; LePage & Banner, 2014; Seidl *et al.*, 2014b).

There are other dimensions to measuring closeness to old-growth conditions in forests. Classic indicators beyond those used here are, for example, the number of large trees over a certain size, or the presence of certain habitats that come along with large trees such as tree cavities or other micro-habitats (Rademacher *et al.*, 2001; Remm & Lõhmus, 2011; Asbeck *et al.*, 2019). Protected areas in general and old-growth reserves in particular play a tremendous role in maintaining forest biodiversity and ecosystem functions. The results of this study show that protecting formerly managed forests can be a viable strategy to create diverse and functioning forests which develop independently of human interference even if development to fully old-growth-like conditions may take several centuries.

5.3. Impacts of climate change on forest composition and structure

I found a strong impact of climate change on forest composition and structure going as far as a shift from a forest dominated by large conifers to a state more reminiscent of Mediterranean forest types with broad-leaved trees of smaller dimensions. These changes were driven by changes in temperature and precipitation only. To understand how these results relate to a possible future of forests, we need to consider also further factors which can drive forest change. Chiefly among those are natural disturbances, both those already frequently observed in Central European forests such as wind, bark beetle and ungulate herbivory (Gregow *et al.*, 2017; Hlásny *et al.*, 2019; Nopp-Mayr *et al.*, 2020) and potential novel disturbances such as fire (Bekar *et al.*, 2020) and novel pests and diseases (Seidl *et al.*, 2018b). These disturbances can in particular work to hasten forest transformation and provide opportunities for reorganization. In this regard, disturbances play different roles in relation to forest resilience to climate change. On the one hand, they can help forests adapt to new climate conditions faster (Thom *et al.*, 2017b), on the other hand novel disturbance regimes may increase the likelihood of non-forest states, particularly when frequency and size of disturbances exceed a threshold where successful regeneration is no longer possible (Turner *et al.*, 2019). This problem can be exacerbated if there isn't a sufficient availability of regeneration from trees that are better adapted to future climate and disturbance regimes, whether that is because these species are simply not present in the landscape or because seedlings of those species are for example preferentially browsed by ungulates (Ramirez *et al.*, 2018).

As is evident from the study, topographical factors can play a large role in forest response to climate change. Topography can have a buffering effect by providing refuges and sheltered sites for regeneration (Hoecker *et al.*, 2020) but can also add additional challenges in making certain stands particularly exposed to frequent disturbances (Seidl *et al.*, 2018a) or causing challenges for regeneration survival (Hoecker *et al.*, 2020).

5.4. The need for resilient forests and the current state of European forests

European forests are facing changes in relation both to environmental factors and to societal demands. Recent climate change has caused a change in mean annual temperature in Europe of between 1.7 and 1.9° C relative to pre-industrial climate (European Environment Agency, 2020) and several particularly hot and dry summers in recent years. Disturbance regimes are changing and forest mortality is increasing (Senf *et al.*, 2018), with natural disturbances often interacting with climate change (Seidl *et al.*, 2017). Both changes in the frequency and severity of disturbances which are already part of the established disturbance regime and novel disturbances are challenging the resilience of European forests.

At the same time, society is raising new demands towards forests, from the need for a renewable biomass source for the emerging bioeconomy (Wolfslehner *et al.*, 2016; European Commission, 2018) to an ever-growing need for forest areas as recreation spaces (Derks *et al.*, 2020). The regulating functions of forests in particular will also have increasing importance especially in moderating the effects of climate extremes. In particular, forests can contribute to climate regulation both on a macro level through carbon sequestration and storage (Luyssaert *et al.*, 2008) and on a local level by influencing the local (micro-) climate through evapotranspiration and shading (Frey *et al.*, 2016). Forests also contribute to stable water provisioning and disaster protection, which is getting more important as extreme weather events become more frequent (Dorren *et al.*, 2004; Kelly *et al.*, 2016; Moos *et al.*, 2018).

Resilient forests are crucial for facing these challenges, particularly when considering the uncertainty that comes with changing environmental conditions and disturbance regimes as well as changing and increasing societal demands for forest ecosystem services. European forests have been shown to be relatively resilient and have been able to recover from disturbances such as bark beetles (Petritan *et al.*, 2015; Winter *et al.*, 2015; Senf *et al.*, 2019, Appendix B). However, future changes may challenge this resilience considerable (Appendix C). In general, older, less diverse forests seem to already be less resilient, highlighting the need to address resilience through management.

5.5. Resilience as a concept in forest research and management

The concept of resilience has become very popular and is frequently included in policy documents and even management guidelines. It can help forest managers, policy makers and scientists to deal with increasing uncertainty and complexity. However, to be truly useful as a management concept and to make fruitful communication possible between forest researchers and managers, we must work to be more precise in defining what we mean by forest resilience and how it relates to the future of forests. Simply establishing "resilient forests" as a management goal is not enough if we do not define what we mean by that. In fact, there is no consensus within the scientific literature whether resilience is a system property, a process or a desirable management outcome (Nikinmaa *et al.*, 2020). Particularly when going into the realm of ecological resilience, we have to understand that resilience *per se* is a neutral term. That is, a system state may be resilient in the sense of remaining stable within a domain of attraction but it may not be the state desired by managers. In this case, the resilience is actually causing difficulties because it makes it harder to achieve management goals. Therefore, at the very least, we must define the "of what" and "to what" whenever we discuss resilience as a desirable forest state (Carpenter *et al.*, 2001) to ensure clear communication. This means that we have to define the forest attributes of interest as well as a target state or range we want them in and also the disturbances and drivers we would like them to be resilient against. Only then can resilience be operationalized as a management target and as a concept that facilitates exchange between scientists and practitioners.

This need for a clear definition and goal-setting suitable to the local forest management context as well as the need for local adaptation of any management strategy means that there are no silver bullet solutions to managing for resilience. What a resilient forest is and how forest resilience can be supported through management varies with local ecological factors as well as well as management needs and targets. Many of the management strategies that can enhance forest resilience are already part of the classic management portfolio. Forest managers can play an important role in helping forests adapt to future climate and disturbance regimes by promoting tree species that are better suited to future conditions and generally fostering species and structure diversity in forests (Aquilué *et al.*, 2020). They can also promote forest resilience by preserving natural buffering capacities within the forest system. This might include avoiding large canopy openings which might negatively influence the microclimate of the forest and expose saplings to more extreme climate. Management should also be adapted to local conditions such as topography on a fine-grained level both in choice of tree species as well as for example in shape and timing of forest management interventions (Seidl *et al.*, 2018a; Aquilué *et al.*, 2020). In general, core tenets of resilience thinking such as learning and adaptation will be crucial to dealing with changing disturbance regimes and climate change, which disrupt traditional management strategies and concepts (Nikinmaa *et al.*, 2020)

Protected areas play an important role in promoting resilience on multiple scales. Protected areas, especially those containing old-growth forests, are often prime examples of forest systems exhibiting resilience-enhancing characteristics such as a diverse composition and structure as well as relatively undisrupted processes of recovery and adaptation. On a larger scale, they contribute to resilience by providing refugia, harboring species diversity which may be relevant for the resilience of surrounding less diverse areas through repopulation, and also through providing climate regulating ecosystem services such as carbon storage and micro-climatic buffering. Finally, on the level of understanding processes of resilience and adaptation to changing conditions, protected areas can be important "laboratories" (Nagel *et al.*, 2013), helping science to understand which processes and conditions make forests resilient, insights which can be transferred to forests where resilience is a management goal that is yet to be attained.

6 Conclusions

Resilience is a burning topic in these times of rapid environmental change. It gives us a conceptual way to consider what happens in the long term, whether our ecosystems can weather these changes or reorganize themselves to keep existing despite them. For forests, we have to consider long time spans and spatial extents to even begin to understand how they will fare in the future. Working with models, we can explore the potential impact of environmental drivers. As shown here, even if abrupt threshold responses of forest ecosystems can be avoided, massive changes are to be expected and forest will likely look very different in the future. This necessarily has an effect on the ecosystem services these forests provide to society, an area that deserves further study. Resilience can be a useful concept to address the mounting uncertainty and complexity related to the future of forests. For resilience to fulfill this role and be helpful in guiding forest management as well as fostering exchange between forest managers and scientists, we need to be clear in our definitions of resilience and the target forest conditions. Forests are often very resilient systems and can recover quickly after disturbance. However, forest ecosystems are facing unprecedented changes and challenges. Forest management, guided by scientific knowledge, can and should support forests in adapting to these challenges to ensure that forests and the services they provide can be sustained in the future.

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9 Appendix

A Simulating forest resilience: A review

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

C Climate change causes critical transitions and irreversible alterations of mountain forests

D Academic CV

Appendix A

Simulating forest resilience: A review

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RESEARCH REVIEW

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Simulating forest resilience: A review

Katharina Albrich[1,2] | Werner Rammer[1,2] | Monica G. Turner[3] | Zak Ratajczak[3] | Kristin H. Braziunas[3] | Winslow D. Hansen[4] | Rupert Seidl[1,2]

[1]Institute of Silviculture, University of Natural Resources and Life Sciences (BOKU) Vienna, Wien, Austria

[2]Ecosystem Dynamics and Forest Management Group, Technical University of Munich, Freising, Germany

[3]Department of Integrative Biology, University of Wisconsin-Madison, Madison, Wisconsin, USA

[4]Earth Institute, Columbia University, New York City, New York, USA

Correspondence
Katharina Albrich, University of Natural Resources and Life Sciences (BOKU) Vienna, Institute of Silviculture, 1190 Wien, Austria.
Email: katharina.albrich@boku.ac.at

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Abstract

Aim: Simulation models are important tools for quantifying the resilience (i.e., persistence under changed environmental conditions) of forest ecosystems to global change. We synthesized the modelling literature on forest resilience, summarizing common models and applications in resilience research, and scrutinizing the implementation of important resilience mechanisms in these models. Models applied to assess resilience are highly diverse, and our goal was to assess how well they account for important resilience mechanisms identified in experimental and empirical research.

Location: Global.

Time period: 1994 to 2019.

Major taxa studied: Trees.

Methods: We reviewed the forest resilience literature using online databases, selecting 119 simulation modelling studies for further analysis. We identified a set of resilience mechanisms from the general resilience literature and analysed models for their representation of these mechanisms. Analyses were grouped by investigated drivers (resilience to what) and responses (resilience of what), as well as by the type of model being used.

Results: Models used to study forest resilience varied widely, from analytical approaches to complex landscape simulators. The most commonly addressed questions were associated with resilience of forest cover to fire. Important resilience mechanisms pertaining to regeneration, soil processes, and disturbance legacies were explicitly simulated in only 34 to 46% of the model applications.

Main conclusions: We found a large gap between processes identified as underpinning forest resilience in the theoretical and empirical literature, and those represented in models used to assess forest resilience. Contemporary forest models developed for other goals may be poorly suited for studying forest resilience during an era of accelerating change. Our results highlight the need for a new wave of model development to enhance understanding of and management for resilient forests.

KEYWORDS
ecosystem modelling, literature review, model development, process-based modelling, resilience processes, simulation model

1 | INTRODUCTION

Forest ecosystems are under increasing pressure from changing environmental drivers and intensifying disturbances related primarily to changes in climate and land use (McDowell et al., 2020; Millar et al., 2007; Scholze et al., 2006; Trumbore et al., 2015). These changes can move ecosystems out of their historical range of variability (Keane et al., 2009), possibly causing unexpected and nonlinear responses, such as abrupt transitions to other ecosystem states (Albrich et al., 2020; Ratajczak et al., 2018). This uncertainty in future ecosystem trajectories presents challenges for ecosystem managers tasked with ensuring that ecosystems will be able to cope with these changes. It is also difficult for researchers to investigate responses to conditions for which no historical analogues exist.

The concept of resilience provides a framework for assessing the response of ecosystems to changing pressures. Resilient forests, that is, those that are able to persist even under changed environmental conditions, are frequently mentioned as a main goal of forest management and restoration (Bone et al., 2016; Keenan, 2015; Rist & Moen, 2013; Seidl et al., 2016). Despite a wide adoption of resilience in applied ecology its specific meaning often remains unclear, as resilience is difficult to operationalize and quantify (Carpenter et al., 2001; Standish et al., 2014). Resilience has many definitions (Box 1; Brand & Jax, 2007; Grimm & Wissel, 1997), but in ecology, resilience is most often used to describe the response of ecosystems to disturbances or other changes in environmental drivers. Resilience here is the ability to maintain a functionally similar state despite changes in disturbances and other drivers, by being resistant or ‘bouncing back’ when the system drifts from its long-term state (Walker et al., 2004).

Assessing the impacts of environmental change is particularly challenging in forest ecosystems, due to their longevity and often protracted responses to change (Standish et al., 2014). Unlike faster systems, such as lakes, where experimental manipulations are routinely used to investigate ecosystem resilience (Schröder et al., 2005), experimental investigations of resilience are difficult in forest ecosystems due to the large time spans and spatial extents that are necessary to obtain inference. These challenges related to space and time make simulation models an important tool in forest resilience research. Models allow the impact of environmental changes that lack past analogues to be investigated. Furthermore, they enable experimentation in silico to assess recovery and collapse over larger spatial extents and temporal durations than would be possible through experimental manipulation (Egli et al., 2018; Seidl et al., 2016). A particular strength of simulation modelling in forest resilience research lies in its ability to consider multiple drivers simultaneously and to quantify their interacting impacts on forest ecosystems. Models allow for a more thorough exploration of these impacts on state variables (e.g., forest cover, biomass) and the potentially large state spaces occurring in nature, enabling the identification of alternative system states.

A comprehensive picture of how simulation models are used in the context of forest resilience, and how important processes are implemented in these models, is lacking to date. Recent years have brought an improved understanding of processes that contribute to forest resilience (e.g., legacies, forest regeneration processes, Johnstone et al., 2016), but model development often lags behind this understanding, meaning that crucial processes of forest resilience may not yet be included in models.

Box 1 Resilience definitions

While many different definitions of resilience exist, the following three are most frequently used in forest ecosystem research (see Nikinmaa et al., 2020). Further considerations of the resilience concept and its definitions can be found in, for example, Grimm and Wissel (1997), Carpenter et al. (2001), Brand and Jax (2007) and Folke (2006).

Engineering resilience (Pimm, 1984) refers to the time a system needs to recover from a disturbance. It assumes the presence of a single equilibrium state that a system deterministically returns to after a disturbance.

Ecological resilience (Holling, 1973; Holling & Gunderson, 2002) is defined as the ability of a system to maintain its functions, structures and feedbacks in the face of disturbance. It acknowledges the presence of multiple equilibrium states, and the possibility that a system will not return to its state prior to disturbance but rather shifts to an alternative state.

Socio-ecological resilience (Walker et al., 2004): focuses on coupled human and natural systems and their ability to stay within a desirable regime (i.e., maintain structures, functions and services) under disturbance. It particularly emphasizes the role of adaptation.

An improved synthetic understanding of the models used to assess resilience could further forest research in at least three important ways: First, it allows researchers aiming to study resilience to identify promising modelling approaches. Second, it can identify novel modelling approaches that have not yet been applied widely to questions of resilience. And third, the identification of resilience mechanisms that have received only limited attention in models could stimulate the development of improved models for simulating resilience. Here, our aim was to provide a review and synthesis of the simulation models used to study forest resilience. Specifically, our objectives were to synthesize (a) which questions of resilience are addressed with simulation models, (b) what types of models are used for specific resilience questions, and (c) whether processes identified as important for resilience in the theoretical/empirical literature are represented in simulation models.

2 | METHODS

2.1 | Definition of resilience

A necessary first step in conducting our review was to operationalize our definition of resilience, enabling us to identify relevant studies. Resilience is a frequently used term with an evolving set of definitions

(Brand & Jax, 2007; Nikinmaa et al., 2020; Ratajczak et al., 2018). We chose an approach suggested by Carpenter et al. (2001), operationalizing resilience by assessing the *resilience of what* (i.e., which forest ecosystem property responds) and the *resilience to what* (i.e., the pressure or driver that triggers a response). This allowed us to compare studies that themselves used very different definitions of resilience, for example, from engineering resilience (i.e., the ability of the system to resist disturbance and the rate at which it returns to equilibrium after a disturbance, as defined by Pimm, 1984; applied e.g., in Seidl et al., 2017) to socio-ecological resilience (i.e., the capacity of a coupled human-natural system to absorb disturbances and maintain its essential functions, processes, and feedbacks, as defined in Adger, 2005 and Walker et al., 2004; applied e.g., in Charnley et al., 2017).

2.2 | Literature search and identification of relevant studies

To identify relevant studies in the scientific literature, we conducted an extensive web search using the academic literature databases Scopus (Elsevier, Amsterdam, Netherlands) and ISI Web of Science (Clarivate Analytics, Philadelphia, PA, USA). We searched for the terms "forest" and "model*" in combination with any of the terms "resilien*", "state shift", "regime shift", "tipping point", "recovery rate", "catastrophic shift", "abrupt shift", "bifurcation" "bistab*" or "collapse" (search terms based on and expanded from Ratajczak et al., 2018). We included only studies published in English. The cut-off date for publications to be included in this study was 6 September 2019.

The search yielded more than 1,200 entries, which were manually checked to filter studies that were of relevance for our research questions. Specifically, we checked whether the study investigated forest ecosystems (e.g., we did not include studies that focused on transitions between grassland and savanna ecosystems, where forest was not one of the possible ecosystem states), used some sort of simulation model (studies using purely conceptual models without numerical simulation, or that consisted of fitting a statistical model to data were not included), and investigated resilience (omitting studies that mentioned the term in the abstract or keywords but whose study objectives were not related to resilience). This selection resulted in a total of 119 studies being included in our review, representing 128 individual model applications (as a few studies included multiple models).

From each study we collected information for several categories (Table 1). General information such as location of the study and the investigated biome and ecosystem type allowed us to identify geographical 'hotspots' of simulation model use in resilience research. We also recorded the name and type of model as well as a set of essential model characteristics (spatial and temporal grain and extent, spatial explicitness, stochasticity, and whether the model was process-based) to better characterize the types of models that are used for simulating forest resilience. We also investigated how resilience was defined in each study, specifically noting the *of what* and *to what* (sensu Carpenter et al., 2001), and recording specific response variables used to quantify resilience where applicable (this includes both dedicated resilience indicators, as defined for example by Scheffer et al., 2015, and relevant measurements of state variables, e.g., biomass, species shares). The responses (*of what*) and drivers (*to what*) were recorded jointly so that relevant response/driver combinations could be identified. As drivers often do not act in isolation, the co-occurrence of different drivers was also analysed.

2.3 | Analysis of process inclusion

The core of our review consists of the analysis of specific ecological processes deemed important for forest resilience and their implementation in models. This catalogue of processes was compiled a priori, and is based on seminal work on forest resilience (Frelich & Reich, 1999; Johnstone et al., 2016; Martínez-Vilalta & Lloret, 2016). We identified three groups of processes of particular relevance for forest resilience: regeneration processes, legacy processes and soil processes. We purposefully kept the set of processes investigated general as we acknowledge that model formulations necessarily vary with different study systems.

Regeneration is a crucial contributor to forest resilience as it strongly influences post-disturbance recovery. Regeneration processes have a large influence on whether the ecosystem is able to recover, or whether it shifts to a different type of forest or a non-forest state (Enright et al., 2014; Johnstone et al., 2016; Martínez-Vilalta & Lloret, 2016). Specifically, we investigated whether *distance to seed source*, *reproductive maturity*, *serotiny*, and *resprouting* – processes related to the availability of reproductive material (seeds and sprouts) – were considered in the models. We also considered the *climate sensitivity of regeneration*, *light availability* (shading effects from mature trees) and *competition from other (non-tree) vegetation*, as these processes often have a strong bearing on the survival of seedlings and saplings.

Legacy processes are mechanisms that lead to information or material being carried over from the pre-disturbance ecosystem into the post-disturbance ecosystem (Johnstone et al., 2016). They are often directly related to regeneration processes, as they can provide starting points for recovery, for example in the case of *aerial and soil seed banks*. We also analysed *live tree legacies*, which are a measure of tree *tolerance to disturbance* and represent an important seed source that is carried over from the pre-disturbance state of the ecosystem (Seidl et al., 2014). Finally, we investigated *persistent stress* as a legacy, that is, whether the model tracks the influence of stress on tree survival over multiple time steps (Anderegg et al., 2015; McDowell et al., 2008).

Soil processes identified as relevant for ecological resilience were primarily related to water and nutrient availability (Fahey et al., 2016; Gazol et al., 2017; von Oheimb et al., 2014). We therefore assessed the implementation of *water availability* and *nutrient cycling* (separately for nitrogen and other nutrients) in the models used to investigate forest resilience. We also hypothesized that *soil erosion* is important for resilience (Flores et al., 2019), and analysed its implementation in the models applied in the resilience literature. All data analysis and visualization was conducted in R (version 3.6.2, R Core Team, 2019), specifically using the packages dplyr (version 0.8.3, Wickham et al.,

TABLE 1 Information gathered from each simulation study of forest resilience

Category	Subcategory	Indicator	Information recorded
General information		Location	As reported by the authors
		Biome	According to categories of Olson et al. (2001)
		Forest ecosystem type	As reported by the authors
Model information		Model type	Categories: analytical/conceptual, biogeochemical, dynamic global vegetation model (DGVM), empirical, landscape, population, state & transition, other
		Spatial explicitness	Is the model spatially explicit?
		Spatial grain and extent	In hectares, pixel size and size of simulated area
		Temporal grain and extent	In years, smallest time step and simulation duration
		Stochasticity	Are any stochastic processes implemented?
		Process-based	Is the model process-based?
Resilience definition		Of what	Categories: forest cover, forest composition, forest structure, forest functioning, ecosystem services, biodiversity
		To what	Categories: climate change, land use, fire, drought, wind, other abiotic, insect, other biotic, generic (no agent given), other (fits none of the above categories)
		Definition	Which definition of resilience do the authors give, if any?
		Quantification	How is resilience quantified?
Resilience processes	Regeneration: are processes related to regeneration implemented in the model?	Reproductive maturity	Do trees have to reach maturity before they can reproduce?
		Serotiny	Is the process of serotiny (regarding seed availability after fire) implemented in the model?
		Resprouting	Are trees able to resprout in the model?
		Distance to seed source	Is spatial dispersal of seeds considered in the model?
		Climate sensitivity	Is regeneration sensitive to climate influence?
		Competition from other vegetation	Is regeneration sensitive to competition from other vegetation (adult trees, herbaceous vegetation)?
		Light availability	Is regeneration sensitive to light availability (influence of canopy layer)?
	Legacy processes: is tree survival and the carryover of information as well as material legacies in the face of disturbance simulated?	Disturbance tolerance	Do live trees remain behind after disturbance?
		Maturity effect on disturbance tolerance	Does the age/size of trees (adult tree versus sapling) influence their environmental response/susceptibility to disturbance?
		Seed bank	Are seed banks (aerial and soil) implemented in the model?
		Persistent stress	Does the model track the influence of stress on tree survival over multiple time steps?
	Soil processes: are soil processes included in the model?	Water availability	Is water availability (soil moisture) a factor influencing forests in the model?
		Erosion	Can erosion (loss of fertile soil) happen in the model?
		Nutrient cycling (nitrogen and other nutrients)	Does the model include dynamic nutrient cycles (for nitrogen and other nutrients)?

2019) ggplot2 (version 3.2.1, Wickham, 2016), reshape2 (version 1.4.3, Wickham, 2007) and networkD3 (version 0.4, Allaire et al., 2017).

3 | RESULTS

3.1 | Use of forest resilience and the geography of its application

The use of resilience as a concept in forest research has increased over time (see Supporting Information Material S1: Figure S1.1). Most of the studies included in this analysis focused on forest resilience in the Americas (North and South) or Europe (Figure 1). The tropical and temperate biomes were particularly well represented. Most studies simulating resilience focused on a single study site or a small number of study locations. However there were also studies covering larger (e.g., sub-continental) areas and many different study sites (e.g., Shuman et al., 2011). Of the 119 studies investigated, 31 (26%) did not specify a location (i.e., the model was built for a certain biome or type of ecosystem but was not linked to a particular study site or landscape) and 2 (1.7%) were global in extent.

3.2 | Drivers and responses in modelling forest resilience

We grouped the studies by the responses (*of what*) and drivers (*to what*) that they addressed. There were 43 unique combinations of drivers and responses, with many studies investigating multiple drivers and responses. The most frequent response variables considered in model-based forest resilience studies were, in order of decreasing frequency, forest cover, forest structure (referring to, e.g., tree size distribution), forest functioning (e.g., primary productivity) and forest composition (e.g., species occurrence and abundance, Figure 2). Overall, metrics of forest structure, function and composition were investigated more frequently compared to indicators linked to these ecosystem responses, such as variables associated with biodiversity and ecosystem services.

The most common drivers (*to what*) assessed in modelling studies were wildfire, climate change and land use (Figure 2). With the exception of fire, drivers related to human activity (such as land use and climate change) were more frequently investigated than natural disturbances (e.g., wind or insect disturbance). The two most commonly simulated drivers (climate change and fire) are also the ones most frequently considered together (Supporting Information Material S1: Figure S1.2). Overall, the most common driver-response combination was fire and forest cover, followed by climate change and forest functioning (Figure 2).

3.3 | What types of models are used to simulate resilience?

The most common model type was landscape models. Analytical models (mostly consisting of a set of ordinary differential equations or similar), dynamic global vegetation models (DGVMs) and population models were also frequently applied to study forest resilience (Figure 3 and Table 2). However, several models could not be clearly classified into one of these broad model types. These include instances of coupling different types of models, for example, a DGVM linked to a state and transition model (Halofsky et al., 2014).

Simulations of resilience were conducted over a wide variety of spatial grains (10^{-4}–10^{8} ha) and extents (10^{0}–10^{9} ha, Table 2). The simulated extent ranged from plot-level to global simulations. There was similar diversity in temporal grain and extent. Most models simulating resilience operate on a yearly time step. While the simulation duration (temporal extent) varied enormously from a few

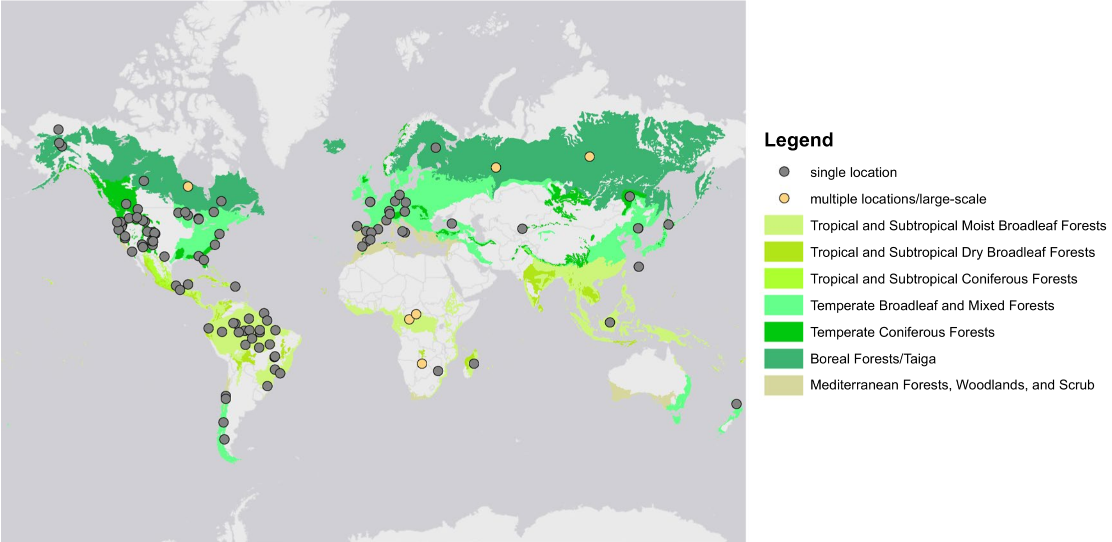

FIGURE 1 Geographical distribution of simulation studies addressing forest resilience. Each dot represents one study. For studies that covered a large spatial extent or included multiple study sites the location is given as the centre point of the area addressed. In addition to the 86 georeferenced studies displayed here our analyses also included 33 studies that had no specified location or were global in their extent. (Biome map from Olson et al., 2001.)

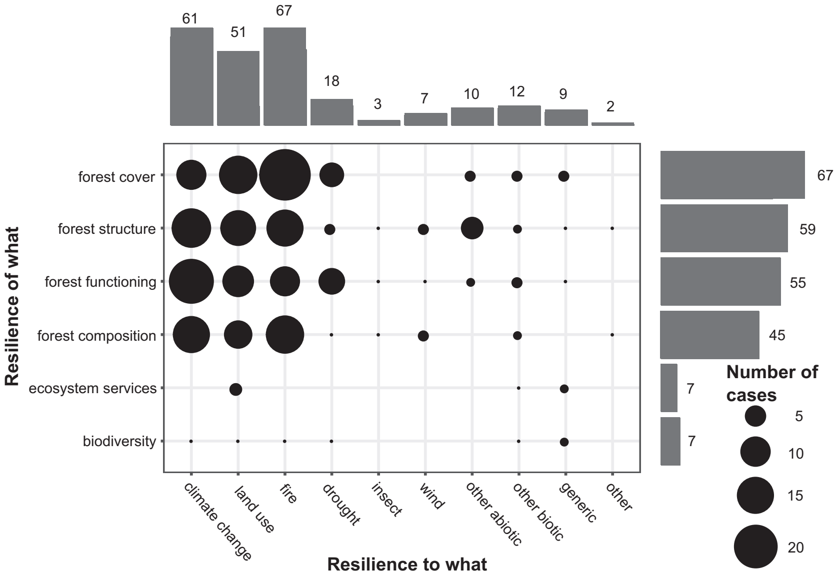

FIGURE 2 Combinations of responses ('of what', *y* axis) and drivers ('to what', *x* axis) in simulation studies of forest resilience

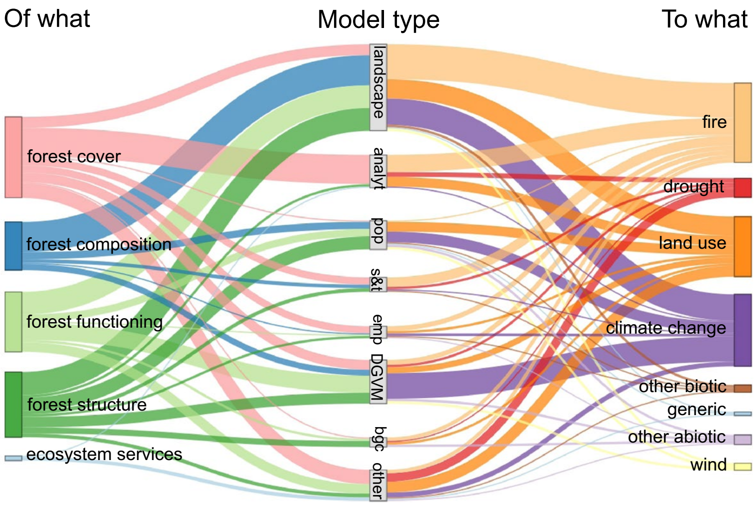

FIGURE 3 Model types used to simulate important response variables (resilience of what) to prominent drivers (resilience to what). Width of bands and bars is proportional to the number of studies found in the literature. For clarity only combinations that had more than three occurrences are shown here. Abbreviations: analyt = analytical/conceptual models; pop = population models; s&t = state and transition models; bgc = biogeochemical models; emp = empirical models; DGVM = dynamic global vegetation models.

years to several thousands of years, most studies covered a study period of less than 200 years (Supporting Information Material S1: Figure S1.3).

Certain model types were preferentially used to address specific drivers and responses (Figure 3). The most frequent response variable (forest cover) was most commonly addressed by simple conceptual models. The resilience of forest composition, forest functioning and forest structure was most often simulated with landscape models. DGVMs were frequently used to model the resilience of forest functioning. Landscape models and DGVMs are also important tools to assess forest resilience to climate change. With regard to resilience to fire, mainly landscape and analytical models were employed, while the effects of land use and climate change were addressed by several different types of models.

3.4 | Implementation of resilience processes in simulation models

Overall, 67% of the model-based studies investigating forest resilience were process-based models, of which 41% were spatially explicit. Furthermore, 42% of models included thresholds and 41%

included feedbacks. 96% of models included a representation of at least one process from our resilience processes catalogue.

3.4.1 | Regeneration processes

Regeneration processes are of high relevance for forest resilience. Yet, only 41% of the model applications considered regeneration processes explicitly (Table 3). Most of the model applications addressing regeneration explicitly considered the effect of reproductive maturity as well as the influence of light availability and climate on seedling survival and regeneration success. In contrast, the influences of competition from ground vegetation or herbivory (Supporting Information Material S3) were rarely considered. Also, only 17% of models simulate regeneration as an emergent property of multiple processes, such as the interplay of dispersal, establishment, and seedling growth. The level of detail with which regeneration was considered in models generally varied with the objective of the study (i.e., different of what/ to what combinations, Table 3).

3.4.2 | Legacy processes

Simulations of processes creating disturbance legacies were rare in the studies investigated (Table 4). Remaining live trees, indicating tolerance to disturbance, were the most common legacy implemented in models (28%). Twenty-two percent of models differentiated between adult trees and saplings/seedlings in terms of susceptibility to disturbances. Seed banks were only simulated in a small number of studies investigating fire, despite the important role of seed banks in the recovery after fire in many ecosystems (Enright et al., 2015; Johnstone et al., 2010). We note, however, that serotiny (reported in the previous section on regeneration processes) equals the inclusion of a canopy seed bank. Approximately 12% of the model applications included some form of stress legacy, that is, where the model is able to simulate the compounding effect of stressors (such as drought) over multiple years, for example through a continuous simulation of carbohydrate reserves in trees (Hansen et al., 2018; McDowell et al., 2013).

TABLE 2 Basic characteristics of the models used to simulate forest resilience

		Spatial		Temporal	
Model type	***n***	**Grain (ha)**	**Extent (ha)**	**Grain**	**Extent (years)**
Landscape	27	10^{-1}	10^{5}	Year	250
		$4\cdot10^{-4}$ to $8\cdot10^{1}$	$1\cdot10^{0}$ to $2\cdot10^{7}$	Day to decade	55 to 3,348
Conceptual/ analytical	22	10^{5}	10^{8}	Year	500
		$2\cdot10^{1}$ to $6\cdot10^{5}$	$4\cdot10^{7}$ to $1\cdot10^{9}$	NA	90 to 10,000
DGVM	19	10^{5}	10^{7}	Day	100
		$5\cdot10^{-2}$ to $3\cdot10^{8}$	$1\cdot10^{2}$ to $3\cdot10^{9}$	Day to year	91 to 333
Population	19	10^{-2}	10^{1}	Year	500
		$2\cdot10^{-3}$ to $1\cdot10^{2}$	$1\cdot10^{0}$ to $3\cdot10^{3}$	Day to decade	5 to 1,575
Biogeochemical	9	10^{6}	10^{8}	Day	180
		$1\cdot10^{5}$ to $1\cdot10^{6}$	$5\cdot10^{7}$ to 10^{9}	Day to year	4 to 8,096
State and transition	8	10^{0}	10^{6}	Year	150
		$1\cdot10^{-1}$ to $4\cdot10^{1}$	$5\cdot10^{2}$ to $6\cdot10^{6}$	NA	50 to 500
Empirical	6	10^{0}	10^{4}	Year	75
		$1\cdot10^{-2}$ to $3\cdot10^{5}$	$1\cdot10^{3}$ to $3\cdot10^{8}$	Year to decade	15 to 4,000
Other	18	10^{-2}	10^{4}	Year	90
		$7\cdot10^{-4}$ to $1\cdot10^{1}$	$1\cdot10^{0}$ to $8\cdot10^{7}$	Day to year	6 to 1,850

Note: DGVM = dynamic global vegetation model. Shown are number of observations (model applications) per model type, median, and 5th–95th percentile range for spatial grain and extent as well as temporal extent of model applications. For temporal grain (time step), the most common value and the highest and lowest resolution are shown.

3.4.3 | Soil processes

Soil processes related to forest resilience were more frequently included in models than regeneration and legacy processes (Table 5). Slightly less than half of the analysed cases considered water availability explicitly. However, water availability was often the only soil-related process. Only around 20% of the applications considered a dynamic representation of the nitrogen cycle. Availability of other nutrients and their effect on ecological resilience were considered only rarely (< 1%, Supporting Information Material S3). Likewise, erosion processes, which influence forest resilience in some systems (Flores et al., 2019), were considered very rarely. Models assessing resilience of forest functioning had the most detailed representation of soil processes across all response indicators. Models that were applied to study the resilience to climate change tended to have a more complex representation of soil processes compared to investigations of other drivers.

4 | DISCUSSION

Human-caused climate change is challenging the resilience of forests. Developing adaptation strategies to mitigate these changes will require understanding of how multiple processes interact to shape resilience. Simulation models are a promising tool because they allow the exploration of a more complete set of compounding factors than field experiments and facilitate the analysis of outcomes over long time periods. However, in our review of the simulation models used for modelling forest resilience, we found that few were explicitly designed for that purpose and many relevant resilience processes are currently not well represented in models. Thus, we call for a new wave of model development that leverages expanding process understanding and data availability (e.g., from remote sensing) as well as growing computational resources.

While we here present the first comprehensive synthesis of models for forest resilience, our analysis has some limitations. One challenge in identifying relevant literature was the ambiguous use of the term resilience. On the one hand it is often used in abstracts and keywords of studies that do not actually investigate resilience based on commonly used resilience definitions. On the other hand, some studies that explicitly deal with modelling critical transitions and alternative stable states of ecosystems do not actually use the term resilience in their title and keywords. We addressed these challenges using multiple alternative keywords and carefully checking the studies we found for relevance before starting the in-depth review process. The issue also underlines, however, that a more consistent and concise application of the resilience terminology in the literature would be desirable. Furthermore, the concept of resilience is intrinsically connected to concepts such as stability, vulnerability and persistence (Grimm & Wissel, 1997). Studies may address similar questions, but choose a different conceptual framework. Thus, some studies that address generally similar issues were excluded from our analysis due to our set of keywords. We focused on resilience because conceptual advances have been rapid and applications of resilience are growing both in the peer-reviewed literature and society (Ratajczak et al., 2018; Selles & Rissman, 2020). Notwithstanding the challenges in identifying the relevant subset of the literature, important insights emerge from our review. We discuss these insights in the following sections, first focusing on the perspective of model users (Section 4.1) and then discussing issues of relevance for model developers and charting a path forward (Section 4.2).

4.1 | Lessons learned for assessing forest resilience

A wide variety of resilience questions can be successfully tackled using models, as shown by the large number of driver-response combinations found in the literature. Furthermore, many studies investigated the ecosystem response to multiple drivers (e.g., Batllori et al., 2017 for fire and drought, and Lucash et al., 2017 with LANDIS-II for climate change, wind and forest management), which highlights a key strength of simulation models, that is, the ability to interactively consider a broad set of simultaneously changing factors. Models can also account for important feedbacks (for example between forest structure, species composition, and disturbances) that play a critical role in forest resilience (Flores et al., 2019; Staal et al., 2015).

Spatial and temporal extent of studies in our review varied widely. As spatio-temporal extent is primarily defined by the specific research question being addressed, this finding underlines that models can provide inference across a wide range of applications. With regard to the temporal dimension, the long simulation durations (with a median of 200 years across all reviewed studies, and some studies extending over several thousands of simulated years, e.g., Bauch et al., 2016; Wild & Winkler, 2008) are a characteristic that sets simulation-based studies apart from experimental and observational studies. A recent review of 89 drought experiments in terrestrial ecosystems found that 80% of drought treatments were less than 5 years in duration (Hoover et al., 2018). The ability to efficiently address centennial time-scales makes models prime tools for assessing resilience questions that go beyond the analysis of individual disturbance events and rather focus on disturbance regimes (and changes thereof; e.g., Kitzberger et al., 2012, with SELES; Hudiburg et al., 2017, with DayCent). While models are a useful tool for simulating extensive time periods, long simulation time can also lead to unrealistic model behaviour due to compounding errors. Careful model evaluation (Oreskes et al., 1994) and the testing of simulations against a wide variety of observed spatial and temporal patterns (Grimm et al., 2005) are thus of particular importance to ensure the utility of long-term simulations.

Our analysis shows that different types of model can provide unique insights on resilience, depending on which type of drivers and responses are of relevance in a given study system. When studying forest cover as the response variable of resilience, for instance, relatively

TABLE 3 The explicit consideration of regeneration processes in models used to simulate forest resilience, parsed by different combinations of resilience of what and resilience to what for the most commonly occurring combinations

				Regeneration processes						
		n	Natural regeneration included (%)	Reproductive maturity (%)	Serotiny (%)	Re-sprouting (%)	Distance to seed source (%)	Climate (%)	Competition (%)	Light availability (%)
All model applications		128	*41.4*	32.0	9.4	24.2	18.8	25.8	9.3	31.3
Of what	**To what**									
Forest functioning	Climate change	21	47.6	38.1	14.3	28.6	23.8	42.9	4.8	28.6
	Fire	9	77.8	66.7	33.3	66.6	66.7	77.7	0.0	66.6
	Land use	10	40.0	40.0	30.0	40.0	20.0	60.0	20.0	50.0
Forest structure	Climate change	16	62.5	50.0	25	37.5	25.0	37.5	6.3	50.0
	Fire	14	35.7	42.9	21.4	35.7	28.6	42.9	0.0	42.9
	Land use	13	76.9	61.5	23.1	61.5	23.1	46.2	7.7	69.2
Forest composition	Climate change	14	71.4	64.3	35.7	50	42.9	64.3	0.0	57.1
	Fire	15	86.7	73.3	26.7	66.7	60.0	60.0	6.7	53.3
	Land use	8	100.0	75.0	37.5	87.5	37.5	62.5	0	75.0
Forest cover	Climate change	9	44.4	44.4	11.1	33.3	22.2	22.	22.2	44.4
	Fire	28	32.1	32.1	7.1	21.4	14.3	10.7	7.1	17.9
	Land use	15	13.3	13.3	6.7	13.3	6.7	6.7	0.0	6.7

Note: Observations are individual occurrences of response/driver combinations. For details on the processes considered see Table 1.

TABLE 4 The explicit consideration of legacy processes in models used to simulate forest resilience, parsed by different combinations of resilience of what and resilience to what for the most commonly occurring combinations

				Legacy processes			
		n	Legacies included (%)	Disturbance tolerance (%)	Susceptibility by age (%)	Seed bank (%)	Persistent stress (%)
All model applications		128	33.6	28.1	21.8	6.3	11.7
Of what	**To what**						
Forest functioning	Climate change	21	38.1	33.3	19.0	4.8	14.3
	Fire	9	88.9	88.9	44.4	0	33.3
	Land use	10	80	70	30.0	0	20
Forest structure	Climate change	16	43.8	37.5	18.8	6.3	25
	Fire	14	50.0	42.9	35.7	0	28.6
	Land use	13	69.2	61.5	38.5	7.7	23.1
Forest composition	Climate change	14	57.1	57.1	35.7	14.3	28.6
	Fire	15	60.0	60.0	53.3	6.7	20
	Land use	8	87.5	87.5	50.0	12.5	25
Forest cover	Climate change	9	44.4	44.4	33.3	33.3	11.1
	Fire	28	21.4	21.4	28.6	10.7	3.6
	Land use	15	6.7	6.7	6.7	0	0

Note: Observations are individual occurrences of response/driver combinations. For details on the processes considered see Table 1.

TABLE 5 The explicit consideration of soil processes in models used to simulate forest resilience, parsed by different combinations of resilience of what and resilience to what for the most commonly occurring combinations

				Soil processes		
		n	Soil included (%)	Water availability (%)	Erosion (%)	Nitrogen cycle (%)
All model applications		128	46.1	46.8	3.9	18.75
Of what	**To what**					
Forest functioning	Climate change	21	76.2	85.7	0.0	38.1
	Fire	9	66.7	77.8	0.0	66.7
	Land use	10	80.0	70.0	20.0	30.0
Forest structure	Climate change	16	62.5	68.8	0.0	31.2
	Fire	14	42.9	57.1	7.1	42.9
	Land use	13	53.8	61.5	0.0	30.8
Forest composition	Climate change	14	71.4	92.9	0.0	57.1
	Fire	15	33.3	53.3	0.0	33.3
	Land use	8	62.5	75	0.0	50.0
Forest cover	Climate change	9	66.7	55.6	0.0	11.1
	Fire	28	17.9	21.4	0.0	7.1
	Land use	15	13.3	6.7	6.7	0.0

Note: Observations are individual occurrences of response/driver combinations. For details on the processes considered see Table 1.

simple models, such as sets of differential equations with varying levels of parametrization, were successfully applied to study transitions between forest and savanna (De Michele & Accatino, 2014; Tredennick & Hanan, 2015). However, when resilience of forest composition, structure and functioning is investigated, landscape models are powerful tools due to their spatially explicit nature and their ability to accommodate complex ecological processes (Scheller & Mladenoff, 2007; Shifley et al., 2017). This implies that more complex models are needed to simulate processes that lead to changes in composition, structure and functioning, whereas the consideration of basic demographic processes (establishment and mortality) in models is enough to reproduce the dynamics of forest cover. Indeed, most of the models that assessed ecosystem functions were landscape models or DGVMs. While choice of model is influenced by multiple considerations of suitability and availability, our review provides a starting point for considering potentially appropriate model families for studying specific questions of forest resilience (Figure 3).

There is no one best model type for a certain resilience question, as illustrated by the wide range of studies addressing forest resilience to fire. Most frequently applied are landscape models, in which spatial processes such as fire spread and seed dispersal into burnt areas can be simulated (e.g., Loudermilk et al., 2017, with LANDIS-II; Keane et al., 2019, with FireBGCv2). However, the second most frequently used model type for studying the resilience to fire is analytical or conceptual models, where fire is generally represented aspatially and with simplified computation of tree mortality. Therefore, model choice depends strongly on the drivers and responses being simulated. We thus advocate for an approach where the appropriate model is chosen based on its ability to simulate the relevant mechanisms of resilience in a given context and study system (e.g., Hansen et al., 2018, with iLand).

Box 2 Future directions

- The models currently in use for simulating resilience have often been developed for other purposes and are not fully capturing relevant processes of forest resilience.
- A new wave of model development is needed, especially focusing on processes not yet well-represented in models (e.g., nutrient cycling, plant trait adaptation, tree regeneration).
- New empirical and experimental studies can contribute to model development by specifically targeting gaps in process understanding. This inter alia requires that the interactions between the model development and experimental/empirical communities are strengthened.

4.2 | Lessons learned for modelling forest resilience

We found a large gap between the processes that are considered to be important mechanisms of resilience in the theoretical and empirical literature (e.g., Flores et al., 2019; Johnstone et al., 2016; Martínez-Vilalta & Lloret, 2016; von Oheimb et al., 2014) and the explicit consideration of these processes in models used to study forest resilience. In other words, processes deemed relevant for resilience (e.g., seed banks, soil erosion and nutrient cycling) are often not included in models. As a result, many models are not yet capable of comprehensively testing which theoretically important processes may underpin future forest resilience. Another possible outcome of missing resilience processes in models could be a systematic underestimation of resilience in simulation studies.

Process representation varies with the spatial scale of models. Landscape models (e.g., iLand, LANDIS-II) are designed to simulate forests on relatively small spatial domains and are thus well suited to simulate critical fine-scale processes and spatial dynamics. Indeed, our analyses revealed that several landscape models are able to capture a large number of relevant forest resilience mechanisms. Conversely, DGVMs and Earth system models that operate across continental to global domains and are successfully used to simulate questions of biome shifts and forest die-back (Gonzalez et al., 2010; Higgins & Scheiter, 2012) are just beginning to represent forest demography with sufficient detail to explore questions of resilience (Fisher et al., 2018; Massoud et al., 2019; U.S. DOE, 2018).

While many types of models can increasingly capture aspects of resilience, most were not designed explicitly for this purpose. Thus, our analysis underscores the need for a new round of model development (Box 2). The resilience processes highlighted in our review (Tables 3–5, Supporting Information Materials S2 and S3) can provide a valuable starting point for such a resilience-focused development of simulation models. While for many of these processes examples of how to model them already exist in the literature, some processes of resilience, such as plant trait adaptation (both local adaptation within populations as well as adaptation over time, such as acclimation processes) remain widely neglected in current models (Longo et al., 2018; Nitschke & Innes, 2008, but see Scheiter et al., 2013 for a model including adaptive trait combinations).

Here it should be noted that not all of the processes considered here are necessarily relevant for all study systems. There are, for instance, no serotinous tree species in Central Europe, which is why this process – important for the resilience of forests to fire in other areas of the world (Enright et al., 2015; Johnstone et al., 2016) – is not included in models applied in this region. While we designed our catalogue of model processes based on literature and tried to make it broadly applicable, there are likely many more processes that are relevant to resilience research, depending on the study system and questions asked. Our catalogue of processes does therefore not claim completeness (but see Supporting Information Materials S2 and S3 for an overview of the full set of processes we investigated, not all of which are analysed in depth here) and the separation into three categories of resilience processes is not always clear-cut (e.g., we addressed seed banks as legacies, but serotiny and resprouting in the regeneration category).

There may also be processes that are not yet understood well enough to be modelled, highlighting the need for further experimental and empirical research (e.g., adaptation/plasticity of plant functional traits, Christmas et al., 2016). Authors frequently mention processes they consider relevant to their question and study system, but that have not been implemented in the applied model. These processes include, for instance, nutrient cycles (Bond-Lamberty et al., 2015), as well as the effect of CO_2 fertilization (Bagdon & Huang, 2014; Longo et al., 2018; Lucash et al., 2017), despite growing evidence that these processes are important for simulating vegetation dynamics (Hickler et al., 2015; Rammig et al., 2010; Reyer et al., 2014). Targeted model comparison experiments – applying models with different levels of mechanistic detail and differing implementations of processes to the same driver data – could shed more light on the uncertainties originating from representing processes in different ways or omitting them from models entirely (Bugmann et al., 2019; Petter et al., 2020).

A new wave of model development also requires improved data on forest resilience and its underlying mechanisms. Multiple authors mention data availability as a key obstacle to implementing more process details in models (e.g., Lucash et al., 2017; Magnuszewski et al., 2015). This highlights that further empirical and experimental work is crucially needed for developing more robust simulations of forest resilience. Specifically, empirical and experimental studies that are explicitly designed to address gaps in models could yield valuable insights. Also remote sensing is increasingly used to study forest resilience (De Keersmaecker et al., 2014; Senf et al., 2019) and can serve as a valuable data source for model-based studies, especially when addressing forest change across large spatial extents and in areas where data are sparse (Levine et al., 2016; Staal et al., 2018). In particular, increasing availability of new datasets could be leveraged to benchmark models and identify process uncertainties. This can in turn direct the design of new experiments that address processes underpinning resilience and feed back into model development (Dietze et al., 2018). In the context of increasing the mechanistic details included in models several authors also discuss the trade-off between model complexity and the computational resources needed to run such increasingly complex models (e.g., Manoli et al., 2017; Mitra et al., 2015). This means that applying more complex models may come at the cost of reduced study periods, a smaller number of simulated replicates, or a narrower set of driver combinations being investigated. Even with steadily increasing computational resources, increasingly complex models could thus result in a reduced inferential potential in certain applications, highlighting that the trade-offs that come with higher process detail should be explicitly considered (Loehle, 1990).

Anthropogenic climate and land use change are profoundly affecting forests, emphasizing the need to understand how these impacts will alter forest ecosystems. Models play an important role in understanding the drivers and scope of these changes and the responses of forest ecosystems. Thus, deliberately developed and applied models can make an important contribution to understanding and managing ecological resilience in a changing world. Our study presents a valuable framework for assessing which currently available models are appropriate for such questions and can act as a starting point for a new generation of model developers.

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DATA AVAILABILITY STATEMENT

Data and code used in the analysis are available at https://doi.org/10.6084/m9.figshare.12958166

ORCID

Katharina Albrich https://orcid.org/0000-0002-5157-523X
Rupert Seidl https://orcid.org/0000-0002-3338-3402

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BIOSKETCH

Katharina Albrich is a PhD student at the University of Life Sciences and Natural Resources supervised by Prof. Rupert Seidl. Her research focuses on the resilience of forests to climate change and disturbances.

SUPPORTING INFORMATION

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

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Simulating forest resilience: a review

Supplementary Materials S1: Supplementary results

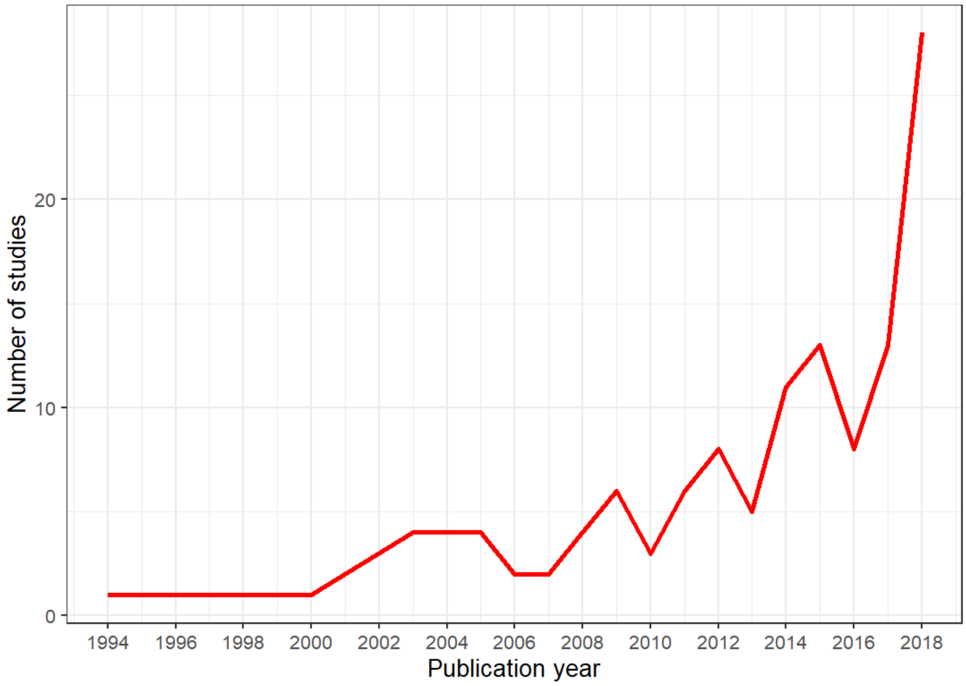

Figure S1.1: Publication of studies related to forest resilience modelling over time.

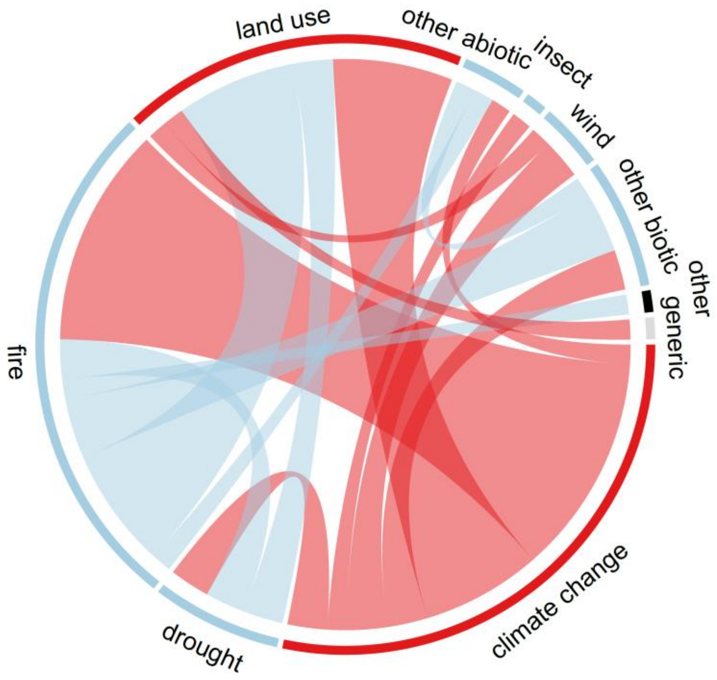

Figure S1.2: Drivers (resilience to what) commonly modelled together. Red stands for primarily anthropogenic drivers, blue for primarily non-anthropogenic.

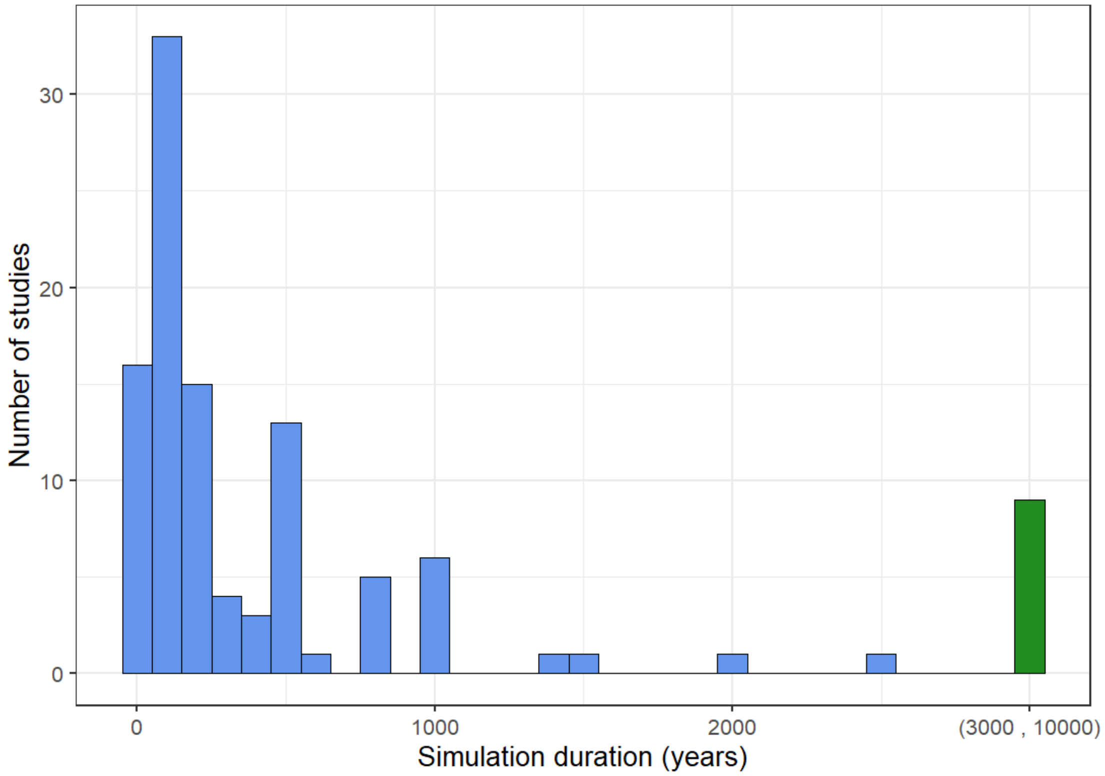

Figure S1.3: Histogram of simulation duration in years. Durations above 3000 years are binned into a single bin (maximum simulation duration was 10000 years).

Simulating forest resilience: a review

Supplementary Materials S2: Catalogue of questions assessed for each study with explanations

Meta-data

- **Title of paper**
- **Name of first author**
- **Publication year**
- **doi**
- **use "resilience": is the term resilience used in the paper**
- **Multiple locations:** are there several discrete study sites (plots/stands/landscapes) mentioned in the study
- **Continent:** continent on which study site is located (chose multiple if more than one location)
- **Country:** country where study site is located (write all if multiple)
- **Biome:** select most closely matching biome (chose multiple more than one location)
- **Dominant forest type:** select from coniferous/broadleaved/mixed (chose multiple more than one location with different forest types)
- **Ecosystem types:** briefly describe ecosystem types (including species) as they are given in the paper. Also include non-forest types if applicable

Simulation model

- **Model:** name of model + extensions used ("unnamed" if there is no specific name for the model)
- **Type of model (select):** choose the category which most closely fits the model described (population model, biogeochemical model, landscape model, dynamic global vegetation model, State and Transition model, empirical model, other)
- **Type of model (self-described):** how do the authors describe the model
- **Additional sources for model:** papers prominently cited which hold additional info about the model (for quick reference when needed)
- **Spatially explicit:** is the model spatially explicit and allows for spatial interactions?
- **Extent of study area:** in ha
- **Spatial grain:** in ha
- **Time step:** what is the smallest time step (highest temporal resolution) the model is operating on?
- **Longest Simulation duration:** how many years are simulated
- **Basic simulation entity:** what is the basic tree entity being modelled (trees, cohorts…)
- **Life forms other than trees (select):** which life forms other than trees (shrubs, herbs, grasses, other) are being modelled?
- **Sensitivity of lifeforms:** are life-forms sensitive to environmental surroundings (climate, substrate, competition) – list all life forms checked in the previous question and add "yes" if adaptive, "no" if not.
- **Sensitivity climate:** in particular, are trees sensitive to climate influences?
- **Growth included:** does the model include tree growth?

- **Mortality included:** is there a mortality process in the model?
- **Establishment included:** is there any establishment process in the model?
- **Competition included:** do trees compete for resources?
- **Stochastic:** are there any stochastic processes in the model?
- **Stochastic (describe processes):** where does stochasticity occur in the model?
- **Process-based:** is the model process-based?

Resilience definition and quantification

- **Definition of resilience:** select engineering (e.g. recovery is discussed) or ecological (e.g. alternative states are discussed) or other/undefined (if it fits neither of the other two categories.
- **Of what (select):** feature of the ecosystem the resilience of which is being investigated, select from general groups forest cover, forest structure, forest composition, forest functioning, ecosystem services, biodiversity
- **Of what (describe):** describe exactly what is being investigated (indicators)
- **To what (select):** wind, fire, insect, pathogen, drought, land use influence, other biotic, other abiotic, generic (no agent mentioned) and other
- **To what (describe):** describe the "to what" in more detail if needed
- **Multiple "of what":** are there multiple "of what" in the study?
- **Multiple "to what":** are there multiple "to what" in the study?
- **Interaction of different "to what" factors:** if multiple "to what" are investigated, are there interactions (e.g., climate change and natural disturbances)?
- **Interaction of different "to what" factors (describe):** which "to what" factors interact?
- **Impact of "to what":** is the "to what" dynamically simulated, (i.e. impact depends on forest vegetation characteristics, etc.) or generic (i.e. killing all trees in a specified cell)?
- **Climate modelled:** is climate part of the model?
- **Climate variability:** is the climate static or is there variability?
- **Management implemented:** is forest management happening in the study?
- **Management considered as a disturbance?** is forest management seen as a disturbance?
- **Quantification of resilience:** which resilience metrics are employed (e.g. recovery time, difference in composition at two points in time,…)
- **Threshold:** is there a threshold in the response variable (as described by the authors)?
- **Alternative states:** do the authors describe alternative states?
- **Alternative states (describe):** which alternative states occur in the study system (e.g. conifer-dominated/broadleaf-dominated or forest/non-forest)?
- **Feedbacks:** are there any feedbacks mentioned?
- **Hysteresis:** does hysteresis occur in the transition between states?

Processes of resilience: Regeneration:

- **Natural regeneration included:** Is natural regeneration being modelled?
- **Multiple regeneration processes:** is regeneration expressed by multiple explicit processes (e.g. seed production, seed dispersal, germination, seedling survival) or in one process or probability of regeneration?

- **Regeneration processes mentioned**: if there are separate regeneration processes, which are these?
- **Reproductive maturity:** Do trees have to reach maturity before they can reproduce?
- **Masting:** does masting occur (annual fluctuations in seed availability)?
- **Serotiny:** does the model include serotiny for fire-adapted species
- **Resprouting**: are trees in the model able to resprout after disturbance
- **Distance to seed source:** Does distance to seed source influence regeneration success?
- **Substrate influence:** does the substrate (soil depth, nutrients…) influence regeneration success?
  Climate influence: is regeneration climate-sensitive?
- **Light availability:** does light availability influence regeneration success (e.g. by shading from canopy trees?)
- **Competition from ground vegetation**: does non-tree competition vegetation (grass, herbs, shrubs,…) influence regeneration success?
- **Herbivory/Biotic disturbances:** is regeneration success affected by herbivory?

Processes of resilience: Legacies

- **Disturbance tolerance:** do life trees remain in place after disturbance and act as seed source (rather than all trees in the disturbance affected area being killed)?
- **Susceptibility by age:** Does the age of trees (adult tree vs sapling) influence their environmental response/susceptibility to disturbance?
- **Seed banks:** does the model allow for seeds to be stored in seed banks (soil, canopy)?
- **Seedling banks**: can seedlings survive a disturbance or are they killed along with the adult trees?
- **Dead plant biomass:** does dead plant biomass stay behind after disturbance (and contribute to regeneration)?
- **Stress legacies:** are trees more susceptible to disturbances and other environmental pressures if they have experienced prior stress?
- **Adaptation/information legacies:** can trees adapt to environmental changes (e.g. by changing allocation patterns)?

Process of resilience: Soil:

- **Soil modelled:** are soil dynamics part of the model?
- **Spatial variation in soil:** are soil characteristics homogenous for the whole simulation area or is there spatial variation?
- **Water availability:** is water availability dynamically modelled?
- **Erosion:** does soil erosion happen in the model?
- **Nitrogen cycle:** is there are dynamic nitrogen cycle with feedbacks to plant-available nitrogen?
- **Other nutrient cycles:** are there other dynamic nutrient cycles with feedbacks to plant-available nutrients.

- **Other comments:** any other relevant features of the study.
- **Investigator:** who entered the study into the database?

Appendix B

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

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

Short title: Legacies of human disturbance

Author list: Katharina Albrich[1,2], Dominik Thom[1,2], Werner Rammer[2], Rupert Seidl[1,2,3]

[1] University of Natural Resources and Life Sciences (BOKU) Vienna, Institute of Silviculture, 1190 Wien, Austria

[2] Technical University of Munich, Ecosystem Dynamics and Forest Management Group, 85354 Freising, Germany

[3] Berchtesgaden National Park, Doktorberg 6, 83471 Berchtesgaden, Germany

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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 natural forests by creating protected areas in formerly managed forests. Here, we investigated (1) if and how such forests return to conditions similar to old-growth, and (2) whether recently observed stand-replacing natural disturbances set them onto an alternative development 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 83 plots, spanning 220 years of forest development after the cessation of management, and compared it to old-growth forests. We analyzed the recovery of nine indicators of forest composition, structure and functioning. To evaluate stand development trajectories after recent natural disturbance we used a process-based simulation model.

Results: Old-growth forests showed a wide range of variability across investigated indicators. Forests converged to old-growth conditions after the cessation of management, with seven out of the nine indicators investigated falling within the indicator range of old-growth at the end of our chronosequence. The variation in tree diameters and the downed deadwood amount were, however, still significantly lower than in old-growth forests after 220 years of unmanaged stand development. Simulations did not indicate an alternative development 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 the protection of formerly managed forests is a valuable strategy to enrich forest landscapes in Europe. Our results indicate that the mountain forests of Central Europe have high ecological resilience, and return to their basin of attraction both after past management and current natural disturbance.

Keywords: primary forest, recovery, protected areas, simulation modelling, chronosequence, forest conservation, forest management

1. Introduction

Pristine old-growth forests have become increasingly rare. In Europe, for example, only 3 % of forests are considered "untouched by man" (FOREST EUROPE 2015). Sabatini et al. (2018) estimate that only 0.7 % of Europe's forest area remains as primary forest. This disappearance 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 natural old-growth forest dynamics (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 micro-climatic 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 with the aim to increase the share of old forests on 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, and how long such a process may take. So far, research on these questions is sparse, particularly in Europe (Vandekerkhove et al. 2009; Paillet et al. 2015).

Answering such questions is often hampered by the limited availability of data on forest ecosystem dynamics going back 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 an age gradient 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 disturbances (Holling & Gunderson 2002) are already on a different development pathway? Since these questions cannot be settled 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 space-for-time 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 varying management history. At the heart of the DWA area 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 biogeochemistry (Pietsch & Hasenauer 2006) in Central Europe as well as for the development of forest management strategies (Mayer 1987). The protected area surrounding the Rothwald was enlarged in several waves, creating a wide gradient in the time since the last management intervention and providing a unique opportunity to study forest development in SFT approach.

Using a combination of field-based observations along a chronosequence and process-based forest landscape model simulations, we here address the questions (1) do formerly managed forests recover towards current old-growth conditions, and (2) do recently observed disturbances initiate alternative vegetation development pathways?

2. Material and Methods

2.1. Study Area

The Dürrenstein Wilderness Area (DWA) is located in Eastern Austria (47°45'20"N 15°02'10"E). It currently encompasses 3,449 hectares of protected area and extends from about 650 m a.s.l. to 1878 m a.s.l. (top of mount Dürrenstein, Fig. 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 further expanded in multiple steps, adding formerly managed forests from the Austrian Federal Forests as well as the Rothschild family (Pekny 2012). In the earliest management periods, management can be described as 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 was generally clear-cut centered with rotation times of around 100 to 160 years. In some areas, management intensity was relatively low due to steepness and accessibility (Pekny 2012; Thom et al. 2018). The entire protected area was designated an IUCN Category Ib Protected Area in 2003, with the last wave of expansion to its current size in 2013 (Splechtna & Splechtna 2016).

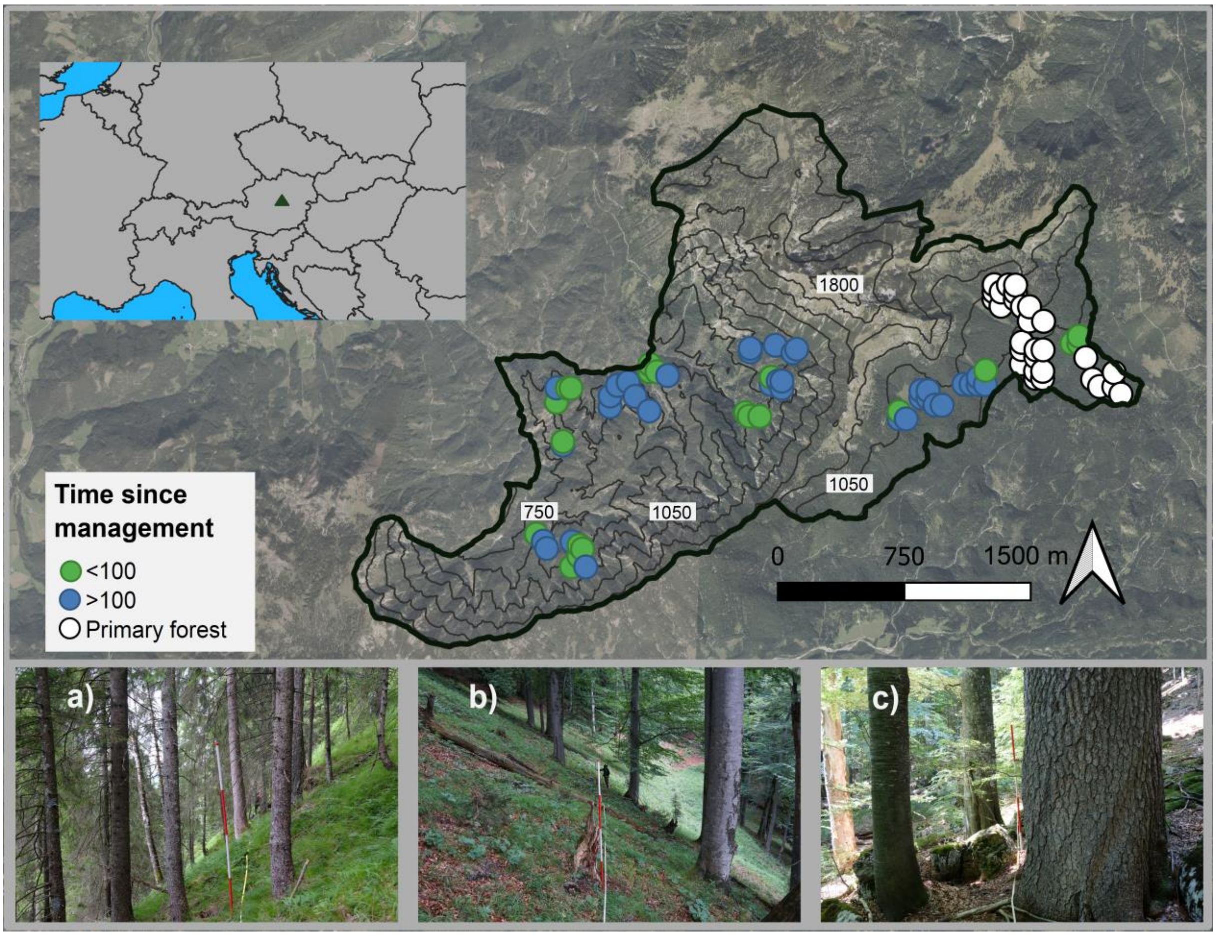

Figure 1: Study area and sample point locations (points, colored by time since management). Photos show examples of conditions on sample plots for age classes: a) <100 years since management, b) >100 years since management, c) Primary forest. (Photos by Rupert Seidl, Daniel Schraik).

The DWA is located in the northern Limestone Alps with dolomite and lime stone 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 L.*), Norway spruce

(*Picea abies (L.) H. KARST*) and silver fir (*Abies alba MILL.*) (Splechtna et al., 2005). The area is characterized by a submaritime climate with long winters and short, relatively cool summers. Annual precipitation is high (up to 2300 mm) and bimodally distributed, with peaks in summer and in 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, stratified by time since last management and elevation zone. We furthermore distributed our sampling evenly between two distinct site types, namely sheltered, relatively flat low to mid-elevation forests with higher shares of conifers and forests on steep slopes at higher elevation and with higher shares of broadleaves (Splechtna et al. 2005). To establish a chronosequence, time since management was derived from historic and current forest management maps and 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 within stands as 50 m long and 4 m wide (200 m^2) transects oriented in a 90° angle to slope direction and separated into 50 4 m^2 subplots (Figure S1). All live trees with a DBH >7 cm in the transect were recorded with DBH, species, and the subplot they were located in. For dead standing trees diameter, height and decay class were recorded. In two 4 m^2 subplots (one at each end of the transect) regeneration subplots were established and 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 broadleaved trees as well as the tree closest to the center of each regeneration subplot. Coarse woody debris was recorded in three 10 m transects originating from the plot center 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 center as well as at the center of the regeneration subplots by means of a Solariscope (Ing.-Büro Behling 2015) to record light conditions. Four plots were located in stands recently disturbed by bark beetles, while for all other plots no visual signs of recent disturbance were identified.

2.3. Statistical Analysis

From the data collected, a total of nine indicators 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 Core Team 2020, R version 3.6.3). Forest Structure was represented through the coefficient of variation in tree diameters, the median tree height, the Total Site Factor as an indicator 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 less than 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 indicators of forest functioning, three aboveground carbon pools were calculated: live tree, snag (standing deadwood) and coarse woody debris on the forest floor (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. 2017), snag carbon was calculated using the approach presented by Ford & Keeton (2017), and for coarse woody debris we followed the method described in Böhl & Brändli (2007). For both deadwood pools, wood density reduction factors were applied for decay classes 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: Indicators used and their definition, calculation and unit (where applicable).

Indicator	**Indicator definition and calculation**	**Unit**
CV DBH	Coefficient of variation of tree diameters	cm
Median height	Median stand height	m
TSF	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* MILL., *Picea abies*, *Pinus sylvestris* L., *Taxus baccata* L.) 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 & 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 & Brändli (2007) with reduction factors for decay classes from Harmon et al. (2011)	t/ha

As a first analysis step, plots were grouped into two managed (<100 years and >100 years old) and one unmanaged (primary forest) categories. We chose 100 years as cut-off as beyond that age increasing disturbance activity and a stronger differentiation in forest structure can be expected, leading to the diversification of forest attributes (Overbeck & Schmidt 2012; Donato et al. 2012; Meigs et al. 2017). Furthermore, 100 years represents the approximate rotation period in surrounding managed forests, with the cutoff distinguishing between forests that have been unmanaged for shorter/ longer than one rotation period. The four plots that were recently disturbed by bark beetles were excluded from this analysis.

We analyzed if the three groups differed significantly in their forest attributes. Non-metric multidimensional scaling (NMDS) using Bray-Curtis dissimilarity was performed to visually explore the multidimensional variable space using the package "vegan" (Oksanen et al. 2019). Subsequently, a PERMANOVA was used to test for significant differences ($\alpha = 0.05$) between the age groups. We tested for significant differences on the level of individual indicators using a Kruskal-Wallis Rank Sum Test with a subsequent Dunn's test with Benjamini-Hochberg adjustment for multiple comparisons (to test which groups were different).

In a subsequent step, we explored the relationship between continuous time since management and the development of the individual indicators using polynomial functions. We calculated the percentage of plots that lie within the variability of old-growth forest (mean plus/minus standard deviation) in order to determine how strongly stands recovering from management deviate from unmanaged reference conditions.

2.4. Simulations

Some of our plots showed clear signs of recent disturbance, and future disturbances are likely to occur (Thom, Rammer, & Seidl 2017b; Thom et al. 2018). To test whether such disturbances set forest development after management off on an alternative trajectory we used a simulation approach.

We employed the simulation model iLand (Seidl et al. 2012) in a stand-level simulation experiment. iLand is an individual-based forest simulation model which can be used to simulate forest dynamics at the stand to landscape scale. iLand is a process-based model with forest dynamics emerging 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 aging, 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. 2012; Seidl et al. 2014; Rammer & Seidl 2015; Seidl & Rammer 2017). Regeneration is simulated spatially explicitly at a grain of 2×2m 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. 2012). The model has been thoroughly tested and parametrized for simulations in the area in previous studies (Thom, Rammer, & Seidl 2017a; Thom, Rammer, & Seidl 2017b).

To simulate the development trajectories of recently disturbed plots (n=4) we utilized input data from nearby Kalkalpen National Park (located 45 km to the west of the DWA), which has similar edaphic and climatic conditions. Soil and climate data were matched to the simulated sites based on elevation, aspect and slope. Time series of historical climate data 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). Each sample plot was represented by a one-hectare simulation area.

We first tested the ability of the model to replicate conditions in the DWA by simulating natural forest development for 1000 years under past climate conditions (reference climate period: 1900-2010), comparing the results to the empirical old-growth data collected from Rothwald forest (Appendix Figure S2). We then focused on the recently disturbed bark beetle plots and used the model to assess whether these forests will develop to a state similar to the observed old-growth forests, or if the environmental changes of the recent past will drive the system to a new state. To that end, we replicated each of the simulated one-hectare cells 500 times. We recreated stand history by initializing the stands in the year 1900 (the approximate year of the last management intervention) with spruce saplings, mimicking the common historic practice of planting spruce after clearfelling (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 was established by forcing the observed stand-replacing disturbance, killing all mature trees and leaving deadwood on site. From this state (representing the state of a recovery trajectory from management interrupted by natural disturbance), the stands were simulated under stable driver conditions (climate resampled from the years 2010-2020) for 700 years. This meant 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 beginning of the simulation, i.e. the stand origin (Table S1). The dynamic disturbance modules for bark beetle and wind were used throughout the full simulation period.

To test whether recently disturbed stands still develop towards reference old-growth conditions in our simulations we extracted the same nine indicators from the model which we used in the analysis of the field data. We fitted polynomial functions to the temporal development of the simulated indicators and compared them to data from old-growth stands of the same site type (higher elevations and steeper slopes, 12 plots). We also calculated the share of simulated plots per indicator 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 two distinct periods: First, we looked at the period between simulation year 200 and 300 (85 to 185 years post disturbance, a similar age bracket to the stands recovering from management observed empirically). Second, we analyzed results for the last 100 years of the simulation, representing the convergence to old-growth conditions after more than 500 years of stand development (Thom, Rammer, & Seidl 2017a).

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 significantly different from old-growth forests for several indicators. Differences decreased for forests that were last cut >100 years ago. Using non-metric multidimensional scaling (Figure 2) and the assessment of stress versus dimensionality (using a scree plot) we found three dimensions to be a suitable level of complexity (stress <0.05). Differences between all three groups were highly significant ($p<0.001$), suggesting that also >100 years after management naturally developing forests still differ from old-growth conditions. A major driver in the separation of groups was regeneration density (number of saplings). The stands which developed for more than 100 years after management were particularly diverse and had overlaps with both other categories in NMDS space (Figure 2).

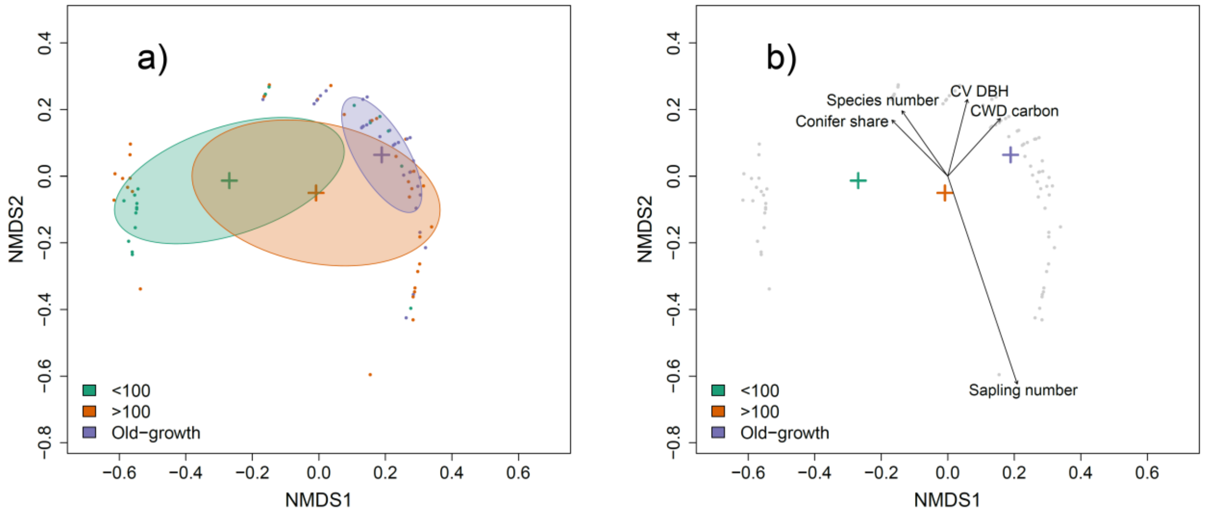

Figure 2: Non-metric multidimensional scaling (NMDS) of the nine indicators of forest structure, composition, and functioning. Shown are the first two axes for three groups of stands (management cessation less than 100 years ago, management cessation more than 100 years ago and old-growth). Crosses indicate the centroids of the three groups in NMDS space. In panel a) the ellipses indicate the standard deviation around the centroid for each group. In panel b) indicators with a significant impact ($\alpha=0.05$) are identified. The length of the arrow is proportional to the strength of the influence. Colored points represent the underlying raw data.

Five out of nine indicators showed significant differences between forests <100 years after the cessation of management and old-growth forests (Table 2). The variation in tree diameters was significantly lower in formerly managed stands compared to old-growth stands ($p=0.009$). Young formerly managed stands were also significantly different from old-growth stands for saplings ($p<0.001$), and had a considerably higher share of conifers ($p=0.001$). 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 lower in stands <100 years after the cessation of management.

The deviation between old-growth forests and forests developing after management decreased for stands >100 years after the cessation of management. Specifically, only two indicators still differed significantly between these two groups, namely the variation in tree diameters ($p<0.001$) and the carbon stored in downed woody debris ($p<0.001$).

Table 2: Group means and standard deviations for each indicator, comparing stands with different time since management to old-growth conditions. Different superscript letters indicate significantly different groups (tested with Kruskal-Wallis test and post-hoc Dunn's test with Benjamini-Hochberg correction).

Indicator	**Time since management**		**Old-growth**
	<100 years	**>100 years**	
CV DBH	0.443±0.124^{a}	0.362±0.205^{a}	0.594±0.244^{b}
Median height	16.7±4.31^{a}	18.8±6.75^{b}	17.9±4.31^{ab}
TSF	0.106±0.113^{a}	0.149±0.147^{a}	0.0986±0.0894^{a}
Sapling number	4,750±13,588^{a}	18,750±32,440^{b}	12,000±14,966^{b}
Species number	1.75±0.531^{a}	1.74±1.01^{a}	1.71±0.7^{a}
Conifer share	76.7±29.4^{a}	34.7±35.2^{b}	37.8±33.3^{b}
Live tree carbon	103±46.6^{a}	128±100^{a}	146±120^{a}
Snag carbon	7.24±12.0^{a}	11.5±29.0^{b}	8.19±20.3^{b}
CWD carbon	0.371±0.688^{a}	2.05±3.48^{b}	3.37±3.02^{c}

Subsequently, we analyzed development trajectories relative to old-growth conditions across the chronosequence of plots to elucidate temporal patterns in more detail (Figure 3). Tree diameter variation declined with stand age and was outside the range of variability of old-growth forests at the end of our chronosequence (age 221). Median tree height and Total Site Factor both showed a hump shaped relationship with stand age and 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 stands were within the old-growth variation (Total Site Factor:

91%). Sapling number first increased with stand age and remained fairly stable after ~150 years, with 81 % of all chronosequence plots falling within the old-growth variability.

Species diversity increased in forests >150 years old, and 54 % of the chronosequence plots 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. 45 % of the chronosequence plots had conifer shares that fell within the range of variation of old-growth forests, which was between 4 and 71 %.

The three carbon pools all showed a weak indication of a hump-shaped relationship with age. The variation of carbon stocks in old-growth forests was very large and chronosequence plots were largely within this range throughout the entire age range. 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 plots were within old-growth variability. For live and snag carbon this rate was 79 % and 94 % respectively.

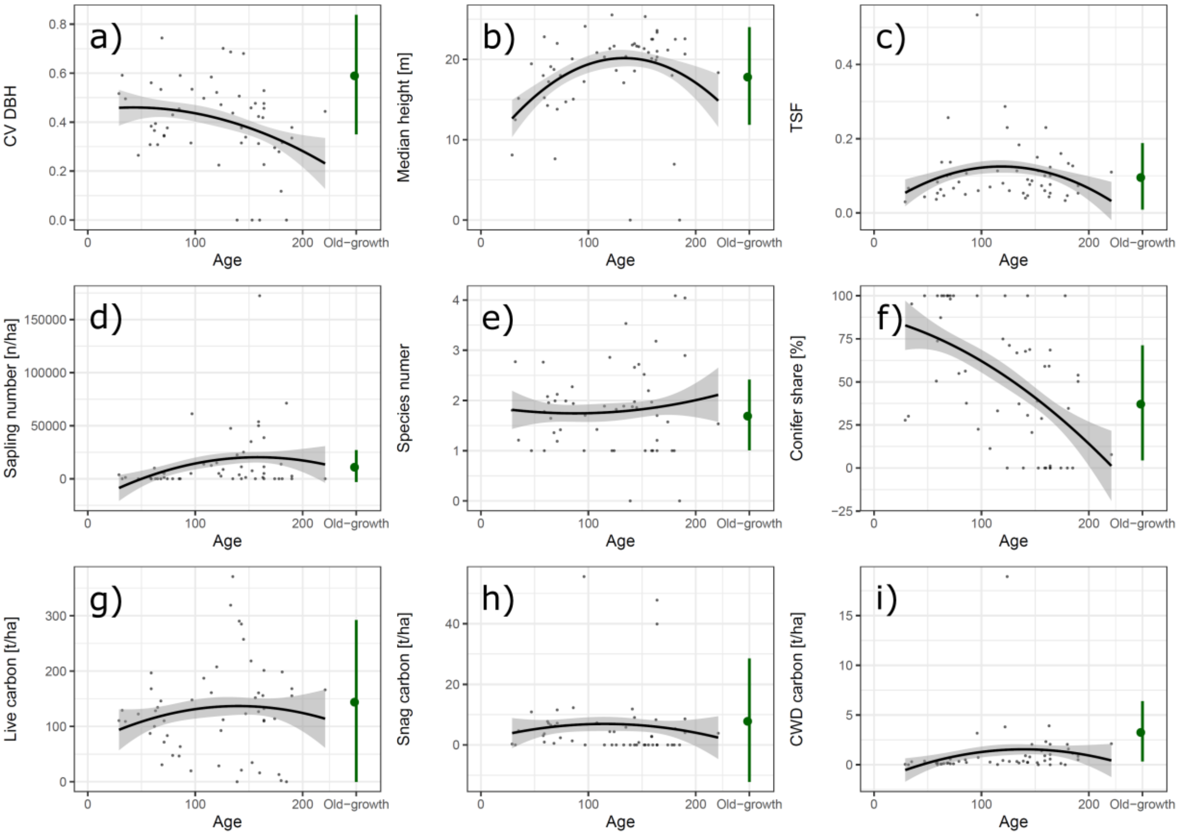

Figure 3: Forest development across age, derived as a chronosequence of time since last clearcut management. The black line shows the mean (polynomial function) with the grey area indicating the variation (plus/minus one standard deviation). Grey points are the individual chronosequence plots. Green point and lines show the mean and variation (plus/minus one standard deviation) of old-growth stands.

Overall, we found that differences between stands describing a chronosequence after the cessation of management and old-growth stands was less pronounced than expected, due to a very high variation in old-growth conditions. In general, most indicators showed a development towards old-growth over time. The two deviations from this pattern were the variation in tree diameters and the share of conifers, for which the trajectories move away from old-growth conditions during our 220-year chronosequence.

3.2. The role of bark beetle disturbance

We used simulation modeling to investigate how recent bark beetle disturbance may alter the trajectories of stands recovering from management. Recent bark beetle disturbance slowed the development to old-growth conditions, but six out of the nine indicators returned to the range of current old-growth forests in the simulations. This indicates that the changed environmental conditions under which the current 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 indicators (Figure 4). While some indicators returned to the range of variability of old-growth forests within a few decades after the disturbance, some 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. 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. As with the development after management, 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 were similar.

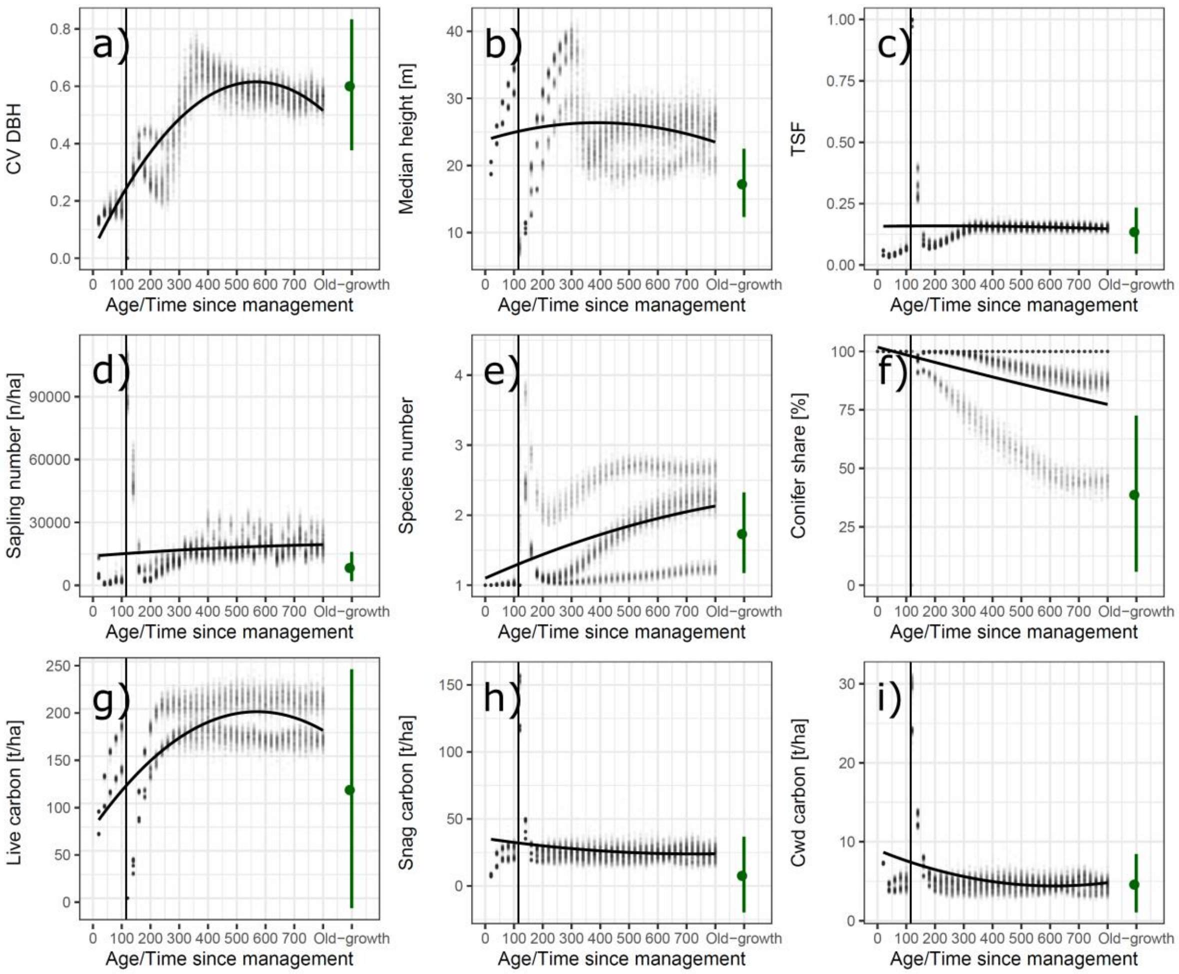

Figure 4: The influence of recent bark beetle disturbance on the stand development trajectory after the cessation of management, simulated with the forest landscape model iLand. Vertical line indicates the occurrence of a stand-replacing bark beetle disturbance (as observed for ~5% of the chronosequence plots). The black line shows the mean development of the indicators (polynomial function) of simulated stands, with the grey area indicating the variation between replicated simulations (plus/minus standard deviation). Grey points indicate individual simulated plots. The green point and lines show the mean and variation of observed old-growth plots.

4. Discussion

Primary forests untouched by human management are becoming increasingly rare. One possible action to counter this loss and ensure that the important roles fulfilled by old-growth forests (e.g. biodiversity refuge, climate regulation, source of ecological understanding) are sustained is to protect formerly managed forest and let them once more develop naturally. How fast a re-convergence to old-growth conditions ensues after the cessation of management remains unclear, however, as extensive management legacies have been documented in previous studies (Thom et al. 2018). Here we combined field observations across old-growth and formerly managed stands with a simulation approach to understand the development of forests after the cessation of management and analyze 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 among forest ecosystem attributes. A key aspect of analyzing the return to a set of reference condition is the definition of such conditions. We here show that old-growth conditions at DWA are highly variable, constituting a very wide basin of attraction for the return of formerly managed forests (Figure 3, Table 2). This wide basin of attraction – particularly distinct for indicators of forest functioning – also meant that some focal indicators returned quickly to states within the range of variability of old-growth forests after the cessation of management. A number of ecosystem indicators even fell within old-growth variation throughout the entire chronosequence after management studied here. This suggests that policies targeting old-growth in conservation need to acknowledge that a broad variety of development stages exist in parallel in these forests.

Beyond the observation that old-growth forests can be very diverse our study indicates forests can take on diverse forms and already exhibit some characteristics of old-growth at relatively young ages (Donato et al. 2012). Multiple factors can contribute to such diverse development pathways emerging already in young stands. These can reach from high variation in environmental and site factors (Sesnie et al. 2009), to reasons related to population dynamics such as seed availability and dispersal (Barbeito et al. 2009) and competition both from trees as well as other plants (Donato et al. 2012). An important factor promoting diverse stand development 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).

Empirical studies investigating the development of formerly managed towards old-growth stands are exceedingly rare, in particular for European forests and for stands where management is relatively far in the past like in our case (Paillet et al. 2015). Those that exist are often focused on the development of deadwood stocks after management cessation and generally find a relatively fast recovery (von Oheimb et al. 2005; Meyer & Schmidt 2011). Observations for other indicators are even rarer, however Paillet et al. (2015) found in a comparison of French forest reserves with recent management history that forest structure and particularly composition recovered slower than deadwood pools after management, which is line with our observations. Other indicators which we did not assess here, particularly those related to the number of very large old trees and the tree cavity habitats they provide (Remm & Lõhmus 2011) may take even longer. Hence, the recovery of the full spectrum of old-growth features takes centuries (Rademacher et al. 2001). Another factor of recovery after management which we did not address here, but which deserves further attention, is the development of soil variables, particularly in relation to carbon and nutrient cycles (Rubio & Escudero 2003; Thom et al. 2019). Overall, our study indicates that attributes of particular value for conservation can emerge already relatively soon after management has ceased, underlining that an increase in the protected forest area can contribute to tackling the global loss in biodiversity (European Commission 2020).

We used a chronosequence approach to analyze 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 questions at hand. 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, controlling for environmental conditions (elevation, slope, aspect). Frequently, old-growth stands are not entirely comparable with formerly managed stands regarding their environmental drivers (e.g. differences in productivity, which might also explain why reference old-growth stands remain untouched by management, Pickett 1989), which reduces the inferential power of a chronosequence considerably. We addressed this problem in our study by distinguishing two distinct site type, and sampling across them in both the Rothwald forest and the formerly managed stands. We selected our chronosequence stands and reference conditions with great care and are thus confident that our chronosequence allows meaningful inference on forest development.

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-cut (the predominant 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 is poorly documented. We excluded all stands that showed visible signs of silvicultural interventions (e.g. cut stumps from tending or thinning operations) in the field and are reasonably certain that stand history is comparable across the chronosequence.

4.2. Resilience of stand development trajectories

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). We here used a simulation model to test whether disturbances occurring under current conditions (warmer temperatures, higher CO2 levels, elevated nitrogen deposition) considerably alter stand development and lead to alternative development pathways. We found that even stands disturbed today largely recovered to reference old-growth conditions within a few hundred years. This recovery towards a reference state that is the result of historical environmental conditions indicates that the mountain forest ecosystems assessed here are resilient against the recent changes in environmental drivers. However, much stronger changes in climate than those observed already are expected in the coming decades, which might result in drastically changed 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 reference state in this study) have a long history of being used as hunting grounds and therefore often carry legacies of high ungulate densities (Mayer & Neumann 1981; von Oheimb et al. 2005). We did not include ungulate browsing in our simulations, which may partially explain the generally higher sapling numbers in the simulation compared to observations. Also, while a tree species diversity comparable to old-growth was already present at young stands in both field data (Figure 3) and simulations (Figure 4), certain species (such as silver fir) can be suppressed through browsing. Ungulates can therefore cause strong alterations in forest composition in the long-term (Didion et al. 2009). While we here focused on tree species diversity, we did not analyze particular species or species groups (such as late-seral species), which might have resulted in a slower return to old-growth conditions (e.g. Seidl 2014).

4.3. Outlook and implications

Old-growth forests are often associated with a dense, multi-storied canopy, big trees and large amounts of deadwood. Here we show that old-growth forests in Central Europe are highly diverse in their structure, composition and functioning. This finding has important implications, as it underlines that old-growth derived reference states for management (e.g., in the context of conservation or close-to-nature forestry) need to be specified in terms of a range of variability (Keane et al. 2009) rather than a narrow set of target conditions.

Here we show that conditions that are comparable to old-growth forests can already emerge relatively early after the cessation of management (c.f. Donato et al. 2012). With regard to many features, forests recovering from management cannot be distinguished from old-growth forests after only a few decades of stand development. This finding suggests that the protection of forests – which is currently one of the most powerful means of strategies to halt biodiversity loss (European Commission 2020) – is able to bring back old-growth structures into landscapes where they have gone largely missing, such as in Central Europe. We note, however, that a 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 features 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 diameters and the amount of downed deadwood still differed considerably from old-growth forests also after two centuries of stand development. This suggests that they are central indicators for gauging how similar or different to old-growth a given forest structure is (Spies 2004). The fact that these indicators 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 in the last century have not yet set these forests on alternative development pathways, and they are still likely to recover to the past basin of attraction that is represented by current old-growth conditions. A 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

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Author Contributions

K.A. and R.S. developed the study design. K.A analyzed the data, conducted the simulation experiment and wrote the manuscript with input from all co-authors.

Data Availability Statement:

Data supporting the findings of this study is available at https://bokubox.boku.ac.at/index.php/#53c02d452e7434a7eaf6569ebda606d2 and will be archived in a permanent repository upon publication of the study.

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Supplementary Material

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

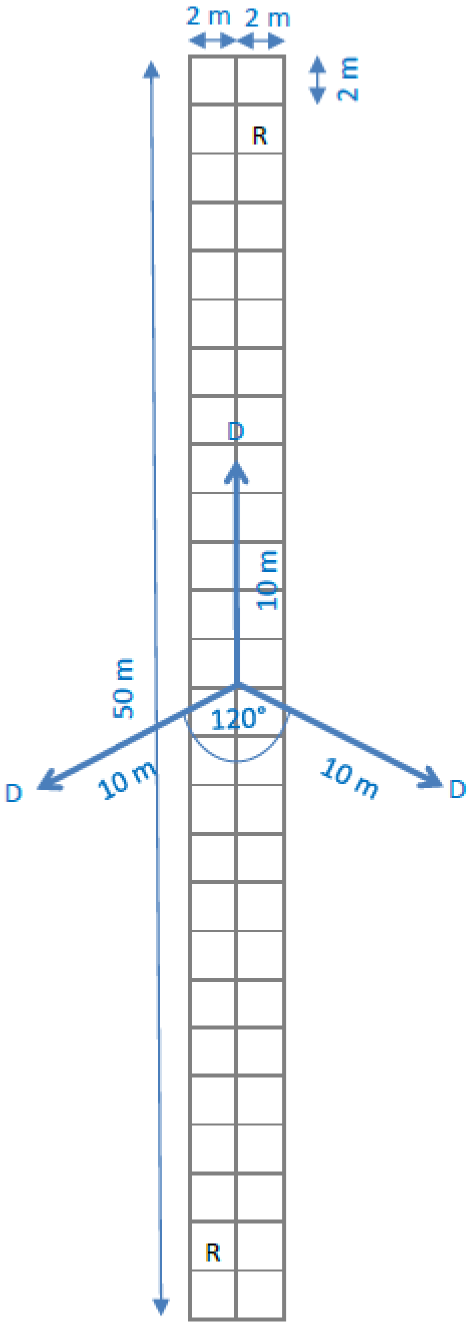

Figure S1: Layout of sample plots, subdivided into 2x2 m subplots. Sample plots were oriented perpendicular to slope directions. The blue transects marked "D" emanating from the plot center were used as line intersect sampling transects to sample coarse woody debris. Subplots labelled with "R" were used for regeneration sampling.

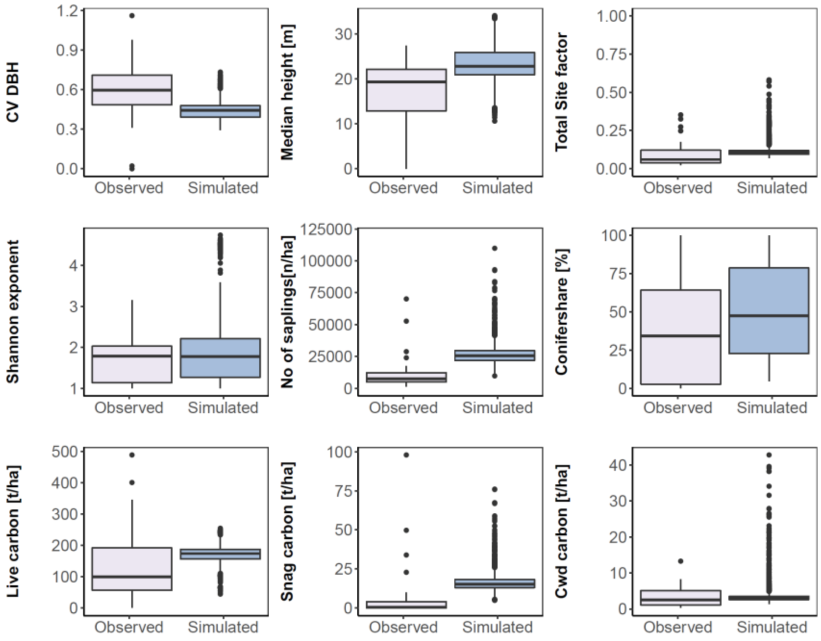

Figure S2: Model evaluation. One run of 7600 hectares for 1000 years under historic climate (climate reference period 1900-2010)

Table S1: Comparison of simulated drivers at beginning of simulated period (1900) and in the equilibration simulation period under current climate (sampled from 2010-2020).

Period	Available Nitrogen [kg ha^{-1} year^{-1}]	CO2 [ppm]	Temperature [°C]	Precipitation [mm year^{-1}]
1900-1910	42.52	298.68	5.38	1376
2010-2020	52.52	404.07	6.64	1489

Appendix C

Climate change causes critical transitions and irreversible alterations of mountain forests

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PRIMARY RESEARCH ARTICLE

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Climate change causes critical transitions and irreversible alterations of mountain forests

Katharina Albrich[1,2] | **Werner Rammer**[1,2] | **Rupert Seidl**[1,2]

[1]Institute of Silviculture, University of Natural Resources and Life Sciences (BOKU) Vienna, Vienna, Austria
[2]Ecosystem Dynamics and Forest Management Group, Technical University of Munich, Freising, Germany

Correspondence
Katharina Albrich, University of Natural Resources and Life Sciences (BOKU) Vienna, Institute of Silviculture, Peter Jordan Straße 82, 1190 Vienna, Austria.
Email: katharina.albrich@boku.ac.at

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Abstract

Mountain forests are at particular risk of climate change impacts due to their temperature limitation and high exposure to warming. At the same time, their complex topography may help to buffer the effects of climate change and create climate refugia. Whether climate change can lead to critical transitions of mountain forest ecosystems and whether such transitions are reversible remain incompletely understood. We investigated the resilience of forest composition and size structure to climate change, focusing on a mountain forest landscape in the Eastern Alps. Using the individual-based forest landscape model iLand, we simulated ecosystem responses to a wide range of climatic changes (up to a 6°C increase in mean annual temperature and a 30% reduction in mean annual precipitation), testing for tipping points in vegetation size structure and composition under different topography scenarios. We found that at warming levels above +2°C a threshold was crossed, with the system tipping into an alternative state. The system shifted from a conifer-dominated landscape characterized by large trees to a landscape dominated by smaller, predominantly broadleaved trees. Topographic complexity moderated climate change impacts, smoothing and delaying the transitions between alternative vegetation states. We subsequently reversed the simulated climate forcing to assess the ability of the landscape to recover from climate change impacts. The forest landscape showed hysteresis, particularly in scenarios with lower precipitation. At the same mean annual temperature, equilibrium vegetation size structure and species composition differed between warming and cooling trajectories. Here we show that even moderate warming corresponding to current policy targets could result in critical transitions of forest ecosystems and highlight the importance of topographic complexity as a buffering agent. Furthermore, our results show that overshooting ambitious climate mitigation targets could be dangerous, as ecological impacts can be irreversible at millennial time scales once a tipping point has been crossed.

KEYWORDS
Alps, climate impacts, forest dynamics, forest simulation model, mountain forest landscape, resilience, topographic buffering

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1 | INTRODUCTION

Recent environmental changes have pushed many ecosystems to the margins of their historic operating space (Duncan, McComb, & Johnson, 2010; Keane, Hessburg, Landres, & Swanson, 2009), increasing the likelihood of abrupt changes in ecosystem characteristics and processes (Scheffer, Carpenter, Foley, Folke, & Walker, 2001). As future changes in the climate system are likely (Good et al., 2011; IPCC, 2013), an important focus of current ecological research is to understand whether ecosystems will respond gradually or abruptly to increasing climate forcing (Turner et al., 2020; van Nes et al., 2016). The growing awareness of tipping points in ecological systems has strongly influenced current targets of climate policy (Schellnhuber, Rahmstorf, & Winkelmann, 2016). Yet, for many systems, it remains unclear whether tipping points exist, and if so, whether limiting climate warming to below +2° is sufficient to prevent critical transitions (i.e., abrupt changes from one ecosystem state to another, Scheffer, 2009). A key question of current ecological research is thus to elucidate how ecosystems respond to increasing levels of warming and quantify the relevant driver–state relationships (Ratajczak et al., 2018).

The concept of resilience provides a powerful framework for studying critical ecosystem transitions in response to environmental change (Johnstone et al., 2016; Ratajczak et al., 2018; Scheffer et al., 2001). Resilience is a broad concept and has been defined in several different ways (Brand & Jax, 2007; Nikinmaa et al., 2020). Here, we focus on ecological resilience, pioneered by Holling (1973) and defined as the ability of "a system to experience shocks while retaining essentially the same function, structure, feedbacks, and therefore identity" (Walker et al., 2006). In this definition, resilience is measured as the amount of perturbation (e.g., change in climate variables) a system can absorb before reaching a tipping point or threshold beyond which it transitions into an alternative state. When a threshold is crossed, systems may also exhibit hysteresis. A hysteretic system will not return to its initial state along the same path even if the driver variable is returned to its pre-threshold level. This means that the driver variable has to be brought to an even lower level to allow the system to return to its initial state. It may also cause a system to be locked in an alternative, possibly undesirable state despite the removal of the initial forcing. Previous forest research on this question has largely focused on the forest–grassland ecotone and on tropical rainforests (Cowling & Shin, 2006; Good et al., 2011; Levine et al., 2016), finding clear evidence for alternative states and hysteresis (Beckage, Platt, & Gross, 2009; Staal, Dekker, Xu, & Nes, 2016; van Nes, Hirota, Holmgren, & Scheffer, 2014). Tipping points and hysteresis remain understudied for extratropical systems (but see e.g., Hansen, Braziunas, Rammer, Seidl, & Turner, 2018, Miller, Thompson, Tepley, & Anderson-Teixeira, 2018, e.g., for potential tipping points in North American systems, and Scheffer, Hirota, Holmgren, Nes, & Chapin, 2012 for an investigation of critical transitions in boreal systems), and to our knowledge no investigation of potential critical transitions exists for forest ecosystems in Central Europe to date.

While resilience research has made large conceptual advances in recent years, applying the concept to specific ecosystems has proven difficult, with measuring and quantifying resilience being particularly challenging (Ingrisch & Bahn, 2018; Reyer et al., 2015; Scheffer, Carpenter, Dakos, & Nes, 2015). In long-lived terrestrial ecosystems such as forests, critical transitions are frequently only apparent years to decades after they have taken place (Hansen et al., 2018; Thrippleton, Bugmann, & Snell, 2018). Furthermore, experimental manipulations—which are an important means to explore resilience to environmental changes (Butitta, Carpenter, Loken, Pace, & Stanley, 2017; Schröder, Persson, & Roos, 2005)—are of limited applicability for studying forest systems at the ecosystem to landscape scale. Simulation models help address these challenges in studying the resilience of forest ecosystems (Egli, Weise, Radchuk, Seppelt, & Grimm, 2018; Reyer et al., 2015; Seidl, Spies, Peterson, Stephens, & Hicke, 2016). They allow the investigation of extended temporal and spatial domains in an efficient manner and can quantify the effect of changes in the environment for which no past analogues exist.

Mountain areas are particularly exposed to climatic changes (Pepin et al., 2015), and life in mountains is strongly temperature limited. This puts mountain ecosystems at particular risk of severe climate change impacts (Palomo, 2017; Thuiller, Lavorel, Araújo, Sykes, & Prentice, 2005), and makes them important study systems for early detection of the potential consequences of climate change (Beniston, 2003). At the same time, mountain ecosystems are characterized by high topographic complexity, which is increasingly recognized as an important factor modulating the impacts of climate change on vegetation (Ashcroft, Chisholm, & French, 2009; Senf & Seidl, 2018). Complex topography may, for example, provide sheltered (e.g., cooler and moister) sites where species can persist even though the general climate becomes unfavorable for them. Such refugia could subsequently be the nuclei of recolonization once environmental conditions return to a more suitable level, overall fostering a more buffered response to climate drivers than in topographically homogenous landscapes (Serra-Diaz, Scheller, Syphard, & Franklin, 2015). Therefore, we hypothesize that complex topography reduces the probability of threshold responses and fosters resilience of mountain ecosystems (Turner, Donato, & Romme, 2013; van Nes & Scheffer, 2005).

We applied an individual-based forest simulation model to study the resilience of a mountain forest landscape in the European Alps to changes in temperature and precipitation. Specifically, we focused our analysis on the response of forest size structure and species composition to climate change. Structurally, a defining characteristic of the current mountain forests of the Alps is the presence and number of large trees, while the key species dominating their potential natural as well as current vegetation composition is Norway spruce (*Picea abies* (L.) Karst.). Both the characteristic size structure and species composition are also relevant to locally important ecosystem services such as timber production, protection from natural hazards and carbon storage (Seidl et al., 2019; Tappeiner, Tasser, Leitinger, Cernusca, & Tappeiner, 2008). Here we quantified the resilience of these attributes to climate change, asking (a) whether there are threshold responses in forest composition and size structure to progressive changes in the climate system, (b) how topographic complexity influences the response of the landscape to climate change, and (c) whether climate-mediated changes in the ecosystem are reversible once the climate forcing is removed. To isolate the role of climate in driving forest change, we analyzed equilibrium size structure and species composition. This allowed us to control for the substantial land-use legacies that are present in forest ecosystems throughout the Alps (Bebi et al., 2017), and to eliminate transient dynamics in the identification of system attractors (Schröder et al., 2005).

2 | MATERIALS AND METHODS

2.1 | Study landscape

The Stubai Valley study landscape is located in the central Alps in Tyrol, Austria (47.10°N, 11.29°E). It is characterized by a strong vertical gradient from 900 m a.s.l. (valley bottom) to the timber line at 2,000 m a.s.l., with the highest mountain peaks exceeding 3,500 m a.s.l. The most important tree species of both the natural and current vegetation are Norway spruce, European larch (*Larix decidua* Mill.), and Swiss stone pine (*Pinus cembra* L.). Mean annual temperature for the period 1961–2014 was 4.1°C, sharply decreasing with elevation (from 7.2°C to 0.6°C, Figure 1). Mean annual precipitation was 998 mm, increasing with elevation (from 826 to 1,163 mm). Historically, the area has been influenced by human land-use such as forest management, grassland management including cattle grazing on alpine pastures, and tourism (Tappeiner et al., 2008). Here we focused on the area of the Stubai Valley that is currently forested, a contiguous land area of 4,811 ha.

2.2 | Simulation model

We used iLand, the individual-based forest landscape and disturbance model (Seidl, Spies, et al., 2012) to simulate forest species composition and size structure under climate change. iLand is a spatially explicit landscape model simulating forest ecosystem dynamics. Detailed descriptions of iLand can be found in Seidl, Rammer, and Spies (2014), Seidl, Rammer, Scheller, and Spies (2012), Seidl, Spies, et al. (2012), Thom, Rammer, and Seidl (2017b), and Thom, Rammer, Dirnböck, et al. (2017); here we focus on describing the core processes of particular relevance for this study. In iLand, the vegetation state is updated annually based on dynamically simulated processes of tree growth, mortality, and regeneration. Productivity is calculated monthly based on a resource use efficiency approach (Landsberg & Waring, 1997) and is contingent on environmental conditions and species traits. Relevant environment variables include climate (temperature, precipitation, radiation, and vapor pressure deficit, all considered at daily resolution) and soil conditions (effective soil depth; sand, silt and clay fractions; and nitrogen availability; all temporally invariant throughout the simulation). Carbohydrate allocation in trees is calculated annually based on allometric ratios and is sensitive to a tree's competitive status. The mortality probability of a tree is influenced both by its carbon balance (stress-related mortality) and by its size and age (species-specific life-history traits). While iLand is also able to simulate tree mortality from natural disturbances and management (Rammer & Seidl, 2015; Seidl & Rammer, 2017; Seidl, Rammer, & Blennow, 2014), we did not include these factors in our study design (see details below). iLand simulates tree regeneration at the grain of 4 m^2 cells (annual time step), and accounts for the processes of seed dispersal and climate-dependent establishment, as well as seedling and sapling growth (Seidl, Spies, et al., 2012). The model simulates the ecosystem water cycle dynamically at daily time steps (spatial grain of 1 ha cells), with water availability directly influenced by precipitation, soil properties (soil depth and texture), and the presence and composition of forest vegetation. The model has been applied and evaluated for multiple landscapes in Central Europe (Dobor et al., 2018; Thom, Rammer, Dirnböck, et al., 2017), including the focal landscape of this study (Supplementary Material Figures S1.1–S1.4, Seidl et al., 2019).

2.3 | Topography scenarios and initial conditions

To investigate the effect of topography on climate responses, we developed three different topography scenarios, hereafter referred to as "complex topography," "intermediate topography," and "uniform topography." The complex topography scenario corresponds to the present topography of the valley with climate and soil properties varying at a grain of 100 m horizontal resolution (see Seidl et al., 2019). Soil input data (soil physical properties, effective soil depth, and plant-available nitrogen) were based on a map of local forest types and their respective soil conditions (Hotter, Simon, & Vacik, 2013) in combination with measurements from the Austrian Forest Soil Survey (Seidl, Rammer, & Lexer, 2009). Climate data were derived by statistically down-scaling climate variables from gridded climate data at 1 km resolution, using local weather station data (see Seidl et al., 2019 for details).

While the complex topography scenario represents the high environmental variability present in the landscape, the uniform topography scenario assumes homogeneous soil and climate conditions throughout the landscape. With regard to soil properties, we used the median values of the complex topography scenario (29.7 cm of effective soil depth, i.e., the soil depth after subtracting coarse materials, 67.4 kg/ha of plant-available nitrogen). We applied the most common combination of sand, silt, and clay fractions to the entire landscape (45% sand, 37.5% silt, and 17.5% clay content). As the driving climate, we assigned a spatially homogeneous climate time series based on the climatology most similar to the landscape mean (temperature = 4.31°C, precipitation = 969 mm, radiation = 10.3 MJ m^{-2} day^{-1}, and vapor pressure deficit = 0.254 kPa).

A third, intermediate topography scenario was created by reducing the heterogeneity of the complex topography scenario. For this

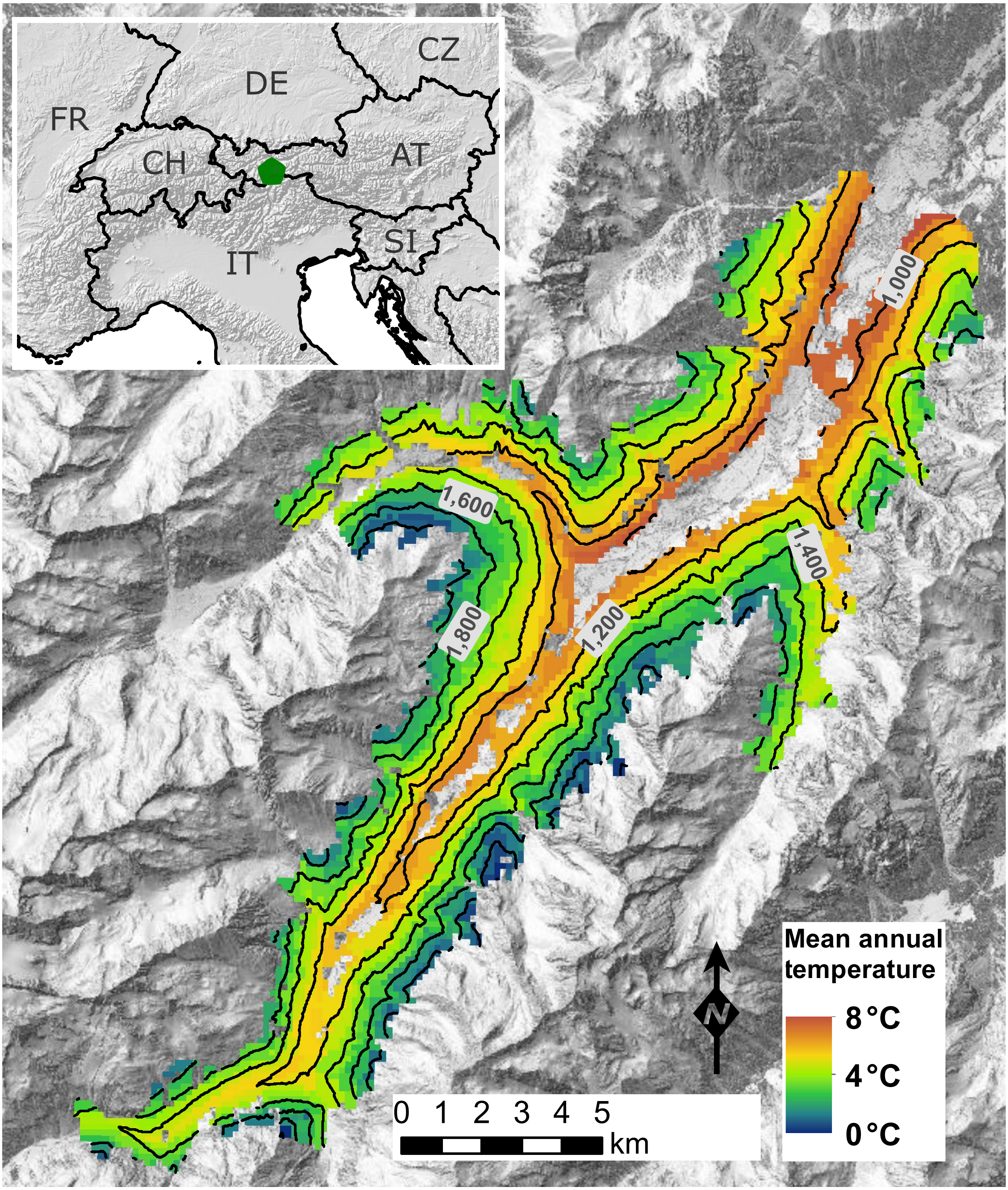

FIGURE 1 Map of the study area, showing the historical mean annual temperature (1961–2014) and the position of the landscape within Central Europe (insert). Isolines are 100 m apart (Basemaps from basemap.at, copernicus.eu, ec.europa.eu)

intermediate scenario, temperature variation in space was rescaled to the 25th and 75th percentiles of the range of the complex topography scenario. Between these rescaled extremes, all pixels were assigned a new climatology following a quantile mapping approach, keeping the gradients of temperature, precipitation, and radiation consistent. Soil variables were aggregated to larger spatial groups to also create intermediate heterogeneity in soils (see Supplementary Material S1 section 2).

Topography not only modulates climate and soil conditions but also influences the dispersal of propagules. We accounted for this effect by assuming different dispersal and migration pathways in the topography scenarios. In addition to seeds from adult trees present on the landscape, forest areas surrounding the landscape can act as seed sources, contributing a small amount of seeds from species not currently present on the landscape (total species pool: 30 central European species, equal immigration probabilities per unit area). In the complex topography scenario, only a small area acts as an external seed source, representing forests adjacent to the study area at the entrance of the valley. This is in line with current conditions, where the influx of seeds occurs mainly from the north and is strongly limited from all other sides by the (partly glaciated) mountain range surrounding the valley. This barrier effect was assumed to be independent of climate scenario. In the uniform topography scenario, new species could migrate into the study area from all sides, representing adjacent forests without natural barriers to seed dispersal. We tested the impact of these two seed source scenarios for the intermediate topography scenario, which was simulated with both seed areas allowing a direct comparison (Supplementary Material Figures S1.5–S1.9). The initial vegetation state for the three topography scenarios—representing the current potential natural vegetation—was derived via spin-up simulations, running iLand for 1,000 years under historic climate (years 1961–2000, randomly drawn with replacement) in the absence of management.

2.4 | Study design

To test for tipping points with increasing climate forcing, we simulated a stepwise change in temperature (between +0°C and +6°C), with each temperature interval lasting 1,000 years. The effect of this stepwise temperature change was evaluated under different precipitation scenarios (between −0% and −30% change in mean annual precipitation) to assess the independent effects of precipitation and temperature. Temperature and precipitation changes were chosen to include potential temperature increases and precipitation losses in the region expected under RCP 8.5 by the end of the 21st century (see Seidl et al., 2019). This allowed us to identify under which combined climate forcing (if any) a critical transition occurs. To ensure realistic temporal variation and autocorrelation of climate variables, we used statistically downscaled future climate scenario data (i.e., from the GCM-RCM combination of HadGEM2-ES and CLMcom-CCLM4-8-17 driven by RCP 8.5, see also Seidl et al., 2019 for details on how the climate scenario was derived) as basis for our climate scenarios. For each stepwise increase in temperature, we identified periods with a minimum length of 20 years in the downscaled climate scenarios where the simulated temperature change matched the respective target (i.e., +1°C: 2001–2022, +2°C: 2016–2046, +3°C: 2036–2067, +4°C: 2055–2075, +5°C: 2061–2091, +6°C: 2079–2099), while climate for the +0°C level was sampled from historical records (1961–2000). We randomly sampled 1,000 years with replacement from these periods to generate stepwise changes in climate. We rescaled precipitation to match the historical mean of the baseline period (1951–2000) while conserving interannual precipitation patterns. We then created four different precipitation change scenarios, corresponding to historical mean annual precipitation and −10%, −20%, and −30% relative to historical conditions. These changes in precipitation correspond to the climate model data used for extracting temperature changes (HadGEM2-ES and CLMcom-CCLM4-8-17 driven by RCP 8.5), ensuring consistency between variables in the generically constructed climate scenarios. We note, however, that a wide variety of precipitation changes are projected for the future in our study area by different climate models (see also Seidl et al., 2019). Climate varied spatially at 100 m resolution based on the underlying topography (see also Section 2.3 above). A single climate series was used for all simulated cells in the uniform scenario, while the climate varied between cells in the complex and (with reduced level of variation) the intermediate scenarios.

To address our research question regarding the reversibility of climate impacts and test for possible hysteresis, we first simulated a stepwise increase in temperature up to +6°C (which is the expected temperature increase in our study landscape by the end of the 21st century under RCP 8.5, Seidl et al., 2019), followed by a symmetrical stepwise decrease in temperature. This sequence of temperature change was simulated for each of the above-described precipitation change scenarios, with precipitation remaining at the same level throughout the respective simulations. We also tested an earlier reversal of the temperature forcing, at warming levels of +4°C (see Supplementary Material Figures S1.10–S1.13 for details). As we were interested in climate-mediated changes in the natural vegetation composition, each change step was simulated for 1,000 years, allowing the system to find a new dynamic equilibrium with climate (see Supplementary Material Figure S1.24 for a conceptual drawing). We evaluated the development of biomass and species composition over time (see also Thom, Rammer, & Seidl, 2017a) and found that a simulation duration of 1,000 years per temperature step was sufficient for the system to obtain a dynamic equilibrium with climate. A doubling of the simulation time did not yield significantly different results (Supplementary Material Figures S1.14–S1.19 but note that larger temperature increments would require longer equilibration times, see Supplementary Material Figures S1.20–S1.23). In all, 10 replicated simulations covering the full 13,000-year sequence of warming and cooling were run for each combination of topography and precipitation to account for stochasticity in the model (e.g., from mortality and regeneration processes).

2.5 | Analysis

We analyzed the resilience of forest size structure and species composition ("of what") to changes in the climate system ("to what"). The forests of our study landscape are currently characterized by a strong dominance of Norway spruce, a species that is important throughout the mountain forests of the Alps (Mayer, 1984). Consequently, we chose the share of Norway spruce (in percent of total basal area) as our focal indicator for forest composition, asking whether this defining species of current mountain forests will still play a dominant role in the late-seral forests emerging under climate change. Current mountain forests in the Alps also have relatively high number of large diameter trees (Bebi et al., 2017). Large trees are important for both biodiversity (Franklin et al., 2002) and ecosystem service provisioning (e.g., in the context of protecting settlements from gravitational natural hazards, where a sufficient number of large trees is needed to fulfill at protective function; Moos et al., 2018). We asked whether this characteristic feature (here quantified as the number of trees per hectare with a diameter at breast height of >30 cm) could be retained under future climate. We assessed the robustness of our findings to different indicator formulations by conducting analyses for alternative diameter thresholds and a broader species portfolio (see Supplementary Material Figures S1.25 and S1.26). We analyzed both indicators at the landscape level, averaging simulation results for the last 50 years of each 1,000-year climate period.

We visually analyzed the two resilience indicators both separately and in combination for tipping points and hysteresis effects after switching from warming to cooling trajectories. A tipping point was defined as a nonlinear change with increasing climate forcing. We identified hysteresis if the simulated system paths for the same climate forcing differed between warming (+0°C to +6°C) and cooling trajectories (+6°C to +0°) of the simulation. To quantify differences in the full species composition and diameter distribution beyond the two focal indicators (number of large trees, Norway spruce share), we calculated the Bray–Curtis Dissimilarity (Bray & Curtis, 1957) between warming and cooling trajectories at the end of each climate period. This index allows for the analysis of differences in species composition between groups and can be calculated both from counts of individuals and from proportions. An index of 0 indicates perfect similarity between two groups (here: the warming and cooling trajectories of the system) while an index of 1 means no overlap. We used the Bray–Curtis Dissimilarity for both species composition and stand size structure, interpreting the number of individuals per 10 cm diameter class similarly to the number of individuals per species. The differences across species and diameter distributions were tested for significance using a PERMANOVA approach. All analyses were done using version 3.5.1 of the R statistical computing language (R Core Team, 2019), in particular applying the packages tidyverse (Wickham, 2017), RSqlite (Müller, Wickham, James, & Falcon, 2018) and vegan (for PERMANOVA and the Bray–Curtis Dissimilarity, Oksanen et al., 2018).

3 | RESULTS

3.1 | Forest tipping points with climate warming

Climate change strongly influenced forest size structure (Figure 2; Supplementary Material Figure S1.27). Topography distinctly modulated the shape of this response. In the complex topography scenario, climate impacts were buffered, and the number of large trees decreased gradually with increasing temperatures, dropping from around 175 trees > 30 cm dbh/ha under current climate to around 50 trees per hectare under the +6°C scenario. In contrast, we found a distinct tipping point in the simulated number of large trees in the uniform topography scenario, with a pronounced shift between warming levels of +1°C and +2°C. The uniform topography scenario resulted in three attractors for forest size structure, with a local optimum at +3°C warming, resulting from a dominance of European beech at this particular warming level. This local optimum shifted to higher warming levels in scenarios with higher water availability (Figure 2). The intermediate topography scenario showed similar behavior with stem numbers reaching their maximum at +2°C, a local optimum at +4°C (regardless of precipitation), and a minimum at +6°C (Supplementary Material Figure S1.5). Overall, the changes from one temperature step to the next in this scenario were more gradual than in the uniform scenario, but less linear than in the complex scenario. More broadly, the number of large trees was reduced under climate change, while the number of smaller trees (especially in diameter classes below 20 cm) strongly increased, resulting in a higher overall stem density under climate change (Supplementary Material Figures S1.7 and S1.27).

Forest composition also changed with climate warming. The basal area share of Norway spruce decreased sharply, with the species being virtually absent from the landscape at warming levels of >5°C (Figure 3; Supplementary Material Figures S1.8 and S1.28). Spruce was initially outcompeted by beech which—at even higher levels of warming—was succeeded by oak (*Quercus robur* L., *Quercus petraea* (Matt.) Liebl.) and Scots pine (*Pinus sylvestris* L.; see also Supplementary Material Figure S1.28). We observed a threshold response under uniform topography, with a 75% decrease in spruce share at +2°C and almost complete extirpation at +4°C. Spruce share declined gradually with increasing warming in the complex topography scenario. In the intermediate topography scenario, spruce decline was intermediate given sufficient external seed sources (large seed area, Supplementary Material Figure S1.6). While it had a more noticeable tipping point in spruce share than the complex scenario, this tipping occurred at higher temperatures than in the uniform scenario (at +3°C of warming, regardless of precipitation and seed availability scenario). Limiting the influx of seeds to the entrance of the valley (small seed area) strongly increased the variability between simulated replicates in the intermediate topography scenario.

The strong elevation gradients in the complex topography scenario created climate refugia for spruce on the landscape (Supplementary Material Figure S1.30). Overall species change was strong across the whole elevation range, with oaks occuring even at the highest elevation (>2,000 m a.s.l.) under +6°C. However, individual spruce trees were able to persist in the highest reaches of the landscape even under the hottest and driest scenarios (cf. the maps in the Supplementary Material S2). At the same time, *P. cembra*, which is the species forming the timber line in the landscape currently, was lost completely at warming levels of above +2°C,

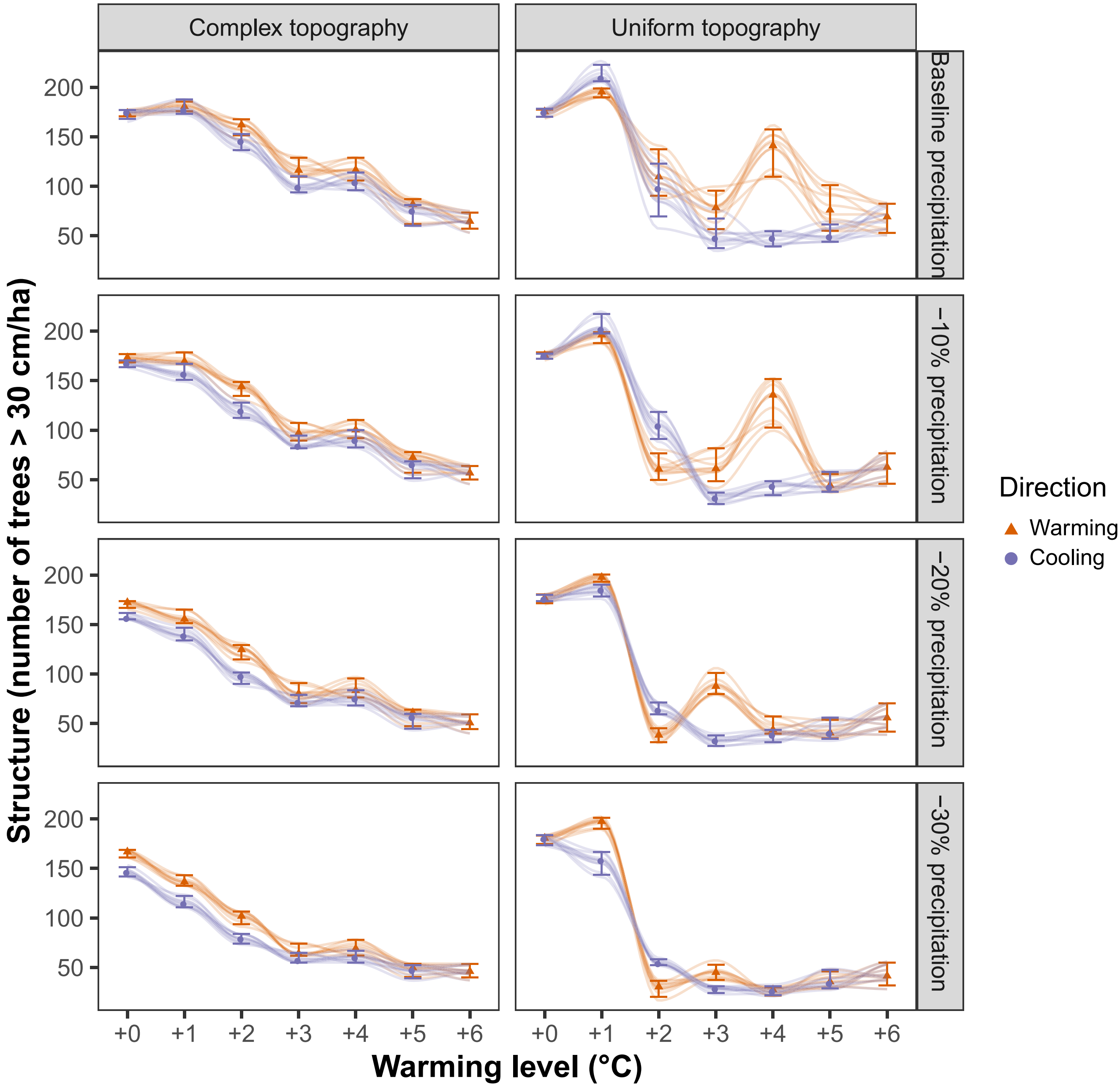

FIGURE 2 The response of forest size structure (here described as the number of trees > 30 cm in diameter) to climate warming (red, triangles) and subsequent cooling (purple, circles). Values describe the state of the landscape at equilibrium (median, 5th and 95th percentiles across 10 replicates) and trajectories for all simulated replicates are shown. Trajectory lines are fitted using a LOESS model

and was not able to return after the climate forcing was reversed (Supplementary Material Figure S1.30).

3.2 | Hysteresis between warming and cooling trajectories

Equilibrium vegetation structure and composition differed between the simulated warming and cooling trajectories, indicating a strong hysteresis effect (Figures 2 and 3). Hysteresis effects were generally stronger under uniform topography compared to complex topography for both indicators. For example, under uniform topography forest size structure exhibited a local optimum at +3°C under warming but not cooling trajectories. The hysteresis effect was stronger for forest species composition than for forest size structure. Under uniform topography, spruce shares remained low in the cooling trajectories until recovering dominance at +1°C. In contrast, spruce share increased gradually and recovery started at higher temperatures during cooling trajectories when topography was complex. This was despite the limiting effect of external seed availability (i.e., seeds of trees not currently present on the landscape entering the simulation only in a limited area at the entrace of the valley) in

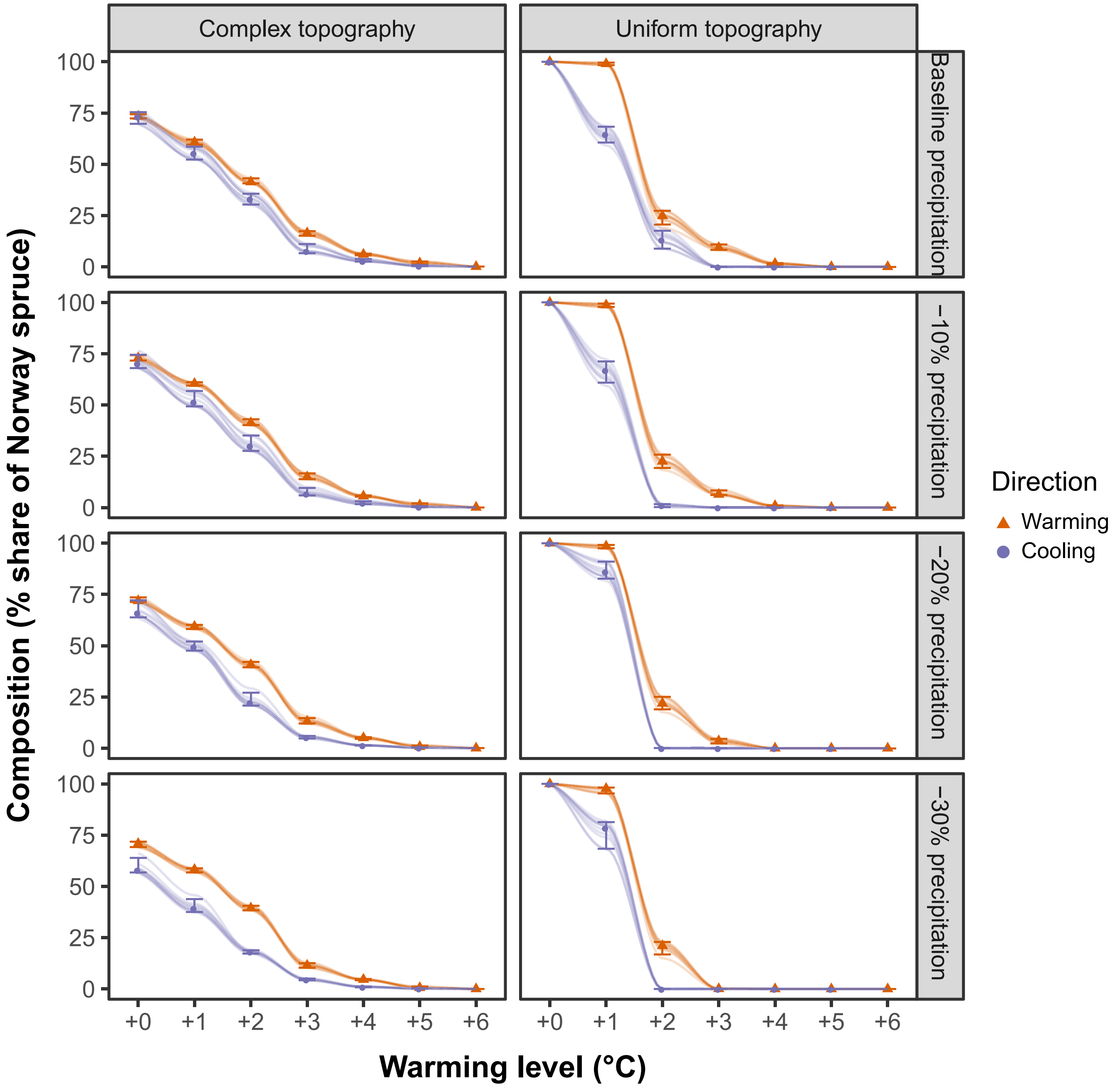

FIGURE 3 The response of forest composition (here described as the share of Norway spruce on total basal area) to climate warming (red, triangles) and subsequent cooling (purple, circles). Values describe the state of the landscape at equilibrium (median, 5th and 95th percentiles across 10 replicates) and trajectories for all simulated replicates are shown. Trajectory lines are fitted using a LOESS model

the complex topography scenario which generally increased hysteresis in species composition (see intermediate topography scenario, Supplementary Material Figure S1.6).

Quantitative analyses across the full species and diameter distribution supported findings from visual analysis of simulation trajectories (Tables 1 and 2). Bray–Curtis Dissimilarity between warming and cooling trajectories was generally lower in the complex topography scenarios across all temperature and precipitation forcings, indicating that uniform topography amplifies hysteresis effects. For forest size structure, the highest dissimilarity occurred at +1°C regardless of precipitation scenarios when topography was uniform. However, when topography was complex, maximum dissimilarity occurred at +2°C under wetter scenarios (−0% and −10% mean precipitation) and at +0°C under drier scenarios (−20% and −30% mean precipitation). These differences in forest size structure were statistically significant at +2°C for all combinations of topography and precipitation scenarios (Table 1). For forest composition, the biggest differences between warming and cooling trajectories occurred at higher warming levels (between +2°C and +4°C) and depended more strongly on the precipitation scenario simulated. With decreasing precipitation, the temperature of the highest dissimilarity decreased, from +4°C at baseline precipitation to +2°C when precipitation was reduced by

TABLE 1 Bray–Curtis Dissimilarity quantifying the difference in forest size structure between warming and cooling trajectories at each temperature step separately for each topography and precipitation scenario. A significant difference indicates the presence of a hysteresis effect. The significance of the differences at each step was tested using a PERMANOVA

	Precipitation scenario							
	Baseline		Minus 10%		Minus 20%		Minus 30%	
	Topography scenario							
Temperature change	Complex	Uniform	Complex	Uniform	Complex	Uniform	Complex	Uniform
0	0.010	0.003	0.038**	0.009	0.078***	0.003	0.117***	0.011
1	0.019	0.366***	0.058***	0.352***	0.066***	0.240***	0.078***	0.376***
2	0.058***	0.053**	0.060***	0.124***	0.059***	0.119***	0.058***	0.135***
3	0.032*	0.221***	0.022*	0.138***	0.025	0.090***	0.017	0.034*
4	0.022*	0.293***	0.025*	0.168***	0.033*	0.042**	0.030*	0.004
5	0.014	0.032	0.017	0.010	0.008	0.008	0.003	0.004

Significance levels
*p < .05,
**p < .01,
***p<=0.001.

TABLE 2 Bray–Curtis Dissimilarity quantifying the difference in forest species composition between warming and cooling trajectories at each temperature step separately for each topography and precipitation scenario. A significant difference indicates the presence of a hysteresis effect. The significance of the differences at each step was tested using a PERMANOVA

	Precipitation scenario							
	Baseline		Minus 10%		Minus 20%		Minus 30%	
	Topography scenario							
Temperature change	Complex	Uniform	Complex	Uniform	Complex	Uniform	Complex	Uniform
0	0.051	0.011	0.092	0.012	0.181*	0.011	0.287***	0.012
1	0.089	0.371***	0.184*	0.363***	0.272**	0.150*	0.356**	0.275**
2	0.161*	0.187*	0.275***	0.266**	0.375***	0.740***	0.374***	0.840***
3	0.303***	0.704***	0.327**	0.824***	0.302**	0.656***	0.209*	0.235*
4	0.316**	0.875***	0.298**	0.792***	0.229*	0.192	0.163	0.022
5	0.243*	0.385**	0.177	0.089	0.106	0.022	0.071	0.024

Significance levels
*p < .05,
**p < .01,
***p<=0.001.

30% (Table 2). Under uniform topography, all simulations returned to their starting point when the temperature forcing was removed completely. Under the complex topography scenario, however, decreasing precipitation resulted in distinctly different size structure and composition of the vegetation even after returning to past temperatures (+0°C forcing level).

3.3 | Ecological resilience to climate warming

The attractor landscape emerging from the joint analysis of forest size structure and species composition showed two distinct basins of attraction (Figure 4). Climate change caused a critical transition between the two attractors. Specifically, a warming of +2°C triggered a transition from the current attractor, characterized by a high dominance of Norway spruce and a high number of trees >30 cm in diameter, to an alternative steady state of little to no Norway spruce and considerably smaller sized trees. Topographic complexity reduced the distance between the two basins of attraction. The intermediate topography scenario showed signs of a third attractor at low warming levels due to differences in forest composition (Supplementary Material Figure S1.9). However, the critical transition at a warming level of +2°C occurred regardless of topographic complexity.

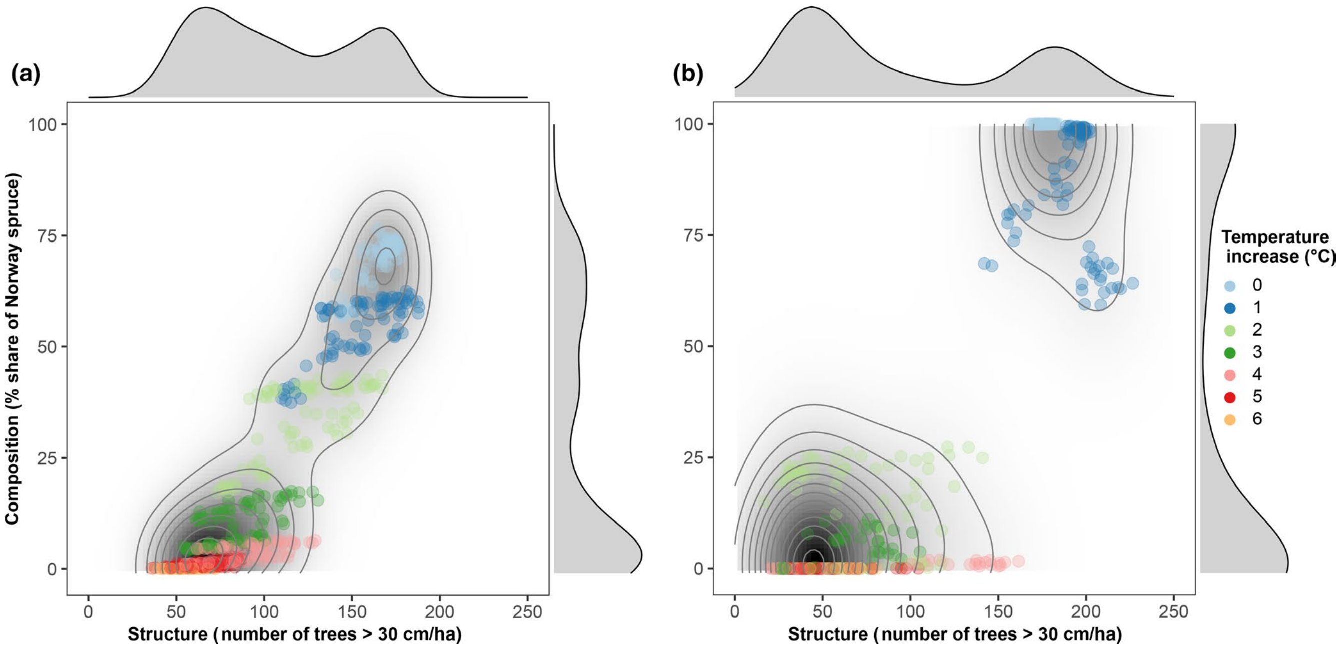

FIGURE 4 Location of the forest landscape in structure–composition attractor space for different warming levels and the complex (a) and uniform (b) topography scenarios over all precipitation scenarios. Marginal plots and isolines give the probability density of all simulated cases, and indicate two alternative stable states for our study landscape

4 | DISCUSSION

4.1 | Forest response to climate change

Climate change has the potential to profoundly alter forest ecosystems. Here we found evidence for substantial shifts in equilibrium forest composition and size structure under climate change for our study system in the European Alps. The response to increasing levels of warming was strongly nonlinear especially in the absence of steep topographic gradients (uniform scenario). Without the buffering effect of topographic complexity, critical transitions occurred even at weak climate forcings of between +1°C and +2°C. Beyond a warming of between +2° and +3°C relative to historic climate, critical transitions of forest composition and size structure occurred in all simulated scenarios. Reductions in precipitation exacerbated this effect, with critical transitions occurring at lower levels of warming, particularly for the forest size structure indicator investigated here. Critical transitions caused the system—currently characterized by a dominance of conifers and the prevalence of many large trees—to change to an alternative stable state with fundamentally different characteristics, namely a broadleaved-dominated system characterized by smaller trees. The alternative state emerging from our simulations is a realistic possibility, as forests dominated by oaks (and pines) of smaller dimensions are the dominant forest types in warm and dry valleys of the Southern Alps (Rigling et al., 2013). However, our simulations did not result in a transition to non-forest, despite simulating warming levels of up to +6°C. Even under the most extreme climate forcings, no more than 2% of the current forest area lost its tree cover after 1,000 simulation years. In contrast to other systems (Enright, Fontaine, Bowman, Bradstock, & Williams, 2015; Hansen et al., 2018; Stevens-Rumann et al., 2018; Tepley, Thompson, Epstein, & Anderson-Teixeira, 2017), large-scale forest loss due to climate change appears unlikely in our study system (but see the following section for methodological limitations).

Topographic complexity buffered the response to climate warming and delayed a landscape-scale transition of forest size structure and species composition. Our results underline that complex topography and spatial heterogeneity contribute to ecological resilience, which is in line with findings from other systems (e.g., Adams, Barnard, & Loomis, 2014, van Nes & Scheffer, 2005; Virah-Sawmy, Gillson, & Willis, 2009). Complex topography supports ecological resilience by decoupling the local conditions from the large-scale average (Daly, Conklin, & Unsworth, 2001), thus providing climate refugia for species (Keppel et al., 2012; Serra-Diaz et al., 2015). We observed topographically mediated refugia in our simulations, with Norway spruce persisting under higher climate forcings in higher elevations and on north-facing slopes (see also Supplementary Material Figure S1.30 and maps in Supplementary Material S2). However, the buffering capacity of topography was limited: as temperature change became more extreme (i.e., beyond +3°C), all simulations transitioned to an alternative warm-adapted stable state regardless of topography and precipitation. Furthermore, complex mountain topography can also have negative effects on major processes of resilience, such as the ability to colonize potential habitat. Mountainous topography, where large areas between forested valleys consist of mountain peaks and glaciers above the timber line, can act as barriers for seed dispersal (Rupp, Chapin, & Starfield, 2001) and thus decrease the adaptive capacity of forests. This could make non-forest states more likely, especially if warm-adapted species are not available to colonize the landscape and replace species lost through climate change.

Our results highlight that climate warming above critical thresholds can have irreversible impacts on forest ecosystems at millennial time scales. We identified hysteresis in driver–state relationships, with forest size structure and species composition differing between warming and cooling trajectories. This is—to our knowledge—the first documentation of hysteresis effects in the response of forest ecosystems to climate warming (but see e.g., Staal et al., 2018; van Nes et al., 2014, e.g., of hysteresis responses to changing levels of precipitation). The irreversible climate impacts found here are particularly noteworthy as they persist even after 1,000 years of simulated forest dynamics under a given level of climate change, while previous analyses found that mountain forests in the Alps reach a new equilibrium with climate after roughly 500 years (Thom, Rammer, Dirnböck, et al., 2017; Thom et al., 2017a). The main processes resulting in irreversible climate effects in our simulations are founder effects (Grime, 1998), with returning cool-adapted specialist species not being able to regain their previous dominance once warm-adapted generalists have taken hold of important parts of the landscape. Species can disappear quickly from an area once the prevailing environmental conditions exceed their fundamental niche, yet it can take them a long time to recolonize these areas via seed dispersal (Meier, Lischke, Schmatz, & Zimmermann, 2012), particularly if dispersal is limited by topography. As both founder effects and dispersal limitation are amplified by complex topography, the complex scenario showed higher levels of irreversibility after returning the temperature forcing to zero compared to the uniform scenario. This suggests that while complex topography can buffer climate impacts, it is also harder to return to previous system states in mountain areas once species have been lost.

In conjunction with founder effects, dispersal limitations can result in species remaining effectively locked out of areas they previously occupied even though the climate conditions have again returned to suitable levels. This "legacy lock" (Johnstone, Hollingsworth, Hollingsworth, Chaping, & Mack, 2010) is only broken once climate conditions return to levels where the previously dominant species regains its competitive advantage. For example, the areas that are dominated by oak under high levels of climate change are initially taken over by pioneer species (particularly Scots pine, *P. sylvestris* L.) once the climate cools and exceeds the temperature niche of oak. These pioneers have a wide physiological amplitude, which allows them to persist on the landscape at all levels of warming (see also Supplementary Material Table S1.1). Norway spruce, the previously dominating species, only slowly reinvades these areas after being almost completely absent from the landscape under extreme levels of warming (except for small refugia in high elevations in the complex topography scenario). The hysteresis effect for forest size structure is linked to the same processes, as the cooling trajectory has higher shares of pioneer species which do not reach the same dimensions as the spruce-dominated vegetation types of the warming trajectory.

4.2 | Methodological considerations

Forest resilience is influenced by complex processes and interactions across temporal as well as spatial domains. Capturing these processes poses a challenge for simulation modeling. iLand is a detailed forest landscape model implementing a high degree of process understanding, yet some processes of potential relevance for forest resilience are incompletely represented in the model. One important example pertains to soil processes: Soil depth and texture are time-invariant in our simulations, ignoring processes such as soil loss through erosion and changes in soil structure, which could have a lasting impact on forest dynamics (Johnston & Crossley, 2002; Johnstone, Chapin, et al., 2010). Furthermore, nutrient feedbacks between vegetation and soil were not dynamically considered in our simulations. We also did not account for the competitive effect of grasses and herbs, which have the potential to interfere with tree regeneration and therefore change forest development pathways (Thrippleton, Bugmann, Kramer-Priewasser, & Snell, 2016). Processes such as soil erosion, accelerated decomposition, and increased resource competition from forest floor vegetation all act to amplify climate change impacts (rather than dampen them). Therefore, our quantification of critical transitions and irreversibility are conservative estimates of the expected effects of climate warming.

In our study, we focused on the responses of forest ecosystems to changes in temperature and precipitation, two important drivers of forest dynamics. However, processes such as natural disturbances (wind, bark beetles, wildfire) and human land-use decisions also influence forest dynamics and resilience. Natural disturbances can enhance forest resilience by fostering response diversity (Dell et al., 2019) but changing natural disturbance regimes could also disrupt forest recovery and therefore reduce resilience (Hansen et al., 2018; Turner, Braziunas, Hansen, & Harvey, 2019). There is a high degree of uncertainty in projections of future disturbance regimes and disturbance interactions as climate changes. In general, disturbances are expected to be an increasingly important factor affecting forests (Lindner et al., 2010; Seidl et al., 2017). For our study landscape, natural disturbances are expected to increase in the coming decades (Seidl et al., 2019). Future efforts should thus assess whether increasing natural disturbances further challenge the climate resilience of our landscape (Enright et al., 2015) or increase its adaptive capacity and therefore decrease hysteresis (Thom, Rammer, Dirnböck, et al., 2017; Thom et al., 2017a).

Rising atmospheric CO_2 concentration can also influence future forest demographics. In the case of our landscape, this could enhance growth and therefore counteract the effects of increased resource limitation from decreased precipitation (Swann, Hoffman, Koven, & Randerson, 2016; Walker et al., 2019). The persistence of such a CO_2 fertilization effect, however, remains uncertain (Reyer et al., 2014).

Finally, large parts of our analysis focused on two indicators chosen to represent the size structure and species composition of our study system. While these indicators are well suited to capture defining characteristics of typical mountain forest ecosystems of the Alps, a broader set of indicators could have shown a more nuanced picture of forest responses to climate change. In the case of trees species composition, an analysis at the species level is insightful, as it reveals multiple transitions between forest types, from a landscape-dominated by spruce to a beech-dominated system, which is succeeded by oak and pine under extreme climate forcing (Supplementary Material Figure S1.28). More detailed analyses of changes (cf. Supplementary Material Figures S1.29 and S1.30 and Supplementary Material S2) can enhance understanding of the impacts of climate change on ecosystem functioning (Mori, Lertzman, & Gustafsson, 2017; Sakschewski et al., 2016), but were beyond the focus of the current analysis. Furthermore, defining thresholds and transitions in forests is difficult because it inter alia depends on the temporal reference frame applied (see e.g., Thrippleton et al., 2018). Here we addressed this issue by reporting climate change effects on equilibrium forest size structure and species composition, which is less sensitive to the time frame of analysis than transient forest dynamics (Schröder et al., 2005).

4.3 | Implications

We show that critical transitions of ecosystems can occur already at warming levels of around +2°C (see also Elkin et al., 2013). This suggests that even if the current political climate targets are met, fundamental changes in the characteristics of important forest ecosystems of the Alps are likely. Changes of the magnitude required for causing critical transitions in our study system are expected to occur until the end of this century even under the most optimistic current climate projections (IPCC, 2013). However, we found that topographical complexity can buffer against climate change impacts and allow for smoother transitions to an alternative stable state. Conversely, this means that regions with low topographical complexity (e.g., large regions in the boreal biome, Scheffer et al., 2012) may be particularly at risk of critical transitions under climate change, as evidenced in out intermediate and uniform topography scenarios. This implies that measures adapting to expected climate change impacts are of paramount importance (Halofsky et al., 2017; Keenan, 2015; Messier et al., 2015; Millar, Stephenson, & Stephens, 2007; Seidl, Rammer, & Lexer, 2011). We also found that climate warming was irreversible on millennial time scales under some scenarios. Given the gap between targets of current climate policy (aiming to limit anthropogenic warming to below +2°C/+1.5°C, UNFCCC, 2015) and actual greenhouse gas emissions, a temporal exceedance of the political target ("overshoot") is likely (Geden & Löschel, 2017; Ricke, Millar, & MacMartin, 2017). While such an overshoot corridor would increase political flexibility in reaching the targets agreed in Paris, our findings show that it could have lasting effects on ecosystems. The nonlinearity and irreversibility of climate impacts demonstrated here thus call for timely and effective action to mitigate climate change.

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available on Figshare at http://doi.org/10.6084/m9.figshare.12091935. Technical model documentation of iLand as well as the executable and model source code are available online at www.iland.boku.ac.at.

ORCID

Katharina Albrich https://orcid.org/0000-0002-5157-523X

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SUPPORTING INFORMATION

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

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Supplementary Material S1 for:

Climate change causes critical transitions and irreversible alterations of mountain forests

Katharina Albrich, Werner Rammer, Rupert Seidl

1. Evaluation of model performance for the Stubai Valley.

The model was tested in depth regarding its ability to reproduce vegetation patterns following the pattern-oriented modelling approach by Grimm et al. (2005). Specifically, we compared model output to inventory data, local yield tables and vegetation maps for the study area. We here present selected results of the evaluation, relevant for the study at hand. For the full set of evaluations performed for the Stubai valley we refer to Seidl et al. (2019, supplementary Material).

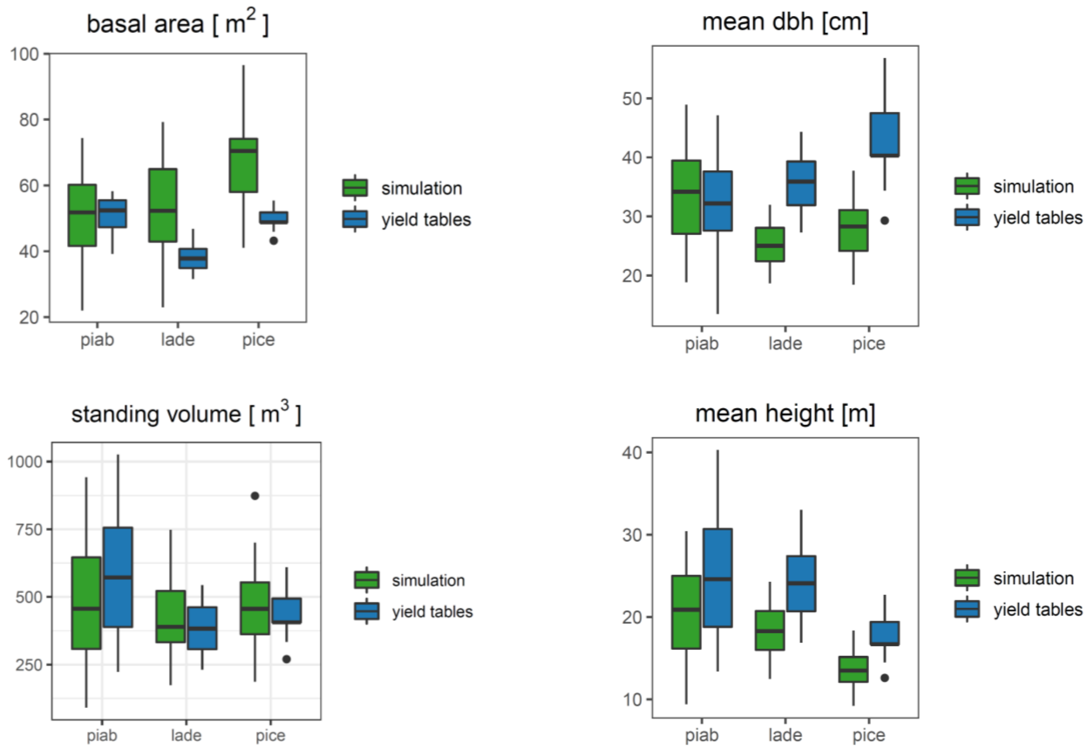

Figure S1.1: Comparison of simulated stand basal area (m^2 ha^{-1}, top left), mean stand dbh (cm, top right), standing volume (m^3 ha^{-1}, bottom left), and mean stand height (m, bottom right) to reference values from yield tables after 70 years of simulation. n= 150 of randomly selected stands distributed throughout the study landscape. Piab= Norway spruce, Lade= European larch, Pice= Swiss stone pine (from Seidl et al. 2019).

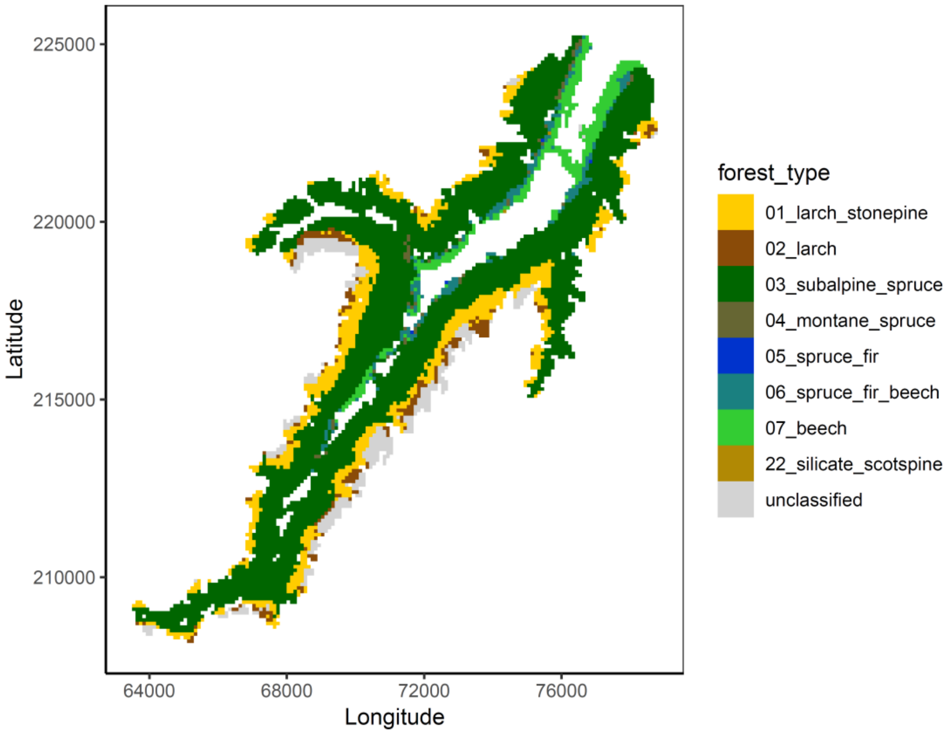

Figure S1.2: Simulated forest types of the potential natural vegetation (from Seidl et al. 2019).

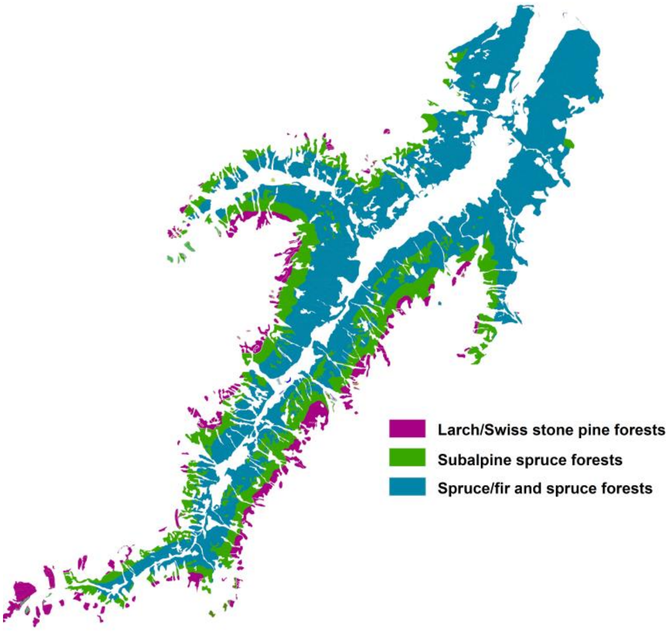

Figure S1.3: Reference forest types from the local forest type classification (Hotter et al. 2013, Seidl et al. 2019)

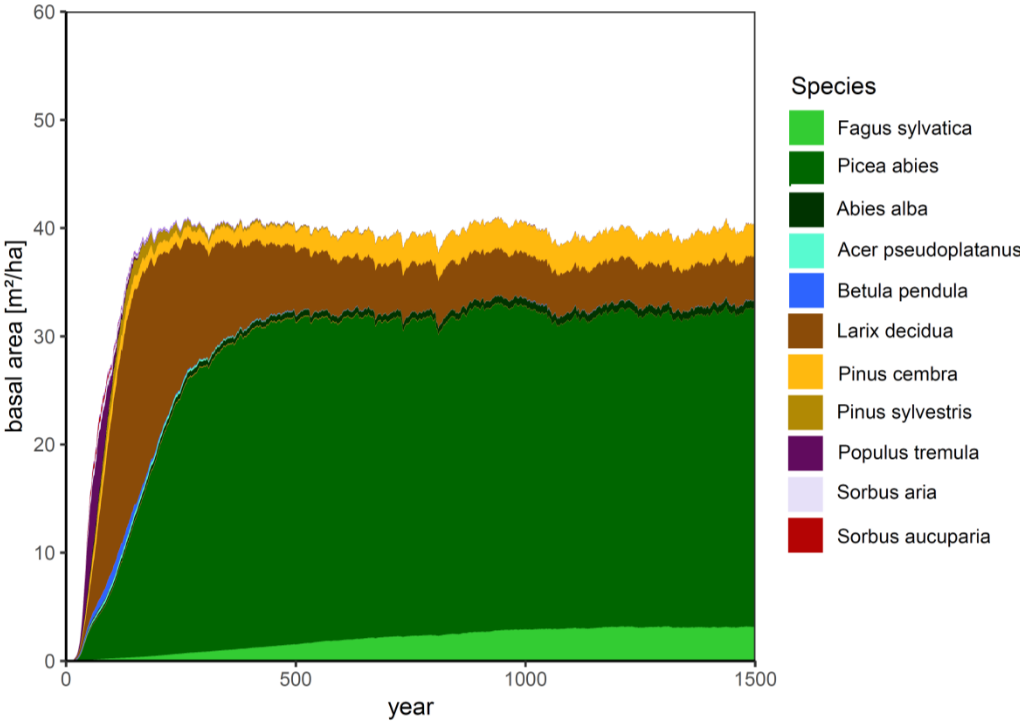

Figure S1.4: Development of succession over 1500 years in the absence of management and natural disturbances (Seidl et al. 2019).

2. Intermediate topography scenario

To further investigate the effect of topography, we designed a third, intermediate topography scenario. For this scenario, we rescaled our climate database so that all temperatures fell between the 25th and 75th percentile of the complex topography scenario (averaged over the entire historic climate data record from 1961-2014). The climate for each 1 ha pixel was mapped to the new range using quantile mapping. Soil variables were aggregated into larger groups to arrive at a smaller range and lower overall variability. We also tested the influence of the external seed area providing seed input in addition to mature trees already present on the landscape. This seed input serves as an important source of new species migrating into the landscape under a changing climate. In the case of the small seed area scenario, also used in the complex topography scenario (see main text), only the forest at the lowest elevation of the valley are receiving external seed input, with mountains and settled areas which surround the rest of the landscape blocking external seed input. The large seed area scenario represents equal seed input from all edges of the landscape. This seed area scenario was also used for the uniform topography scenario.
In the intermediate topography scenario, we simulated 10 replicates for each combination of precipitation change and seed area scenario, resulting in 80 simulation runs.

Overall, the climate response of the intermediate topography scenario lay between the complex and uniform scenarios, both for the individual indicator changes as well as with regard to the occurrence of tipping points (Fig. S1.5, Fig. S1.6). However, species dominance levels differ from the other scenarios at intermediate levels of landscape-scale climate and soil variation (Fig. S1.8). The seed area size mainly influences the variability between simulation replicates (higher with small seed area) and hysteresis.

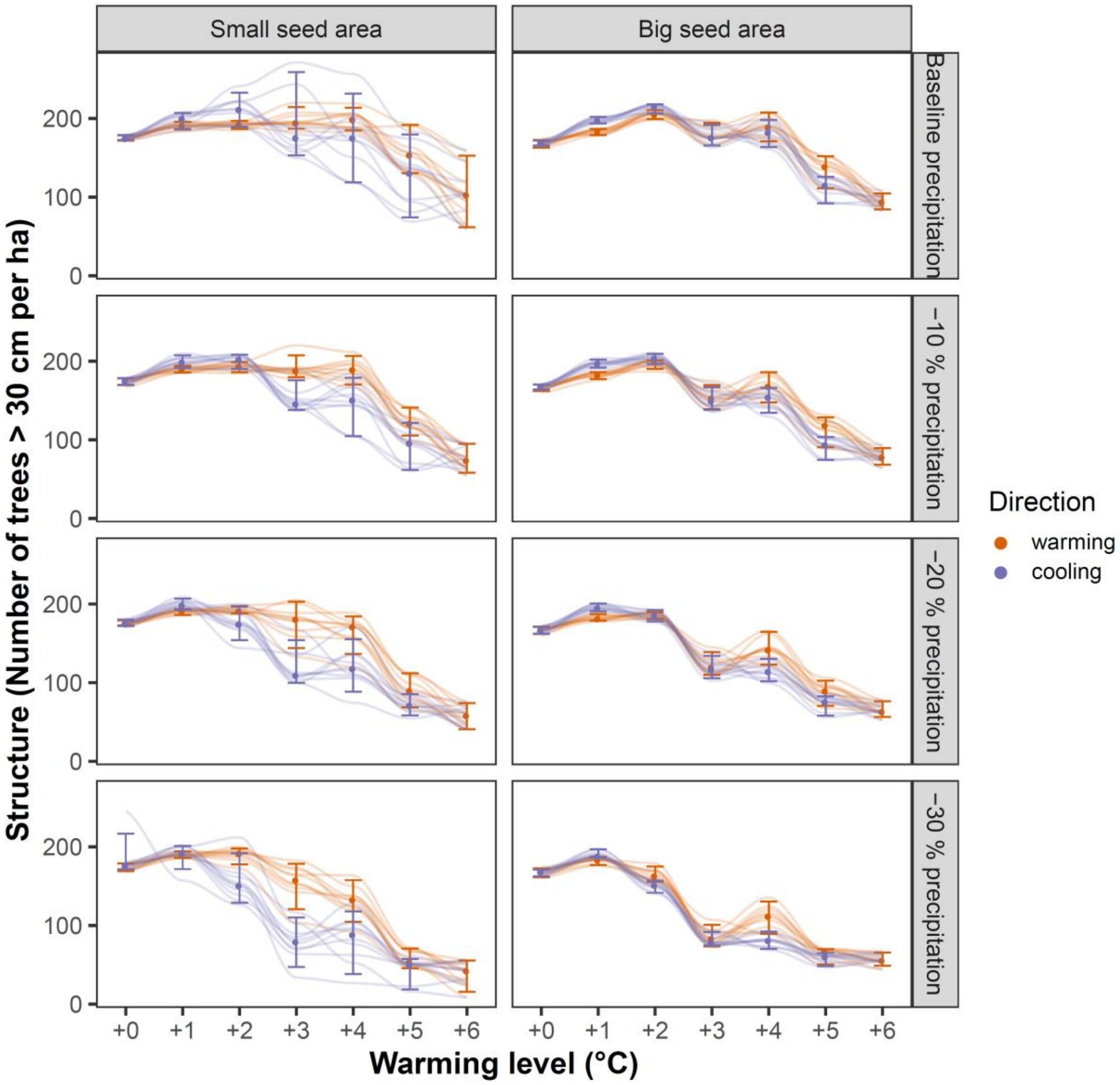

Figure S1.5: The response of forest structure (here described as the number of trees >30 cm in diameter) to climate warming (red) and subsequent cooling (purple) in the intermediate topography scenario. Values describe the state of the landscape after 1000 simulation years (median, 5th and 95th percentile across 10 replicates) and trajectories for all simulated replicates are shown. Trajectory lines are fitted using a LOESS model. Small seed area refers to external seed only entering from a small area at the bottom of the valley, large seed area means that the entire surrounding of the landscape acts as a seed source.

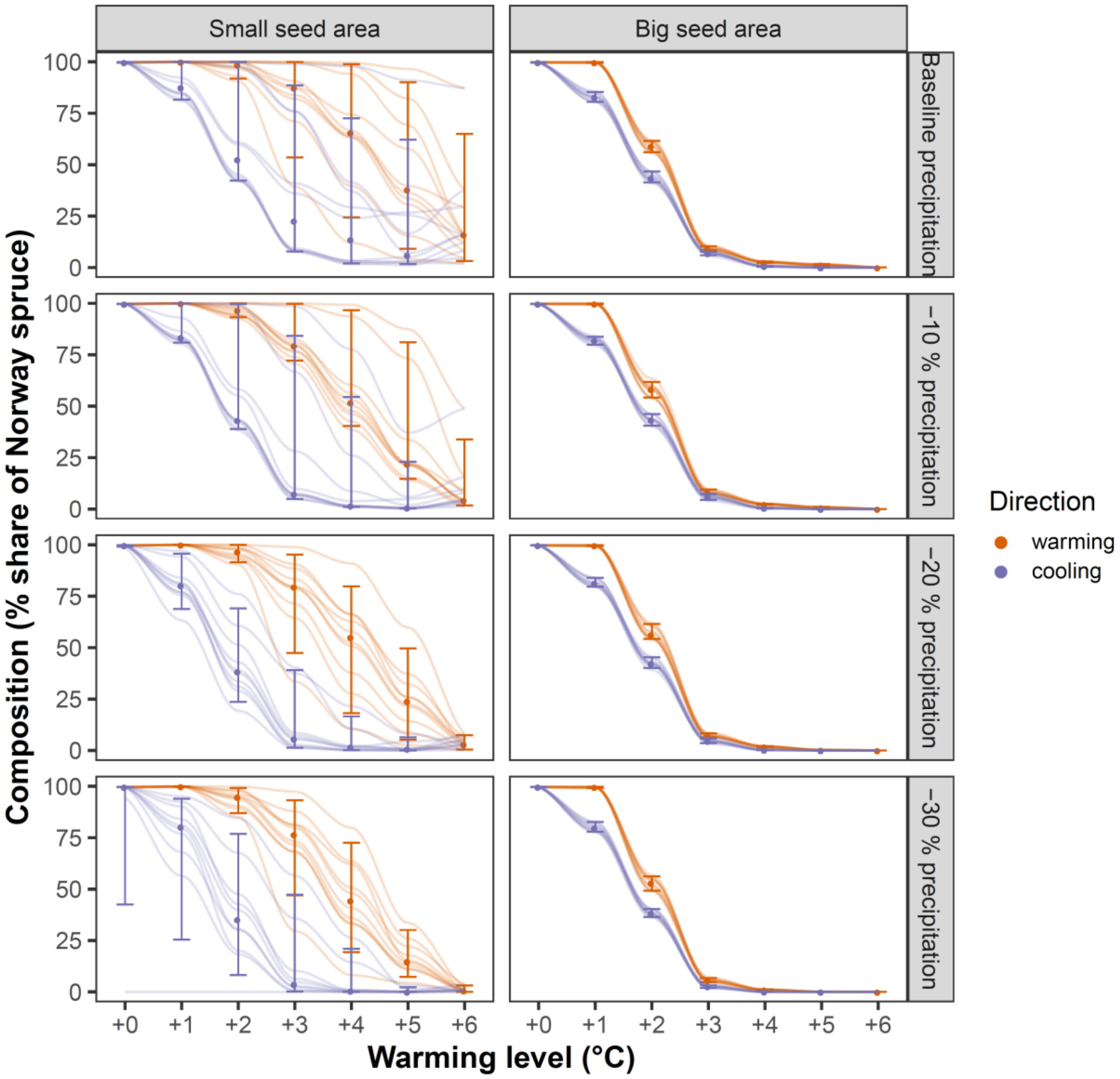

Figure S1.6: The response of forest composition (here described as the share of Norway spruce on total basal area) to climate warming (red) and subsequent cooling (purple) in the intermediate topography scenario. Values describe the state of the landscape after 1000 simulation years (median, 5th and 95th percentile across 10 replicates) and trajectories for all simulated replicates are shown. Trajectory lines are fitted using a LOESS model. Small seed area refers to external seed only entering from a small area at the bottom of the valley, large seed area means that the entire surrounding of the landscape acts as a seed source.

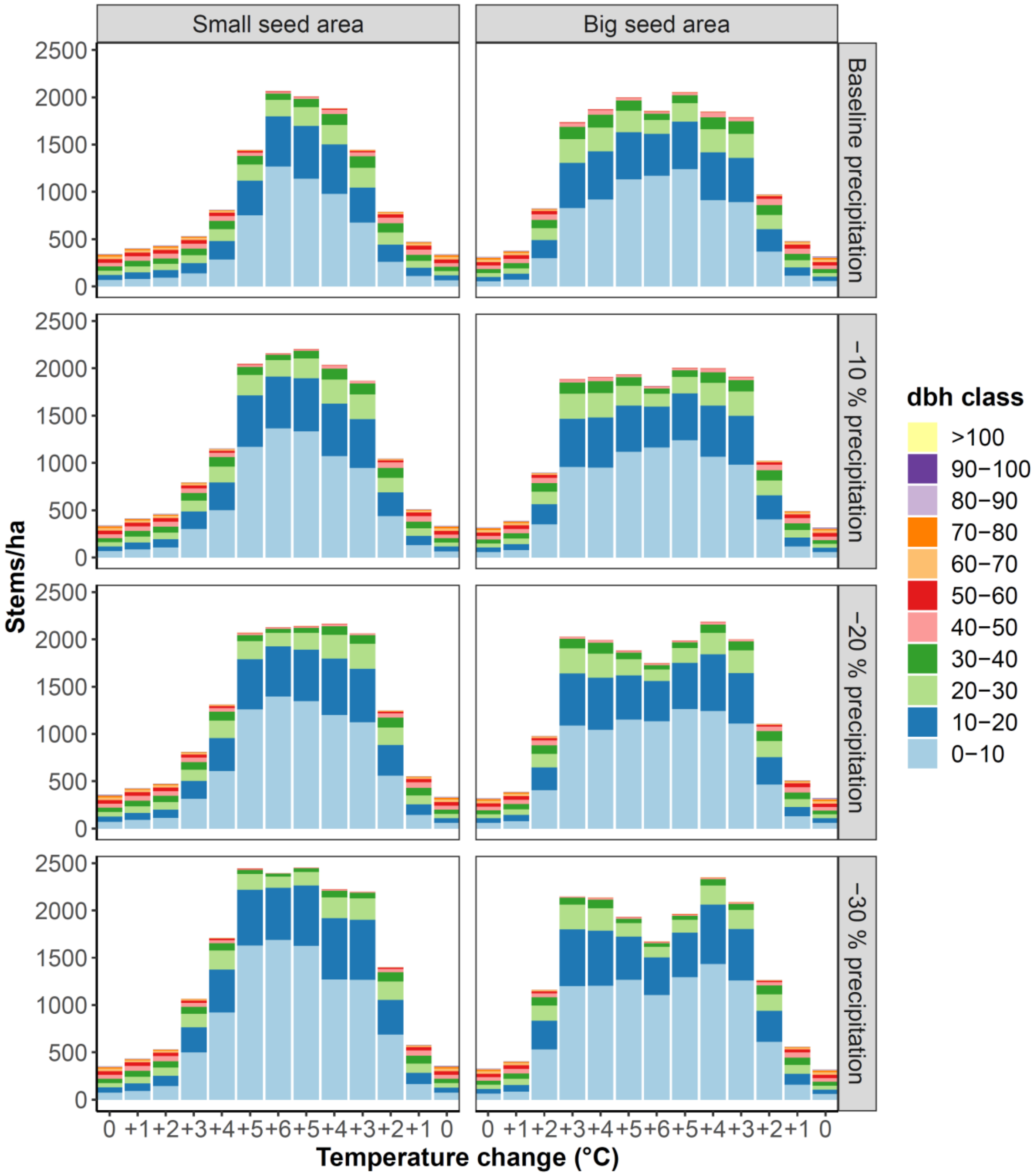

Figure S1.7: Simulated forest structure after 1000 simulation years at each temperature step (number of stems in DBH classes per ha) in the intermediate topography scenario. Small seed area refers to external seed only entering from a small area at the bottom of the valley, large seed area means that the entire surrounding of the landscape acts as a seed source.

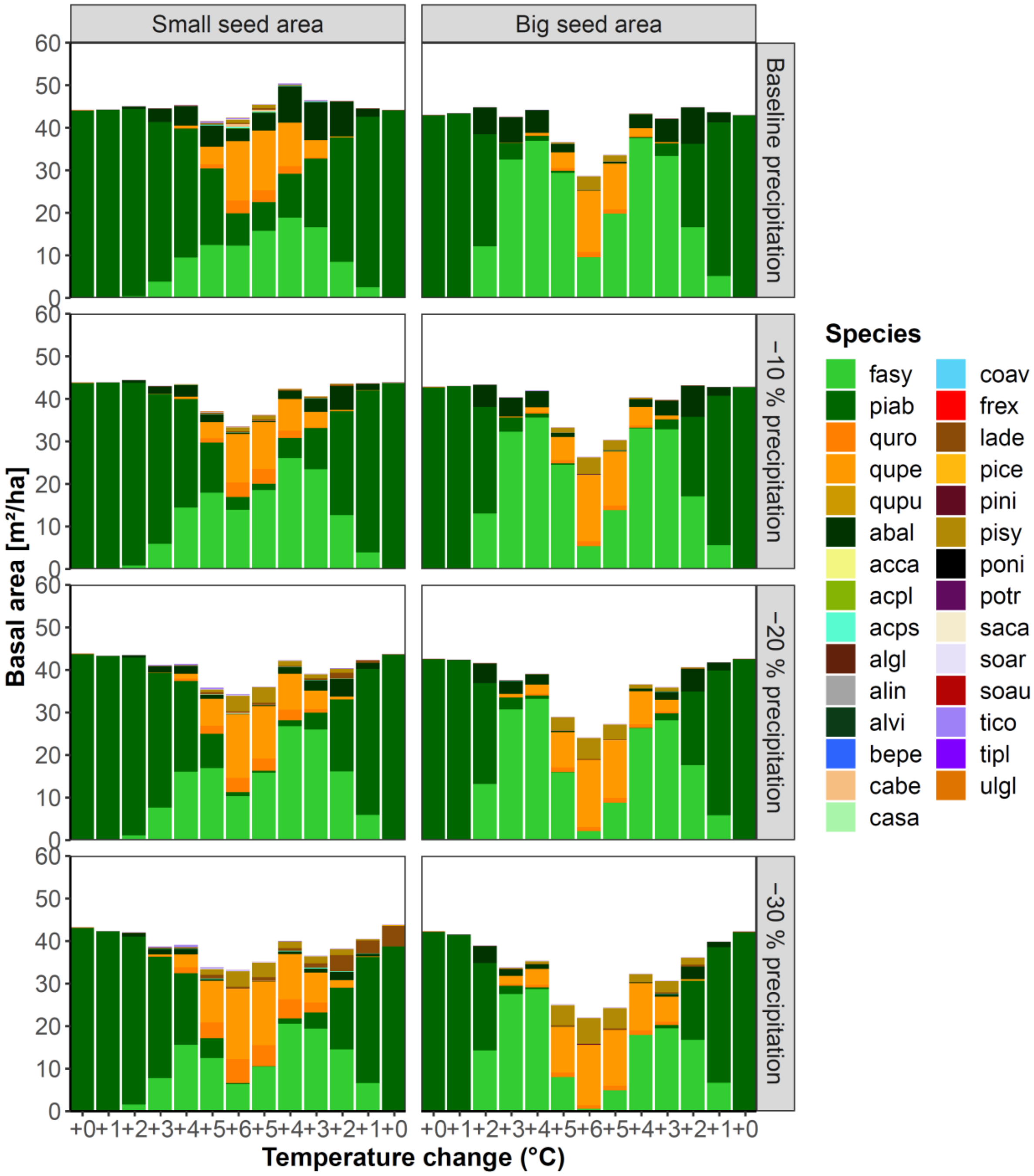

Figure S1.8: Simulated forest composition after 1000 simulation years at each temperature step in the intermediate topography scenario (basal area for each tree species). Species codes: abal=Abies alba, acca=Acer campestre, acpl=Acer platanoides, acps=Acer pseudoplatanus, algl=Alnus glutinosa, alin=Alnus incana, alvi=Alnus viridis, bepe=Betula pendula, cabe=Carpinus betulus, casa=Castanea sativa, coav=Corylus avellana, fasy=Fagus sylvatica, Frex=fraxinus excelsior, lade=Larix decidua, piab=Picea abies, pice=Pinus cembra, pini=Pinus nigra, pisy=Pinus sylvestris, poni=Populus nigra, potr=Populus tremula, qupe=Quercus petrea, qupu=Quercus pubescens, quro=Quercus robur, saca=Salix caprea, soar=Sorbus aria, soau=Sorbus aucuparia, tico=Tilia cordata, tipl=Tilia platyphyllos, ulgl=Ulmus glabra). Small seed area refers to external seed only entering from a small area at the bottom of the valley, large seed area means that the entire surrounding of the landscape acts as a seed source.

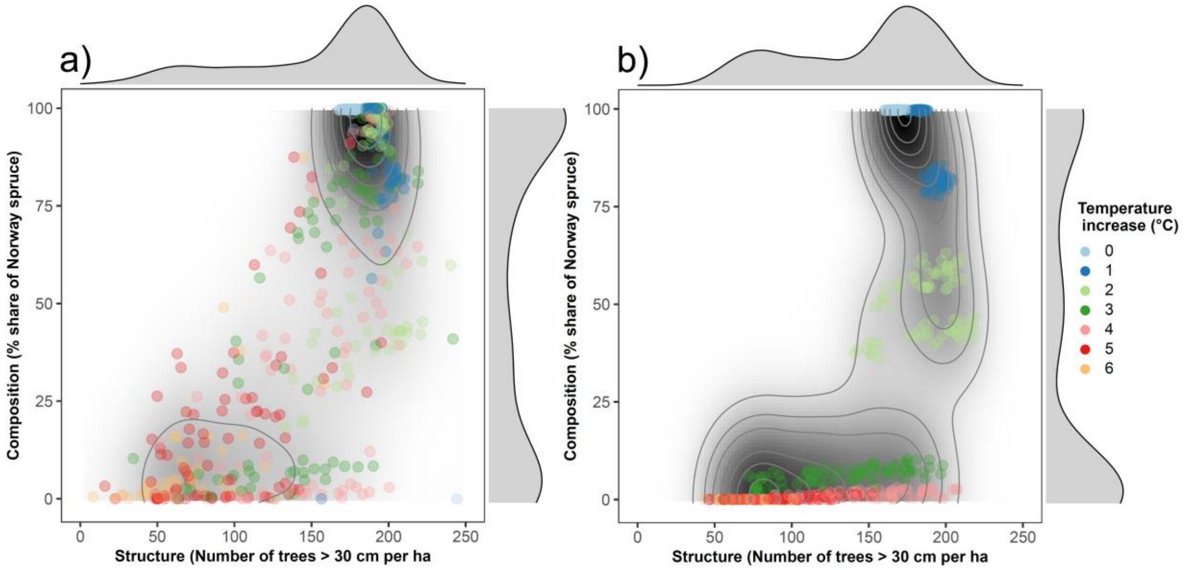

Figure S1.9: Location of the forest landscape in structure-composition attractor space for different warming levels and the small (a) and large (b) seed area scenarios over all precipitation scenarios in the intermediate topography scenario. Marginal plots and isolines indicate the probability density of all simulated cases.

3. Sensitivity to different simulation designs

3.1. Earlier reversal of climate forcing

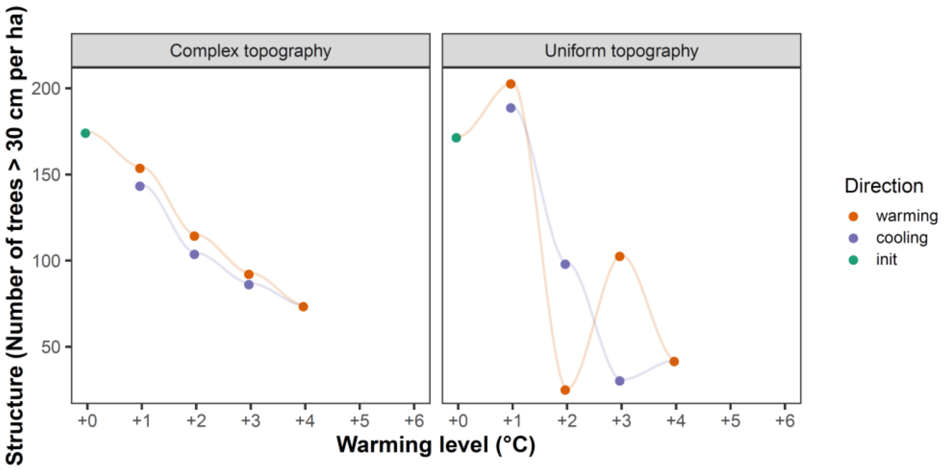

Figure S1.10: The response of forest structure (here described as the number of trees >30 cm in diameter) to climate warming (red) and subsequent cooling (purple). Shown is one simulation trajectory at -20 % precipitation relative to historic climate. The temperature forcing is reversed at +4°C relative to historic climate here.

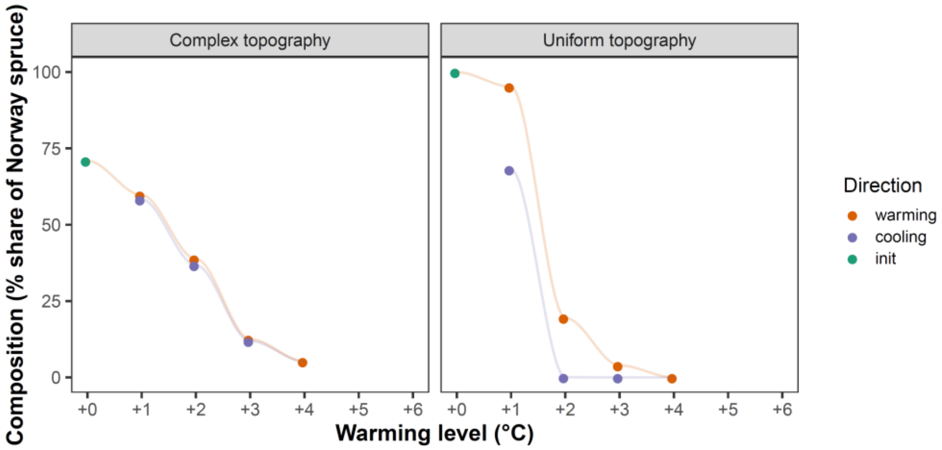

Figure S1.11: The response of forest composition (here described as the share of Norway spruce on total basal area) to climate warming (red) and subsequent cooling (purple). Shown is one simulation trajectory at -20 % precipitation relative to historic climate. The temperature forcing was reversed at +4°C relative to historic climate here.

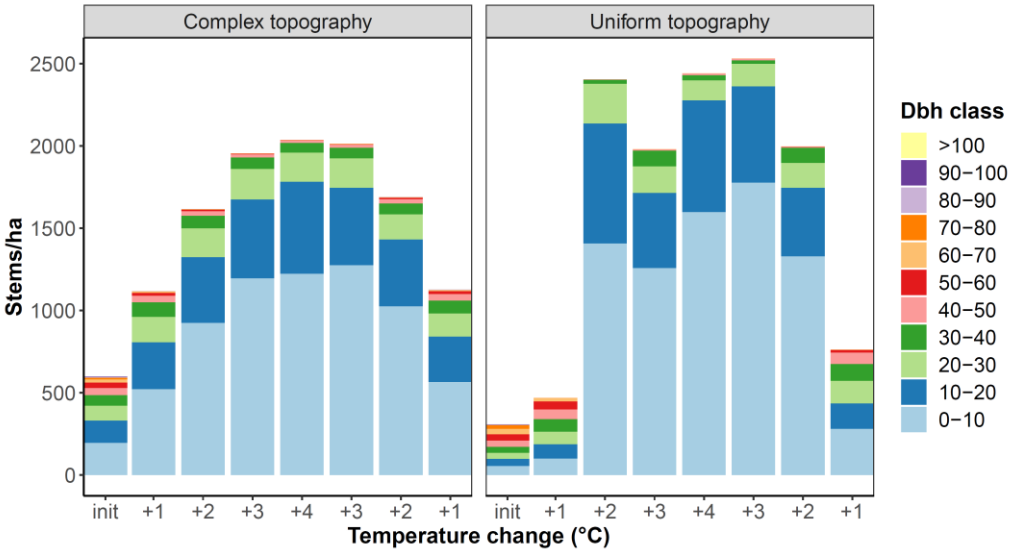

Figure S1.12: Simulated forest structure after 1000 simulation years at each temperature step (number of stems in DBH classes per ha). Shown is one simulation at -20 % precipitation relative to historic climate. The temperature forcing was reversed at +4°C relative to historic climate here.

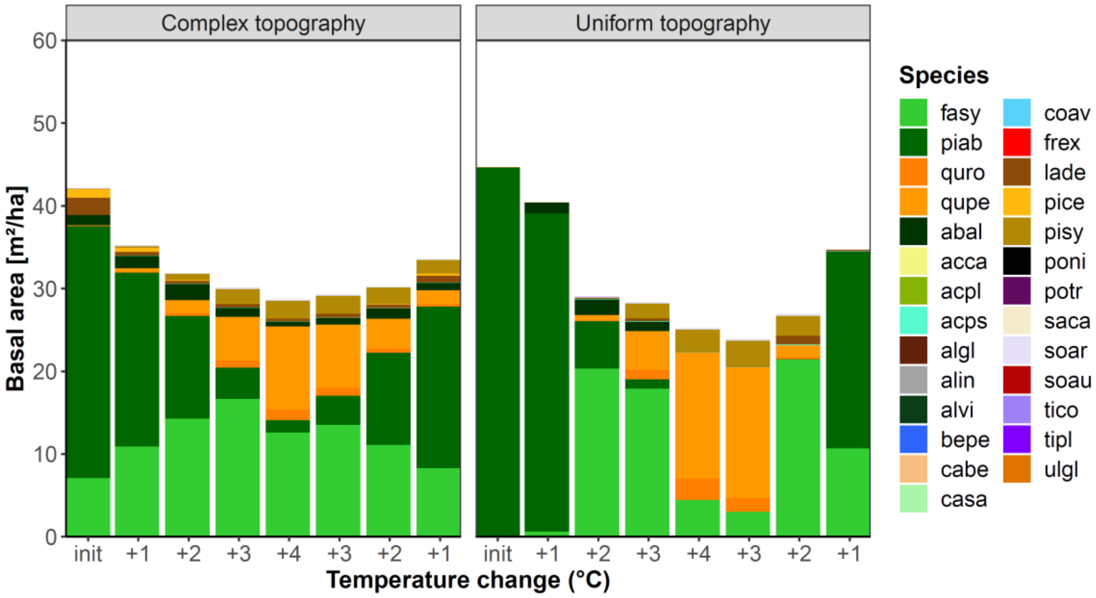

Figure S1.13: Simulated forest composition after 1000 simulation years at each temperature step (basal area for each tree species). Shown is one simulation at -20 % precipitation relative to historic climate. The temperature forcing was reversed at +4°C relative to historic climate here. Species codes: abal=Abies alba, acca=Acer campestre, acpl=Acer platanoides, acps=Acer pseudoplatanus, algl=Alnus glutinosa, alin=Alnus incana, alvi=Alnus viridis, bepe=Betula pendula, cabe=Carpinus betulus, casa=Castanea sativa, coav=Corylus avellana, fasy=Fagus sylvatica, Frex=fraxinus excelsior, lade=Larix decidua, piab=Picea abies, pice=Pinus cembra, pini=Pinus nigra, pisy=Pinus sylvestris, poni=Populus nigra, potr=Populus tremula, qupe=Quercus petrea, qupu=Quercus pubescens, quro=Quercus robur, saca=Salix caprea, soar=Sorbus aria, soau=Sorbus aucuparia, tico=Tilia cordata, tipl=Tilia platyphyllos, ulgl=Ulmus glabra)

3.2. Longer simulation durations at stable temperature

Figure S1.14: Stem diameter distribution after 1000 simulation years (averaged over the simulation years 950-1000) and 2000 simulation years (averaged over the simulation years 1950-2000) at +0°C relative to historic climate. Shown are single runs at baseline precipitation and -20% precipitation relative to historic climate. Simulations were run for a total of 2000 years under historic mean temperature.

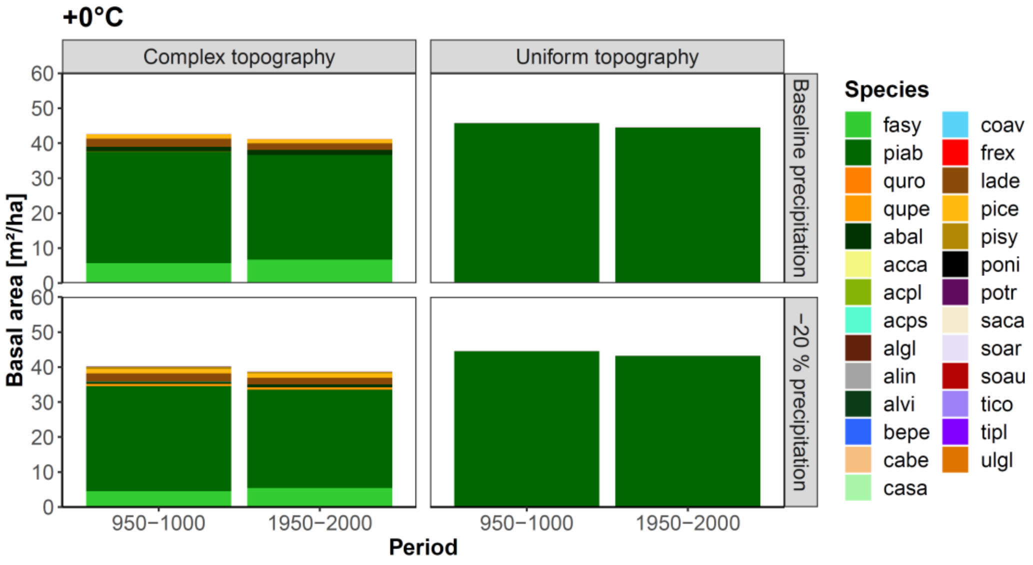

Figure S1.15: Comparison of species composition after 1000 simulation years (averaged over the simulation years 950-1000) and 2000 simulation years (averaged over the simulation years 1950-2000) at +0°C relative to historic climate. Shown are single runs at baseline precipitation and -20% precipitation relative to historic climate. Simulations were run for a total of 2000 years under historic mean temperature.

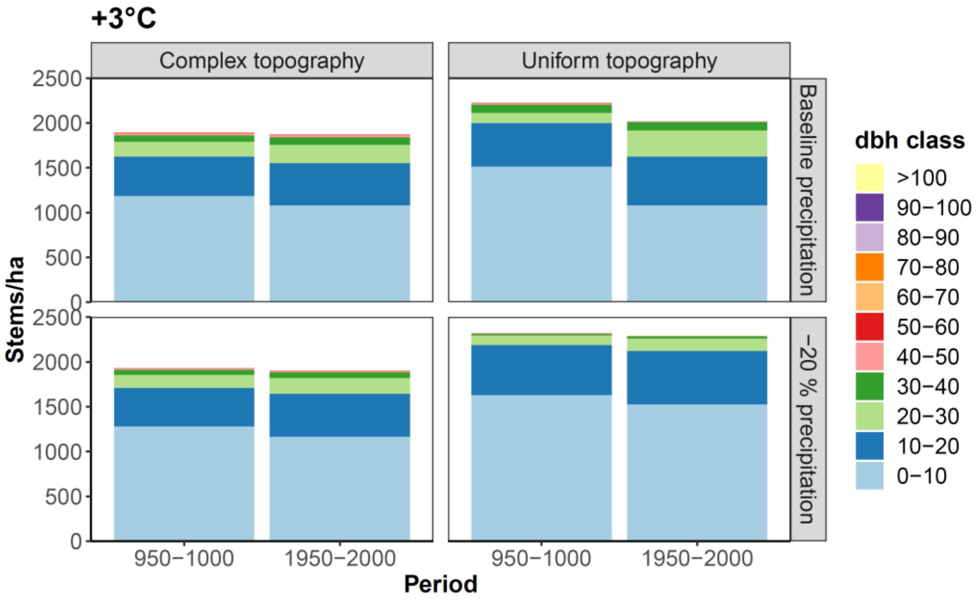

Figure S1.16: Stem diameter distribution after 1000 simulation years (averaged over the period from 950-1000) and 2000 simulation years (averaged over the period from 1950-2000) at +3°C relative to historic climate. Shown are single runs at baseline precipitation and -20% precipitation relative to historic climate. Simulations were run for a total of 2000 years at +3°C relative to historic climate.

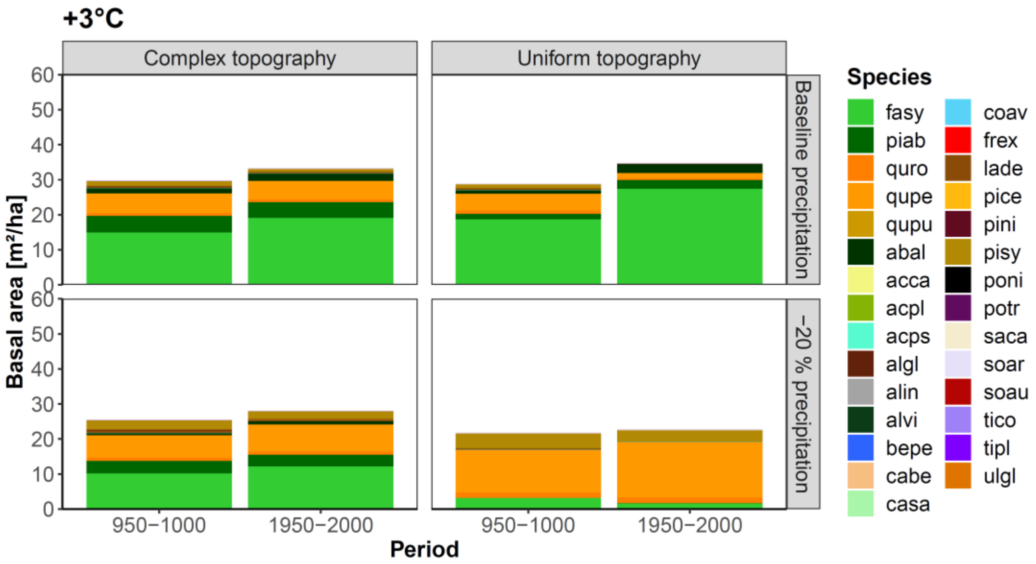

Figure S1.17: Comparison of species composition after 1000 simulation years (averaged over the simulation years 950-1000) and 2000 simulation years (averaged over the simulation years 1950-2000) at +3°C relative to historic climate. Shown are single runs at baseline precipitation and -20% precipitation relative to historic climate. Simulations were run for a total of 2000 years at +3°C relative to historic climate.

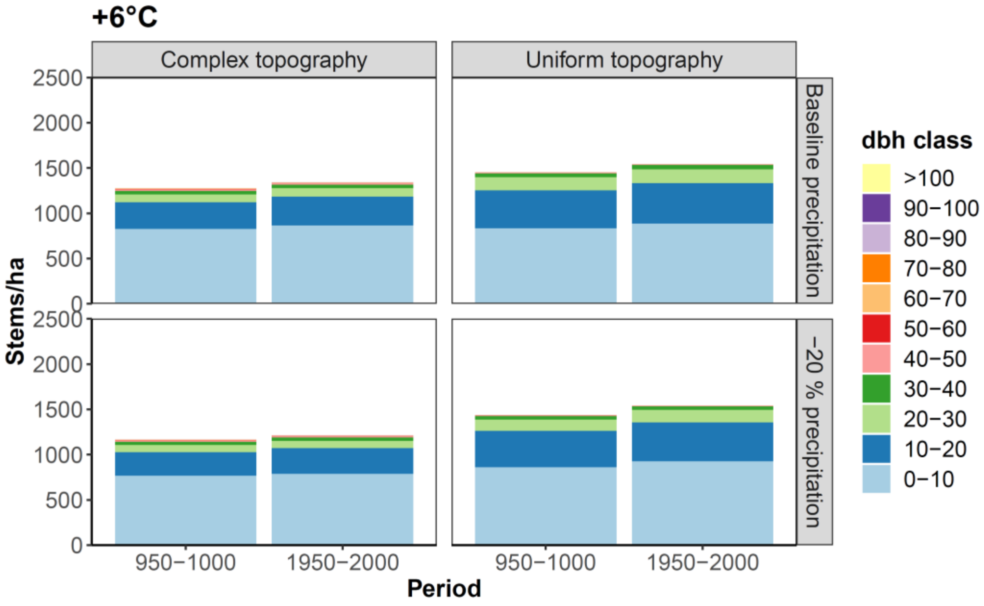

Figure S1.18: Stem diameter distribution after 1000 simulation years (averaged over the simulation years 950-1000) and 2000 simulation years (averaged over the simulation years 1950-2000) at +6°C relative to historic climate. Shown are single runs at baseline precipitation and -20% precipitation relative to historic climate. Simulations were run for a total of 2000 years at +3°C relative to historic climate.

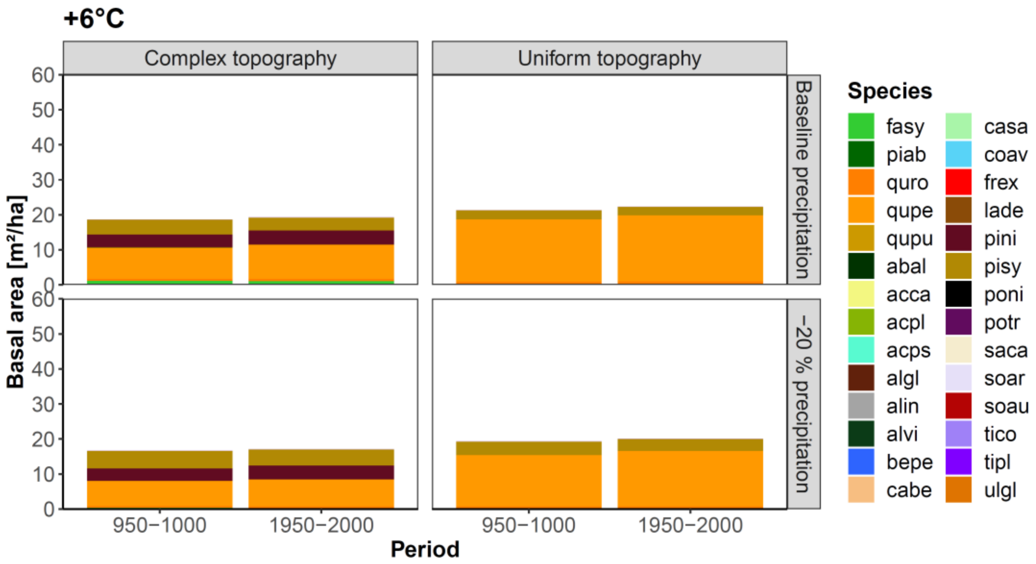

Figure S1.19: Comparison of species composition after 1000 simulation years (averaged over the simulation years 950-1000) and 2000 simulation years (averaged over the simulation years 1950-2000) at +6°C relative to historic climate. Shown are single runs at baseline precipitation and -20% precipitation relative to historic climate. Simulations were run for a total of 2000 years at +6°C relative to historic climate.

3.3. Bigger increments of warming within 1000-year time steps

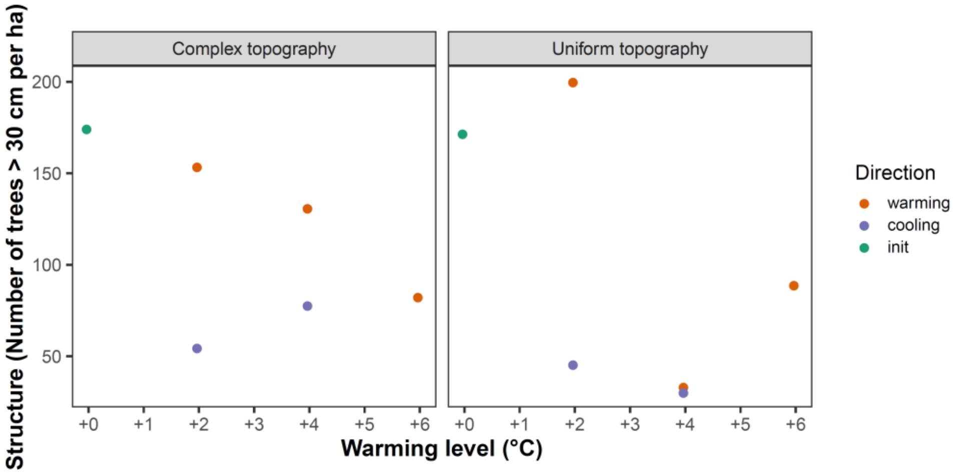

Figure S1.20: The response of forest structure (here described as the number of trees >30 cm in diameter) to climate warming (red) and subsequent cooling (purple). Shown is one simulation at -20 % precipitation relative to historic climate. Temperature was raised by two degrees each 1000 years. The landscape failed to equilibrate to a 2°C change within 1000 years, we therefore did not draw the connecting lines.

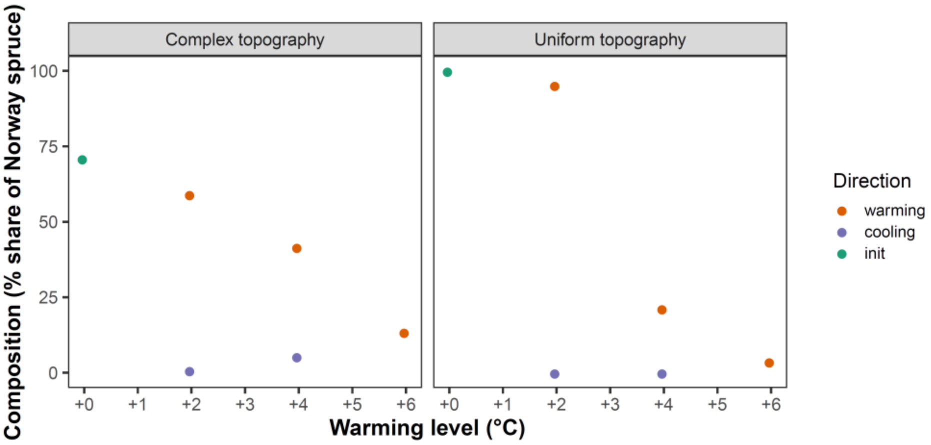

Figure S1.21: The response of forest composition (here described as the share of Norway spruce on total basal area) to climate warming (red) and subsequent cooling (purple). Shown is one simulation at -20 % precipitation relative to historic climate. Temperature was raised by two degrees each 1000 years. The landscape failed to equilibrate to a 2°C change within 1000 years, we therefore did now draw the connecting lines.

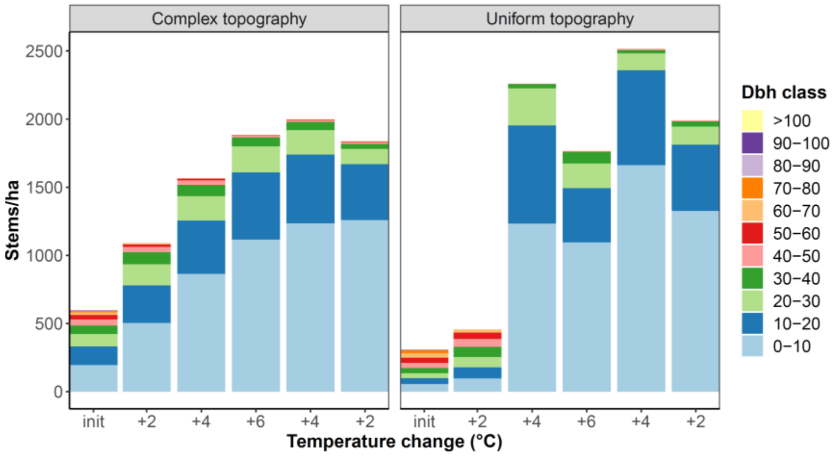

Figure S1.22: Simulated forest structure after 1000 simulation years at each temperature step (number of stems in DBH classes per ha). Shown is one simulation at -20 % precipitation relative to historic climate. Temperature was raised by two degrees each 1000 years. The landscape failed to equilibrate to a 2°C change within 1000 years.

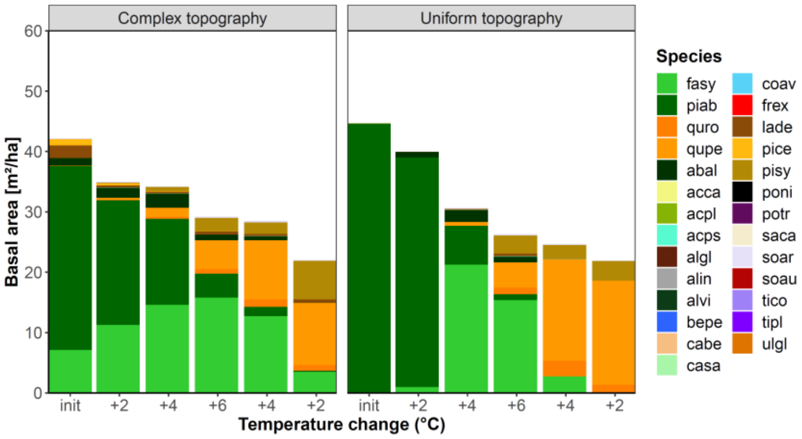

Figure S1.23: Simulated forest composition after 1000 simulation years at each temperature step (basal area for each tree species). Shown is one simulation at -20 % precipitation relative to historic climate. Temperature was raised by two degrees each 1000 years. The landscape failed to equilibrate to a 2°C change within 1000 years. Species codes: abal=Abies alba, acca=Acer campestre, acpl=Acer platanoides, acps=Acer pseudoplatanus, algl=Alnus glutinosa, alin=Alnus incana, alvi=Alnus viridis, bepe=Betula pendula, cabe=Carpinus betulus, casa=Castanea sativa, coav=Corylus avellana, fasy=Fagus sylvatica, Frex=fraxinus excelsior, lade=Larix decidua, piab=Picea abies, pice=Pinus cembra, pini=Pinus nigra, pisy=Pinus sylvestris, poni=Populus nigra, potr=Populus tremula, qupe=Quercus petrea, qupu=Quercus pubescens, quro=Quercus robur, saca=Salix caprea, soar=Sorbus aria, soau=Sorbus aucuparia, tico=Tilia cordata, tipl=Tilia platyphyllos, ulgl=Ulmus glabra)

4. Simulation design

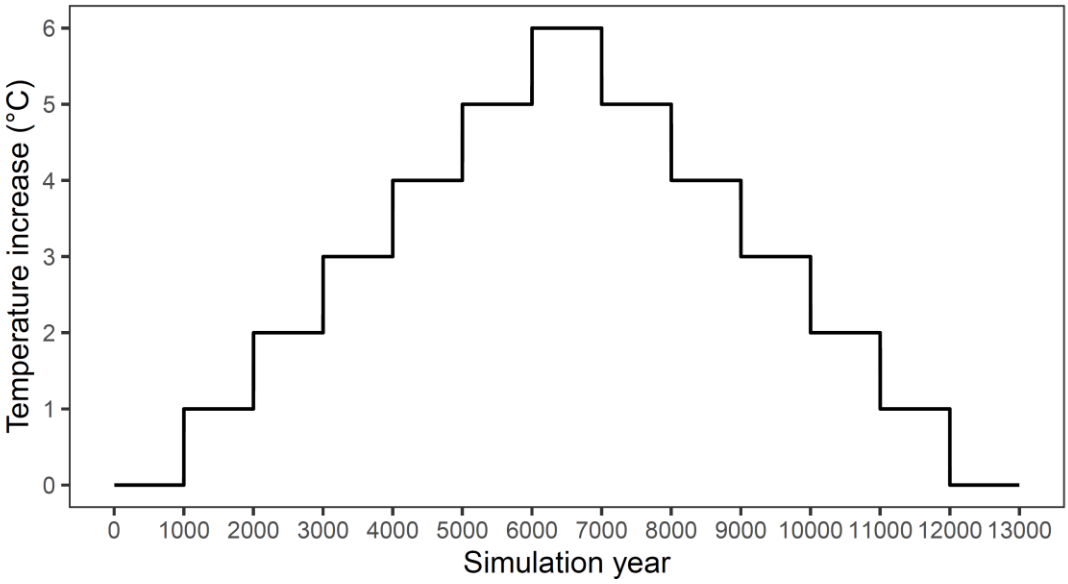

Figure S1.24: Sequence of temperature change (mean change across sampled period) during the simulation.

5. Sensitivity analysis for alternative indicator definitions

5.1. Forest structure: Varying diameter thresholds

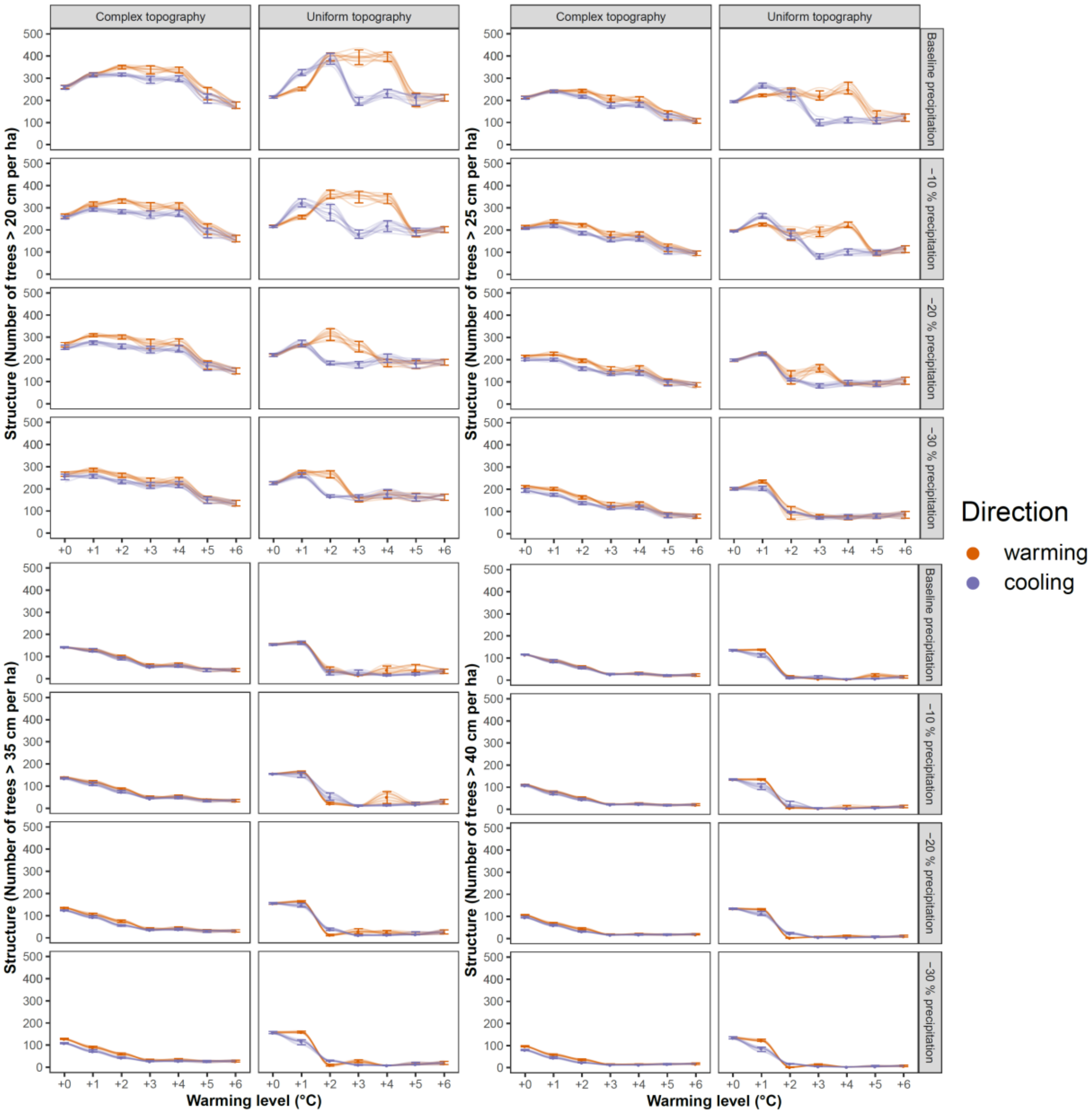

Figure S1.25: Sensitivity to different diameter thresholds used in the definition of the forest structure indicator. Shown are thresholds of 20 cm (top left panels), 25 cm (top right), 35 cm (bottom left) and 40 cm (bottom right). Lines give the number of trees per hectare larger than the respective threshold value.

S5.2. Forest composition: Alternative definition of the indicator

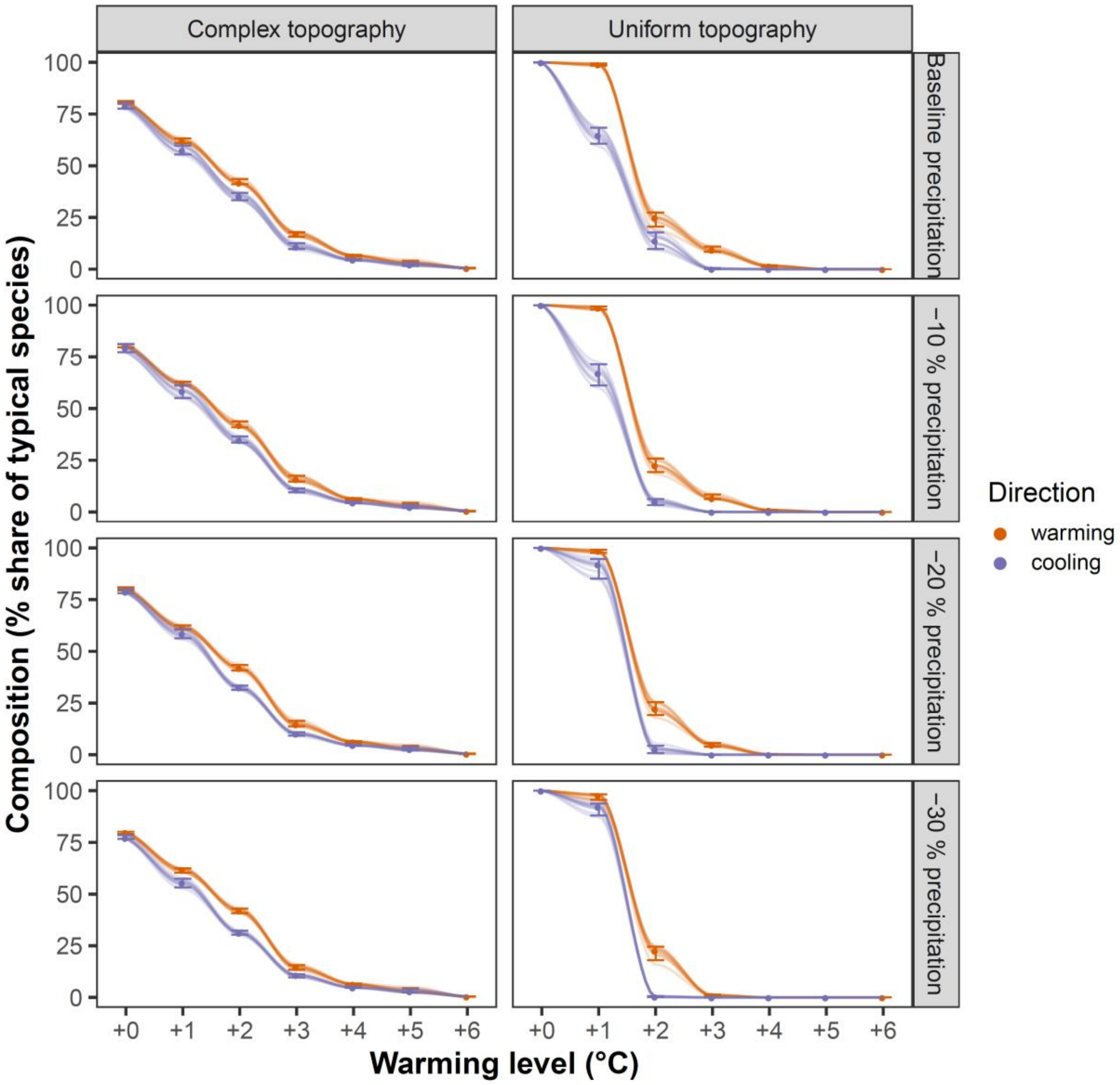

Figure S1.26: Response to warming when including additional species (Larix decidua and Pinus cembra) in the indicator used to define forest composition.

6. Changes in forest structure and composition

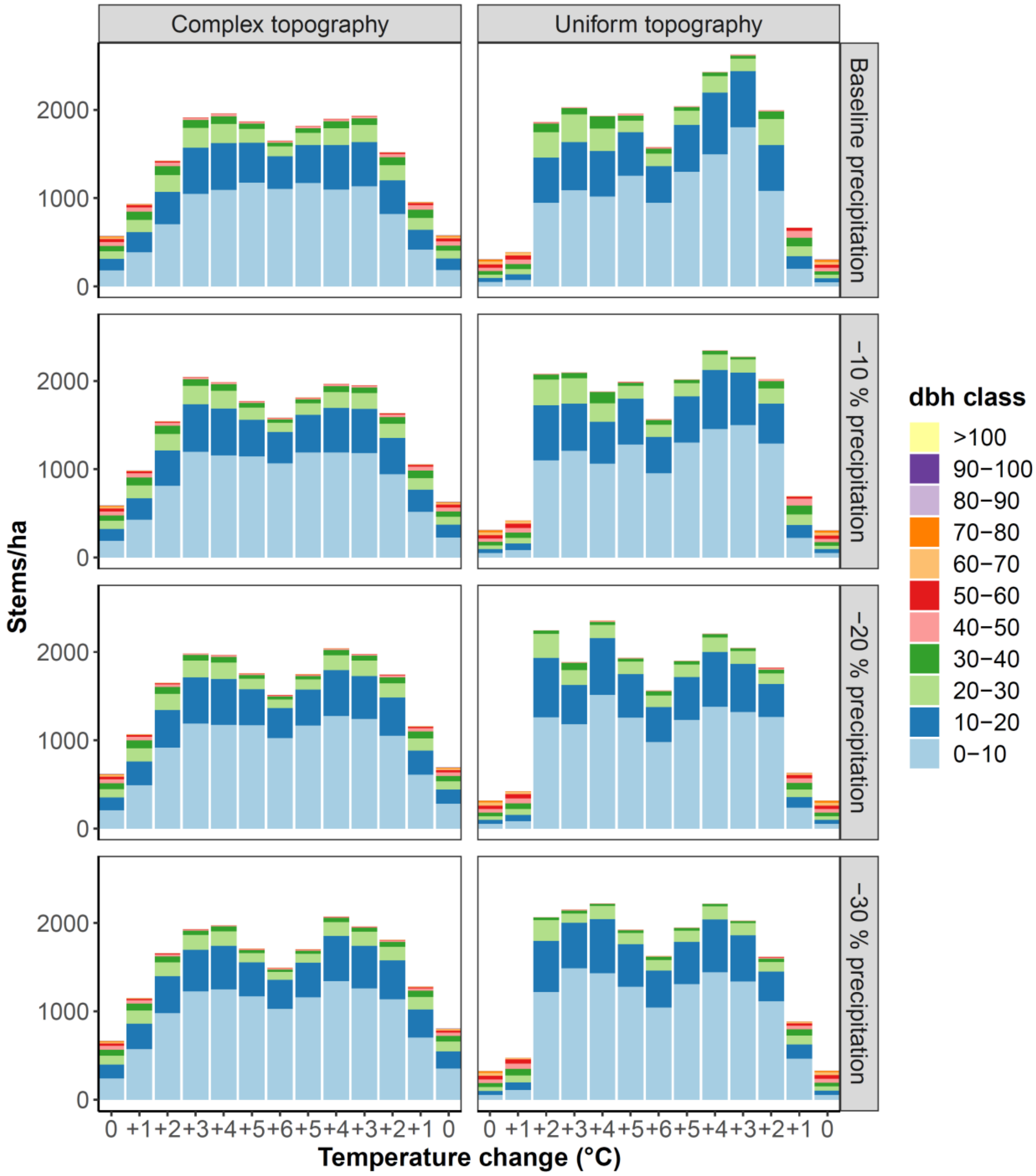

Figure S1.27: Simulated forest structure after 1000 simulation years at each temperature step (number of stems in DBH classes per ha).

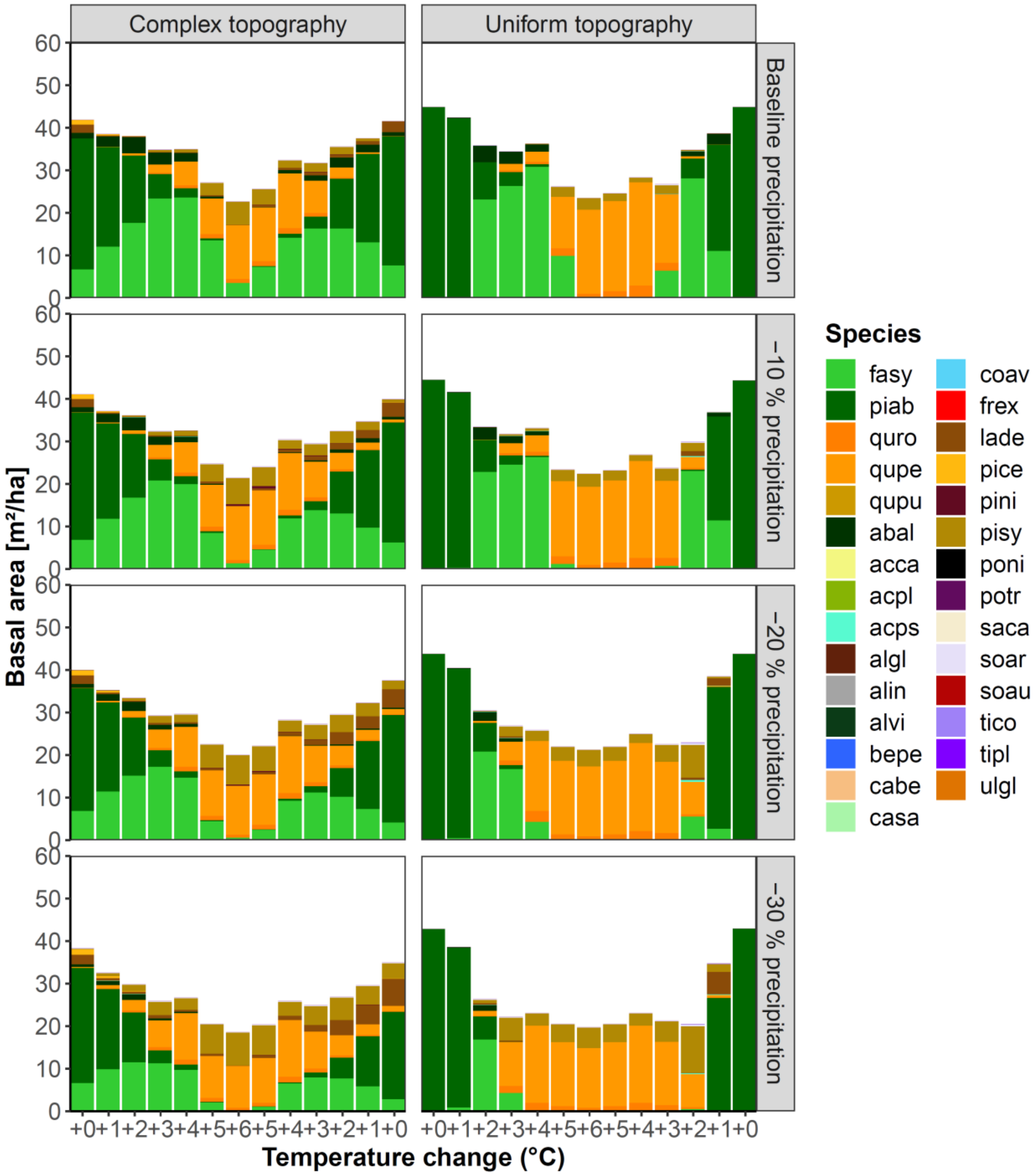

Figure S1.28: Simulated forest composition after 1000 simulation years at each temperature step (basal area for each tree species). Species codes: abal=Abies alba, acca=Acer campestre, acpl=Acer platanoides, acps=Acer pseudoplatanus, algl=Alnus glutinosa, alin=Alnus incana, alvi=Alnus viridis, bepe=Betula pendula, cabe=Carpinus betulus, casa=Castanea sativa, coav=Corylus avellana, fasy=Fagus sylvatica, Frex=fraxinus excelsior, lade=Larix decidua, piab=Picea abies, pice=Pinus cembra, pini=Pinus nigra, pisy=Pinus sylvestris, poni=Populus nigra, potr=Populus tremula, qupe=Quercus petrea, qupu=Quercus pubescens, quro=Quercus robur, saca=Salix caprea, soar=Sorbus aria, soau=Sorbus aucuparia, tico=Tilia cordata, tipl=Tilia platyphyllos, ulgl=Ulmus glabra)

7. Development of forest composition and structure across elevational bands

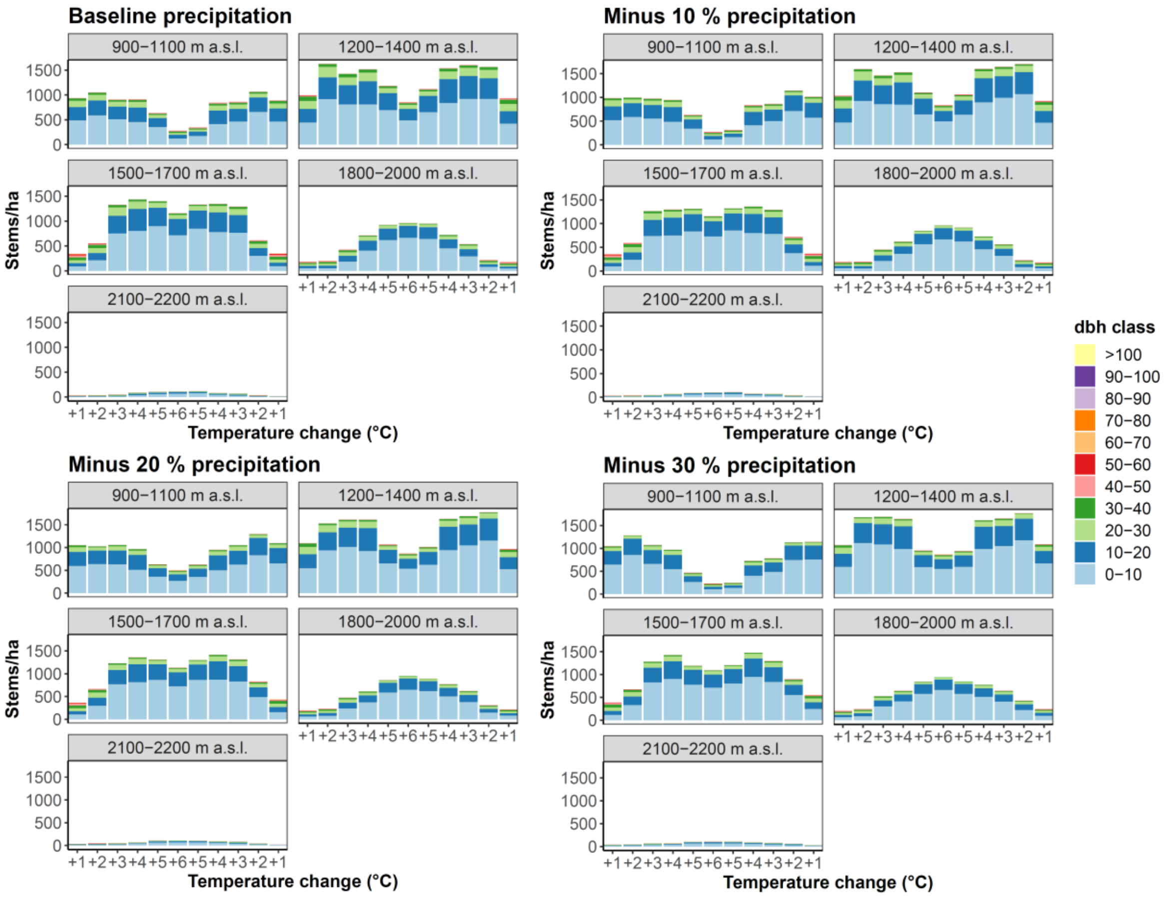

Figure S1.29: Simulated forest structure after 1000 simulation years at each temperature step (number of stems in DBH classes per ha across 300m elevational bands. Shown is one simulation per precipitation scenario.

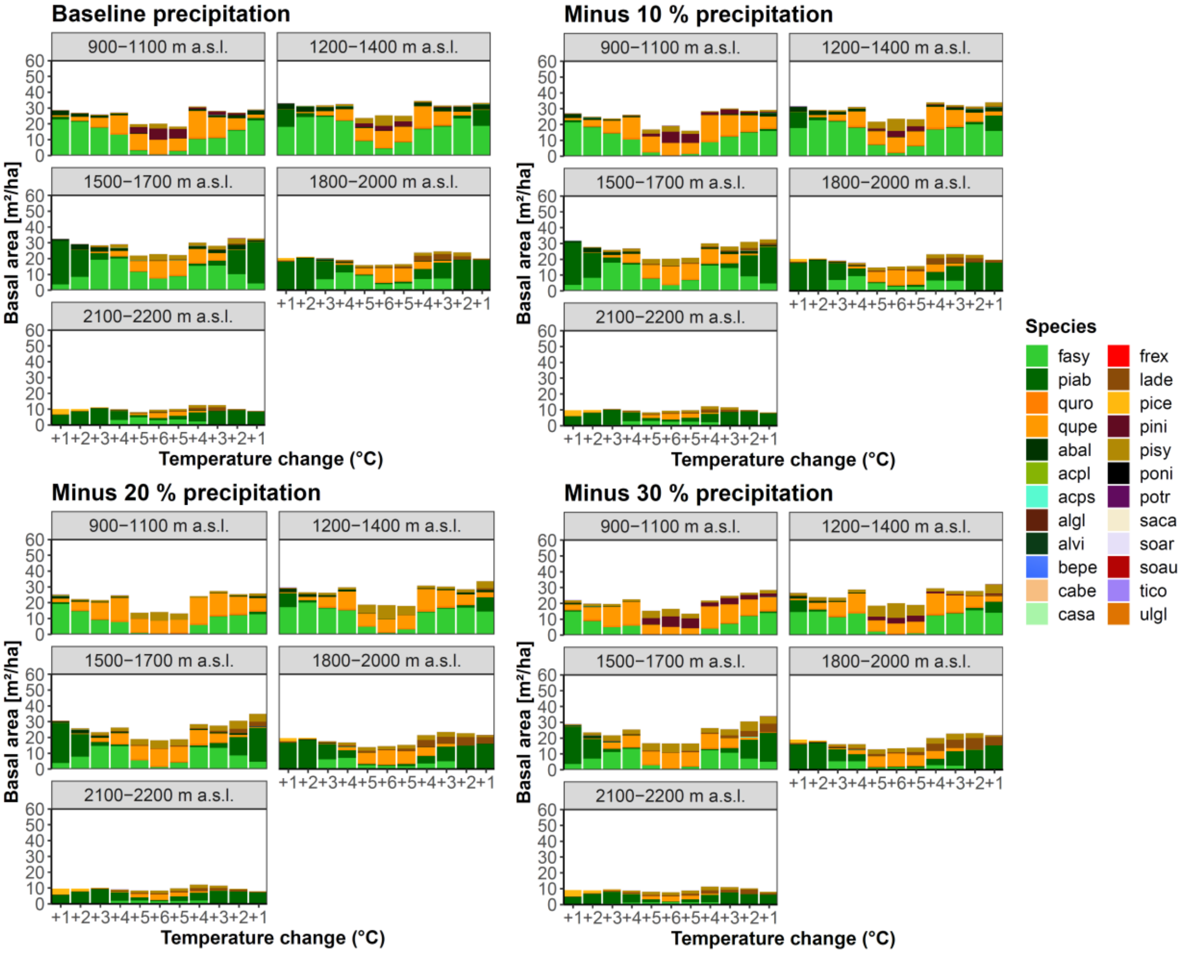

Figure S1.30: Simulated forest composition after 1000 simulation years at each temperature step (basal area for each tree species) across 300m elevational bands. Shown is one simulation per precipitation scenario. Species codes: abal=Abies alba, acca=Acer campestre, acpl=Acer platanoides, acps=Acer pseudoplatanus, algl=Alnus glutinosa, alin=Alnus incana, alvi=Alnus viridis, bepe=Betula pendula, cabe=Carpinus betulus, casa=Castanea sativa, coav=Corylus avellana, fasy=Fagus sylvatica, Frex=fraxinus excelsior, lade=Larix decidua, piab=Picea abies, pice=Pinus cembra, pini=Pinus nigra, pisy=Pinus sylvestris, poni=Populus nigra, potr=Populus tremula, qupe=Quercus petrea, qupu=Quercus pubescens, quro=Quercus robur, saca=Salix caprea, soar=Sorbus aria, soau=Sorbus aucuparia, tico=Tilia cordata, tipl=Tilia platyphyllos, ulgl=Ulmus glabra)

8: Potential drivers of hysteresis

Table S1.1: Optimal and minimal temperature for tree growth by tree species as well as the difference between these temperature points illustrating the temperature amplitude for tree growth of each species.

Species	Optimal temperature (°C)	Minimal temperature (°C)	Amplitude (°C)
Abies alba	21	0	21
Acer campestre	24	3	21
Acer platanoides	24	3	21
Acer pseudoplatanus	21	3	18
Alnus glutinosa	20	2	18
Alnus incana	22	3	19
Alnus viridis	18	1	17
Betula pendula	17	0	17
Carpinus betulus	23	5	18
Castanea sativa	25	5	20
Corylus avellana	22	3	19
Fagus sylvatica	19	3	16
Fraxinus excelsior	20	3	17
Larix decidua	19	-1	20
Picea abies	17	-2	19
Pinus cembra	11	1	10
Pinus nigra	25	1	24
Pinus sylvestris	23	1	22
Populus nigra	21	2	19
Populus tremula	21	2	19
Quercus petraea	23	5	18
Quercus pubescence	23	5	18
Quercus robur	23	5	18
Salix caprea	21	1	20
Sorbus aria	22	3	19
Sorbus aucuparia	22	3	19
Tilia cordata	24	5	19
Tilia platyphyllos	24	5	19
Ulmus glabra	24	3	21

Appendix D – Academic Curriculum Vitae

Education

01/2017 - 04/2021	PhD in Forest Sciences University of Natural Resources and Life Sciences, Vienna Title: Investigating the resilience of forest ecosystems to changing climate and disturbance regimes
10/2014 – 01/2017	MSc in Forest Sciences (with distinction), with a specialization in "Multifunctional forest management", University of Natural Resources and Life Sciences, Vienna Thesis title: Effects of forest management on the provisioning of ecosystem services under climate change in a mountain forest landscape
09/2010 – 10/2014	BSc in Forestry University of Natural Resources and Life Sciences, Vienna

Professional Experience

01/2017 – present	Research Assistant Institute of Silviculture, University of Natural Resources and Life Sciences, Vienna
06/2015 – 01/2017	Student Research Assistant Institute of Silviculture, University of Natural Resources and Life Sciences, Vienna
02/2015 – 03/2015	Carbon Reporter for Singapore LULUCF-MRV Austrian Natural Resources Management and International Cooperation Agency (ANRICA)
07/2013 – 01/2014	Student Research Assistant Institute of Forest Growth, University for Natural Resources and Life Sciences, Vienna

Honors and Awards

2018	IUFRO Student Award for Excellence in Forest Science (ISA)
2018	Scholarship for short-term scientific research abroad for a research visit to the University of Wisconsin-Madison, USA
2017	Dr. Wilfrieda Lindner Wissenschaftspreis for an excellent master thesis in Forest Sciences
2017	Karl Schleinzer Foundation Award for excellent academic performance

Publications

Academic

Publications with grey background are the papers included in this dissertation

2021

Albrich, K., Thom, D., Rammer, W., & Seidl R. (submitted). The long way back: Development of Central European mountain forests towards old-growth conditions after the cessation of management

2020

Albrich, K., Rammer, W., Turner, M.G., Ratajczak, Z., Braziunas, K.H., Hansen, W.D., & Seidl, R. 2020. Simulating forest resilience: A review. *Global Ecology and Biogeography* 29: 2082–2096.

Petter, G., Mairota, P., **Albrich, K.,** Bebi, P., Brůna, J., Bugmann, H., Haffenden, A., Scheller, R.M., Schmatz, D.R., Seidl, R., Speich, M., Vacchiano, G., & Lischke, H. 2020. How robust are future projections of forest landscape dynamics? Insights from a systematic comparison of four forest landscape models. *Environmental Modelling & Software* 134: 104844.

Albrich, K., Rammer, W., & Seidl, R. 2020. Climate change causes critical transitions and irreversible alterations of mountain forests. *Global Change Biology* 26: 4013–4027.

2019

Seidl, R., **Albrich, K.**, Erb, K., Formayer, H., Leidinger, D., Leitinger, G., Tappeiner, U., Tasser, E., & Rammer, W. 2019. What drives the future supply of regulating ecosystem services in a mountain forest landscape? *Forest Ecology and Management* 445: 37–47.

2018

Albrich, K., Rammer, W., Thom, D., & Seidl, R. 2018. Trade-offs between temporal stability and level of forest ecosystem services provisioning under climate change. *Ecological Applications* 28: 1884–1896.

Seidl, R., **Albrich, K.**, Thom, D., & Rammer, W. 2018. Harnessing landscape heterogeneity for managing future disturbance risks in forest ecosystems. *Journal of Environmental Management* 209: 46–56.

Other

Albrich K., 2017. Der Weg zurück zum Urwald - BOKU-Forschungsprojekt zur Waldentwicklung nach Aussernutzungstellung. Wildnis News Nr. 3, 12/2017

Seidl R., **Albrich, K.,** Thom, D., Rammer, W. 2016. Multifunktionalität am Prüfstand, Österreichische Forstzeitung, 12/2016, 24-25

Academic presentations

Albrich, K., Rammer, W., Turner, M.G., Hansen, W., Ratajzk, Z., Braziunas, K., Seidl, R. (2019): Simulating forest resilience – a review. Symposium "Perspectives of forest modeling", Leipzig , Germany

Albrich, K; Rammer, W; Seidl, R (2018): Resilience of mountain forest ecosystems to climate change. Cool Forests at Risk? - The critical role of boreal and mountain ecosystems for people, bioeconomy, and climate (IBFRA18), Laxenburg, Austria

Albrich, K; Rammer, W; Thom, D; Seidl, R. (2017): Providing multiple ecosystem services in the face of changing disturbance regimes. IUFRO 125th Anniversary Congress, Freiburg im Breisgau, Germany

Albrich, K.; Thom, D.; Rammer, W.; Seidl, R. (2016): Impact of different management strategies on the provisioning of forest ecosystem services under climate change. [Poster], COST Action [FP1304] event: PROFOUND Joint MC/WG meeting, Krakow, Poland

Teaching

2017	Grundlagen der Waldbewirtschaftung (Basics of Forest Management), practical exercises, University for Natural Resources and Life Sciences, Vienna
2013	Forstliche Biometrie I (Forest Biometrics I), practical exercises, University for Natural Resources and Life Sciences, Vienna
2013	Zustandserhebungen und Ertragsprognosen (Forest Assessment and Yield Forecasting), practical exercises, University for Natural Resources and Life Sciences, Vienna

Reviewer for Scientific Journals

Ecosphere, Scandinavian Journal of Forest Research, Austrian Journal of Forest Sciences, Journal of Vegetation Science, Global Change Biology, Biodiversity and Conservation, Applied Vegetation Science, Science of the Total Environment