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Doctoral Dissertation

Patterns and processes of natural disturbances in temperate forests: A multi-scale approach

Submitted by

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Affidavit

I solemnly swear that I have compiled this work solely and without external help, have not utilized any sources outside those permitted and that the sources used have been given verbatim or quoted textually in the places indicated.

Vienna, January 2022 Andreas Sommerfeld

Preface

This cumulative thesis consists of three publications which all have undergone peer reviews and are freely available (see below for respective DOIs). All publications, including their supporting materials, can be found in Section 9 (Appendices A – C) of this thesis. The synthesis presented here aims to commonly frame all three publications and conclude the principle parts of the publications. I will give a brief summary of all essential parts, enabling the reader to follow my line of arguments. However, for a detailed description of the experimental design, applied methodologies, complete results, and in-depth discussion please refer to each individual paper in the Appendices.

For the first publication „Patterns and drivers of recent disturbances across the temperate forest biome“ (Appendix A) I contributed to the study design, managed the incoming data, ran data analysis and wrote the first draft of the manuscript. My responsibilities in the second publication „Do bark beetle outbreaks amplify or dampen future bark beetle disturbances in Central Europe?“ (Appendix B) were contributing to the study design, processing necessary input data for landscape setup in the forest simulation model iLand, implementing the simulation runs, analyzing the output data and writing the manuscript. For the third publication „Effects of disturbance patterns and deadwood on the microclimate in European beech forests“ (Appendix C) I was responsible for the planning and implementation of the field work, contributed to the study design and to the manuscript.

This thesis was embedded in the RESIN Project funded by the Austrian Science Fund (FWF) through START grant Y895-B25.

I hope I contribute with this thesis to the understanding of forest disturbance in general, and specifically contribute to an enhanced perception of the influence of disturbance patterns and forest vegetation feedbacks. Additionally, I hope the reader will find this thesis useful to inspire and advance their own research.

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

Sommerfeld, A., Senf, C., Buma, B., D'Amato, A. W., Després, T., Díaz-Hormazábal, I., S. Fraver, L. E. Frelich, Á. G. Gutiérrez, S. J. Hart, B. J. Harvey, H. S. He, T. Hlásny, A. Holz, T. Kitzberger, D. Kulakowski, D. Lindenmayer, A. S. Mori, J. Müller, J. Paritsis, G. L. W. Perry, S. L. Stephens, M. Svoboda, M. G. Turner, T. T. Veblen Seidl, R. (2018). Patterns and drivers of recent disturbances across the temperate forest biome. Nature Communications, 9(1). doi: 10.1038/s41467-018-06788-9

Sommerfeld, A., Rammer, W., Heurich, M., Hilmers, T., Müller, J., & Seidl, R. (2021). Do bark beetle outbreaks amplify or dampen future bark beetle disturbances in Central Europe? Journal of Ecology, 109(2): 737– 749. doi: 10.1111/1365-2745.13502

Thom, D., Sommerfeld, A., Sebald, J., Hagge, J., Müller, J., & Seidl, R. (2020). Effects of disturbance patterns and deadwood on the microclimate in European beech forests. Agricultural and Forest Meteorology, 291. 108066.
doi: 10.1016/j.agrformet.2020.108066

Or this thesis in its entirety:

Sommerfeld, A. (2022) Patterns and processes of natural disturbances in temperate forests: A multi-scale approach. Dissertation, University of Natural Resources and Life Sciences (BOKU), Vienna p. 119

Abstract

Forest ecosystems are a crucial part of Earth‘s biosphere and are therefore critical for human well-being. Forests are essential for the provision of ecosystem services and are a refuge of biodiversity. Nevertheless, forests are under increasing pressure from changes in the climate system and land-use changes. A principle effect of climate change, besides immediate effects on environmental factors such as temperature, is the alteration of forest disturbance regimes. During recent decades, disturbance activities have increased in many areas across the globe, and are likely to increase further. Increases have affected all spatial scales but our understanding of the basic variability of forest disturbances, occurring feedbacks within the vegetation-disturbance system and implications for ecosystem services remains limited.

Here I used a variety of methodical approaches to explore disturbance patterns and processes at three distinct spatial scales. On the global scale, I used data from remote sensing coupled with in-depth local ecological information. I quantified the variability of disturbance activity and analyzed if climate is the main driver of observed variability, and if human influence had a modulating effect. On the landscape scale, I used simulation modelling to examine bark beetle effects on forest diversity and subsequent outbreaks. On the stand level, I studied experimentally altered disturbance patterns (*aggregated* and *distributed*) and different deadwood types to disentangle their effects upon forest microclimate.

Globally, disturbance patterns were highly variable and shaped by disturbance agent and tree species traits. Inside protected areas disturbances were smaller and more complex than in areas affected by human land use. High disturbance activity was consistently linked to warmer and drier than average climate. On the landscape scale, bark beetle outbreaks were strongly amplified by climate change, but disturbance-mediated changes in forest structure and composition dampened future disturbance activity. On a stand level, the buffering capacity of closed forest canopies was higher in warm and dry years, while spatially *aggregated* disturbances led to increased light penetration and a lower microclimatic buffering capacity.

Disturbance patterns on the global scale showed substantial spatio-temporal variation within temperate forests. On a finer landscape level, I found that forest diversity provides important dampening feedbacks, suggesting that homogenizing post-disturbance forests could elevate the future susceptibility to large-scale bark beetle outbreaks. A reduced microclimatic buffering capacity of disturbed forest canopies at the stand scale underlined the negative effect of *aggregated* disturbance patterns on the mitigating effects of forest canopies on climatic extremes.

Keywords: climate change, disturbance interactions, diversity, forest composition, forest structure, iLand, landscape model, microclimate, protected areas, remote sensing, simulation model, forest disturbances

Deutsche Kurzfassung

Waldökosysteme sind ein essentieller Bestandteil der Biossphäre und damit auch von entscheidender Bedeutung für die menschliche Existenz. Wälder liefern wichtige Ökosystemleistungen und sind Hotspots der Biodiversität. Dennoch sind Wälder unter zunehmendem Druck durch wachsende menschliche Landnutzungsansprüche und klimatische Veränderungen. Der Klimawandel beeinflusst die Waldentwicklung durch direkte Effekte wie Temperaturerhöhung aber auch durch indirekte Effekte wie Veränderungen in den Störungsregimen der Wälder. In den letzten Jahrzehnten haben Störungen in vielen Gebieten der Welt zugenommen und eine weitere Zunahme durch fortschreitende Klimaveränderungen liegt nahe. Diese Störungszunahmen betreffen alle räumlichen Ebenen, das Verständnis über grundlegende Variation im Störungsregime, Rückkopplungen auf die Vegetation und die Auswirkung auf Leistungen der Wälder ist jedoch unzureichend.

In dieser Arbeit wurden unterschiedliche Methoden genutzt um die Muster und Prozesse von Störungen auf verschiedenen Skalenebenen genauer zu untersuchen. Auf globaler Ebene habe ich Fernerkundungsdaten mit detaillierten ökologischen Hintergrundinformationen verknüpft. Dabei habe ich Störungsereignisse quantifiziert und überprüft ob klimatische Einflüsse die Hauptursache dafür waren. Zusätzlich habe ich überprüft ob menschliche Einflüsse das Auftreten oder die Gestalt von Störungen beeinflusst haben. Auf Ebene der Landschaft habe ich ein Simulationsmodell genutzt um Effekte von Borkenkäferausbrüchen auf die Diversität von Wäldern und die zukünftige Störungsdynamik zu untersuchen. Auf Ebene der Bestände habe ich untersucht, ob experimentelle Störungsanordnungen (konzentriert und verteilt) und verschiedene Totholzarten Effekte auf das Mikroklima in der Fläche haben.

Die räumlichen Muster von Störungen waren global gesehen äußerst variable und ließen sich am besten durch die Art des Störereignisses (z.B. Windwurf) und die Eigenschaften der betroffenen Baumarten erklären. Innerhalb von Schutzgebieten waren Störungen kleiner und komplexer geformt als in Gebieten wo ebenfalls menschliche Bewirtschaftung stattfindet. Gebiete in denen die höchste Störungsaktivität festgestellt wurde, waren durch wärmeres und trockeneres Klima geprägt. Ebenfalls auf Landschaftsebene wurden Borkenkäferausbrüchen durch klimatische Einflüsse erheblich verstärkt. Das Ergebnis dieser Störungen sind Waldstrukturen und Baumartenzusammensetzung, welche die Wahrscheinlichkeit zukünftiger Borkenkäferausbrüchen jedoch stark verringern. Auf Ebene der Einzelbestände konnte ich feststellen, dass die mikroklimatische Pufferwirkung des Kronendachs auf gestörten Flächen, besonders in warmen und trockenen Jahren, stark nachließ.

Die globalen Störungsmuster zeigten erhebliche räumlich-zeitliche Variationen, jedoch gibt es Hinweise darauf, dass Störungen im Klimawandel das Potenzial haben Waldökosysteme zu transformieren. Allerdings treten auch abpuffernde Rückkopplungen durch einen vielfältigeren Waldaufbau nach Störungen auf. Die abpuffernden Effekte auf Landschaftsebene können jedoch durch eine Homogenisierung gestörter Flächen zunichte gemacht werden. Die Ergebnisse der Einzelbestände zeigen darüber hinaus, dass räumlich konzentriert auftretende Störungen die positiven mikroklimatischen Effekte des geschlossenen Kronendachs reduzieren können.

Schlagwörter: Fernerkundung, iLand, Interaktion von Störungen, Klimawandel, Landschaftsmodell, Mikroklima, Schutzgebiete, Simulationsmodell, Störungen, Diversität von Wäldern, Waldstruktur, Waldzusammensetzung

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1. Introduction

The world has changed for forest ecosystems. Global climate change, the ongoing land-use change, and invasions of novel insects and pathogens into new territories are causing immense challenges for forest ecosystems across the globe (Lambin & Meyfroidt, 2011; Liebhold et al., 2017; Seidl et al., 2014). Quantifying the impacts of change and estimating their consequences is thus a fundamental task for forest research and of great importance for society.

The state of forest ecosystems matters, as forests are hotspots of biodiversity (Rahbek et al., 2019) and play a key role in Earth's carbon cycle (Gower, 2003; Mitchard, 2018). Specifically, forests are capable to contribute to climate change mitigation by sequestering carbon (Fahey et al., 2010; Vass & Elofsson, 2016) on a global scale, as well as dampening local climate extremes (De Frenne et al., 2019). Forests provide further ecosystem services that are crucial for humans livelihoods such as timber, fuel wood, food, water supply and purification, medicinal plants and recreation (Krieger, 2001; MEA, 2005). These forest functions are likely to be substantially altered under a changing forest disturbance regime.

Disturbances are key components of forest ecosystems and are also contributing to biodiversity and adaptive capabilities of forests (Gutschick & BassiriRad, 2003; Kulakowski et al., 2017; Thom & Seidl, 2016; Turner, 2010). In this thesis I refer to the definition of disturbance from Pickett & White (1985), defining disturbances as "any relatively discrete event that disrupts the structure of an ecosystem […] and changes resource availability or the physical environment.'' Disturbances occur on a wide range of scales but we often lack understanding how these processes interact between these scales (Raffa et al., 2008; Turner, 2010). Emergent patterns of higher-scale processes are sometimes hard to predict, even if lower-scale processes are well understood (Peters et al., 2004). Furthermore, underlying processes of disturbance patterns observed at higher scales might not be identified correctly if interactions are unknown (Peters et al., 2004). Therefore, it is important to incorporate multi-scale linkages among processes. Here, I aim to improve the understanding of linkages among scales (e.g. local expert knowledge combined with global satellite data; bark beetle dispersal in a landscape-scale study) to gain a more comprehensive insight to the implications of spatio-temporal patterns of forest disturbances.

Within the last 50 years climate change has affected forest ecosystems in many aspects (Keenan, 2015; Lucier et al., 2009) including climate-induced changes in disturbance regimes (Dale et al., 2001; Seidl et al., 2017, 2011). Large parts of the world have experienced increases in disturbance occurrence and severity from multiple disturbance agents such as insect outbreaks (Kautz et al., 2018), wild fires (Westerling, 2016) and drought (Millar & Stephenson, 2015). The drivers of changes within the disturbance regimes are global, but responses thereon were mainly investigated in well-studied landscapes (Lindenmayer et al., 2011; Seidl et al., 2016; Turner, 2010). Therefore, it was not possible to conclude if recent bark beetle outbreaks in Europe differ from those in Northern America with regard to their climate sensitivity, or if recent wild fires in Australia create similar patterns as those in Southern America. A globally consistent analysis would provide insights to these questions. Additionally, it would be possible to answer if recent disturbances were consistently driven by climate and how disturbance variability was modulated by local factors such as topography and human influence.

Satellite remote sensing in general is an appropriate tool to answer questions on a global scale. Opportunities for forest disturbance research specifically arise from openly available datasets on disturbances (Hansen et al., 2013) that offer high spatial resolution and are globally consistent to enable large-scale comparisons. Despite all advantages of global mapping of forests (Kuemmerle et al., 2013), causal relations and ecological background information cannot be detected from space. Therefore, ground truthing methods such as local expert questionnaires (White et al., 2005) are needed to provide additional information and foster a meaningful interpretation.

At the scale of forest landscapes, disturbances are able to create specific patterns in forest structure and composition which in turn are capable of affecting future disturbances in these landscapes. Resultant processes of disturbance such as vegetation feedbacks on future disturbances act on the one hand on extended spatial scales and on the other hand they also act on temporal scales ranging from decades to millennia. Simulation modelling is an appropriate tool to accommodate these challenges of extended spatial and temporal scale. Process-based simulation models can examine the complex interactions of multiple disturbance agents, disturbance legacies and feedbacks from forest vegetation. Furthermore, simulation modelling empowers the usage of dynamic reference trajectories (e.g. *undisturbed* forest development), which can be used to isolate and quantify the strength of an effect of interest (Dobor et al., 2018).

At the stand level, disturbances shape forest stands directly by altering the microclimate and creating disturbance legacies like deadwood. Although microclimatic effects are crucial for forest health and forest development, previous research has primarily focused on microclimatic differences between forested areas and open areas (Baker et al., 2014; Wright et al., 2010), as well as quantitative effects of canopy closure on microclimate (Davis et al., 2019; Hardwick et al., 2015). However, forest research lacks insights about how spatial patterns of small-scale disturbances impact microclimate, especially given that small-scale disturbances are on the rise

(Senf et al., 2018). Potential effects of deadwood on microclimate have received little attention too (Kovács et al., 2017), although effects are possible in terms of water storage in downed deadwood and shading by standing deadwood.

Appropriate tools for the research on forest stand level are commonly observational and experimental studies. It is important to keep in mind most observational studies only cover a short span of the life cycle of a forest. However, experimental studies provide valuable insights into the immediate changes of environmental conditions and reactions of trees thereon. Another advantage is that studies on stand level observe the same spatial and temporal scale at which microclimatic conditions affect tree physiology. Although field-based research and it's scientific presence has declined (Carmel et al., 2013; Ríos-Saldaña et al., 2018), it is nonetheless important to answer questions on a fine-scaled level and inform and enable higher-level methodologies such as simulation modelling and data synthesis research.

As mentioned above, every ecological research question on each spatial scale requires appropriate tools - there is no one method to resolve them all. However, it is important to build linkages between spatial scales and identify cross-scale interactions (McMahon & Diez, 2007) to better understand the interactions among forests, climate and disturbances. Accounting for scale in ecological analysis is essential to the fundamental understanding of patterns and processes (Chase & Leibold, 2002; McMahon & Diez, 2007; Menge & Olson, 1990). The importance of cross-cutting themes such as spatio-temporal interdependencies has gained general appreciation and academia attempts to integrate them comprehensively into ecological education (Klemow et al., 2019).

2. Objectives

The aim of my thesis was to consolidate fundamental knowledge about patterns and processes of forest disturbances on different spatio-temporal scales. On a global scale, I wanted to address what drives recent disturbances and how disturbances shape landscape patterns in temperate forests. On the landscape scale, I wanted to demonstrate how patterns of disturbances frame future disturbances. And on the stand scale, I wanted to illustrate how disturbance patterns configure forest floor conditions by altering the forest canopy. My thesis was partitioned into three different sections each focusing on a distinct spatial scale:

Specifically, I wanted to

1.) Quantify the variability of recent disturbances, provide an analysis if disturbances were consistently driven by climate, and determine if human influence modulates patterns of natural disturbances in temperate forests.

2.) Simulate bark beetle disturbances on landscape scale, evaluate their effects on forest structure and composition as well as analyze how disturbance-mediated forest dynamics determine future bark beetle activity.

3.) Contrast the microclimatic buffering capacity of forest canopies between years with different climatic conditions, quantify the effects of spatial disturbance patterns on available light and microclimate, and examine if deadwood presence and type affects the microclimate.

3. Material and methods

This thesis is composed of three publications which are thematically linked to each other, but rely upon distinct methodological approaches to accommodate the given scale (Figure 1). Paper I (Appendix A) was a study which integrates remote sensing and questionnaire data to unveil disturbance patterns and drivers. Paper II (Appendix B) was a simulation model application using processes of forest development to examine the effects of forest structure and composition on future disturbance risk. In Paper III (Appendix C), I used experimental treatments to detect effects of disturbance patterns and disturbance legacies on the microclimate.

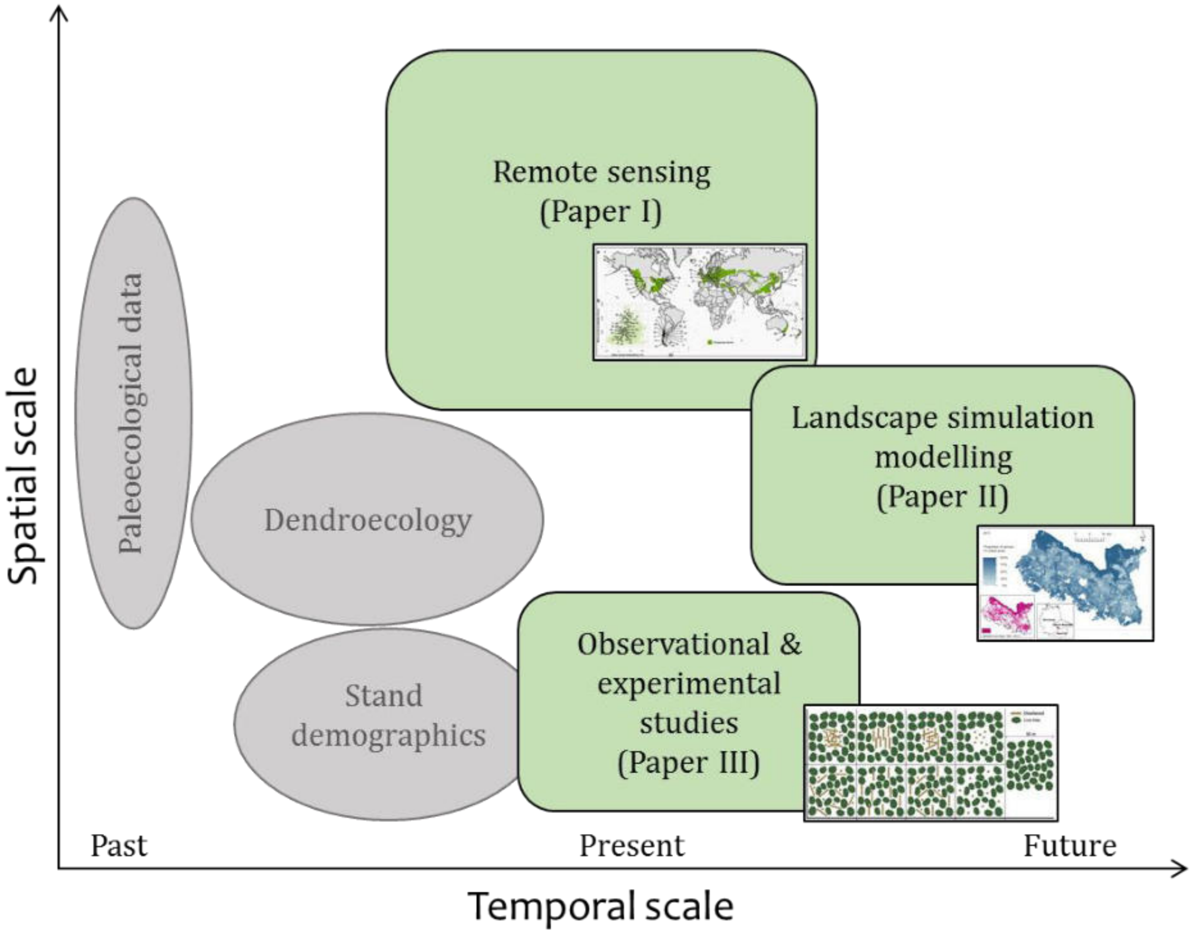

Figure 1: Conceptual diagram with typical methods for studying disturbances on different spatial and temporal scales. Green boxes indicate methods applied in this thesis with an illustrative figure from each publication.

3.1 Study landscapes

The first publication used a global network of temperate forest landscapes including the Bavarian Forest National Park (hereafter referred as BFNP). Publications II and III are entirely situated in the BFNP.

3.1.1 Global temperate forest network

I compiled a network of 50 study landscapes distributed throughout the temperate forest biome, based on the definitions by Olson et al. (Olson et al., 2001). The landscapes were selected if they were protected under IUCN category I or II (e.g. Wilderness Areas or National Park core zones). Studying protected areas allowed me to largely exclude anthropogenic disturbances and focus the main analyses on natural disturbances. Landscapes had to comprise at minimum of 2,000 ha contiguous forest cover and local experts had to provide ecological context information (regarding all present tree species, main disturbance agents, and tree species actually affected by disturbances) for each landscape. I analyzed in total 50 landscapes across 16 countries on five continents, compiling a forest area of 3,9 million ha (see Appendix A for details). The study landscapes covered a wide climatic gradient of the temperate forest biome, with mean annual temperatures ranging from −0.3°C to 14.8°C, and mean annual precipitation sums between 517 mm and 2,315 mm.

3.1.2 Bavarian Forest National Park

The Bavarian Forest National Park is a forested landscape in Southeastern Germany, situated within the Bohemian Forest, the largest low-range mountain forest in Central Europe. The topography is moderate with an elevation range from 655 m to 1,420 m above sea level. Mean annual temperature ranges from 3.5°C to 7.0°C and annual precipitation ranges from 1,000 mm to 1,900 mm. The dominant tree species include Norway spruce (*Picea abies* L.) at mid to high elevations and silver fir (*Abies alba* Mill.) as well as European beech (*Fagus sylvatica* L.) mixed with spruce at lower elevations. Natural tree species composition was heavily affected by humans at least since 500 BC, which has reduced the proportion of silver fir (van der Knaap et al., 2020). The cultivation of spruce was expanded in the 16th century due to an increasing demand of wood for manufacturing, and in the 19th century due to the emergence of commercial forestry. Founded in 1970, BFNP is Germany's oldest national park and the landscape with 24,000 ha extent was protected in two phases, with an extension of the initial protected area in 1997. The BFNP saw the largest unsuppressed bark beetle outbreak in Central Europe in recent history, characterized by two distinct outbreak waves (1996 – 2000 and 2005 – 2010).

3.2 Methods

3.2.1 Global scale remote sensing study

For the network of protected landscapes, I consulted local experts for all 50 landscapes by means of questionnaire concerning ecological context information on disturbance agents and dominant tree species. Furthermore, I used forest cover maps and annual forest loss maps from 2001 to 2014 at a 30 m resolution (originating from global LANDSAT data) from the *Global*

Forest Change data set (Hansen et al., 2013). I calculated two landscape-level metrics and two patch-level metrics to describe disturbance patterns within the landscapes. For the landscape level I used percent of landscape disturbed 2001 – 2014, and edge density of all disturbed patches within the forested area of a landscape. At the patch level I used area-weighted mean patch size, and area-weighted mean perimeter-area-ratio. To identify similarities in disturbance patterns I used Gaussian finite mixture models as an approach for unsupervised clustering for landscapes featuring similar disturbance patterns. In order to select the optimal number of cluster centers I used the Bayesian Information Criterion (BIC). The resulting clusters were then characterized with regard to their main disturbance agents and tree genera, data which originated from the questionnaire. Additionally, I included two complementary plant traits, i.e. "maximum potential tree height" and "mean wood density" corresponding to disturbance susceptibility and disturbance resistance, which were weighted based on tree species shares. For each cluster, I compiled relative occurrences of disturbance agents and tree species and weighted trait means. Differences in traits among clusters were tested using two-tailed pairwise approximate Kruskal–Wallis tests.

In order to contrast natural disturbances with coupled human and natural disturbances, I compared both types of disturbance in close proximity. Specifically, I contrasted disturbance patterns in our study landscapes (e.g. protected areas) and in the adjacent unprotected surroundings. I compared the patch-level metrics between inside and outside the boundaries of protected landscapes. Differences were then tested among clusters using two-tailed pairwise approximate Kruskal–Wallis tests.

For the purpose of identifying the drivers of spatial and temporal disturbance dynamics I tested the influence of topographic complexity and annual climatic variability using generalized linear mixed models (GLMMs). As response variable I used binary disturbance maps indicating whether a pixel was disturbed in the respective year or not. The GLMM was specified using a binomial error distribution and a logit link function. Topographic complexity was measured using the topographic ruggedness index (TRI), obtained from a digital elevation model at 30 m spatial resolution. TRI was calculated using a window size of 7 x 7 Pixels and TRI values were subsequently scaled to zero mean and a standard deviation of one. Thus, positive TRI values indicate a higher than average topographic complexity and vice versa. For climate variability I obtained time series of mean annual temperature and precipitation sums. Climatic data was also scaled to zero mean and a standard variation of one to obtain climatic anomalies with positive values indicating colder/ dryer than average climate and vice versa. I tested variable time lags between climatic anomalies and disturbances signals, selecting the time lag best supported by the data using Akaike's Information Criterion (AIC). Furthermore, I allowed for an interaction term between precipitation and temperature to account for potential modulating effects between these two variables. In order to select the best model I compared three candidate models for each cluster: a full model containing spatial (TRI) and temporal (climatic anomalies) predictors, a model containing spatial (TRI) predictors only and a null model containing only an intercept while maintaining the random effects structure of the GLMMs. The subsequent model comparison was done using the AIC and log- likelihood tests.

3.2.2 Landscape scale modelling study

On the landscape scale I used the simulation model iLand (Seidl et al., 2012) to project the forest development at BFNP. Furthermore, I quantified the feedbacks between structural and compositional diversity and climate-mediated bark beetle dynamics. iLand is spatially explicit, process-based and dynamically simulates processes on a hierarchical multiscale structure. In this multiscale structure processes were simulated on the scale of 1.) individual trees (e.g. resource competition, growth and mortality), 2.) stand level (e.g. water and carbon cycles), and 3.) landscape level (e.g. seed dispersal and disturbances). The ability to dynamical simulate disturbances was one of the main advantages of iLand. Windthrows and bark beetle outbreaks were simulated explicitly, as they often interact and are the two most important disturbance agents in BFNP. Bark beetle dynamics in iLand account for beetle development, phenology and model beetle dispersal spatially explicit. iLand accounted also for the processes of host colonization, tree defense and temperature dependent winter mortality (Seidl & Rammer, 2017). For this study it was crucial that iLand is capable of realistic outbreak simulation and that incorporated linkages between spatial scales (e.g. landscape wide host susceptibility with local barks beetle dispersal) yield reasonable outbreak patterns. Therefore, I extensively tested spatial and temporal patterns of simulated bark beetle infestations against observational data from BFNP (Kautz et al., 2011; see Appendix B). A more detailed description of iLand can be found in Seidl et al., (2012) and Thom et al. (2017). The model code and executable as well as an extensive online documentation are available at http://iland-model.org.

Landscape setup and initial characteristics

Simulation runs in BFNP were initiated in the year 2011, after the most recent bark beetle outbreak waves from 1996 to 2010. The landscape model was initialized with the latest available plot-level forest inventory data from 1992, and updated with aerial surveys of observed bark beetle disturbances (Kautz et al., 2011). Data on soils and climate were available at a 100 m × 100 m grid.

I used four different climate scenarios to run the simulations. Historical climate data from 1980 to 2015 was used as a reference period for constructing a baseline climate scenario by randomly drawing years with replacement. In addition, I simulated three different climate change scenarios, representing different combinations of representative concentration pathways (RCP 4.5 and 8.5) and climate models (ICHEC-EC-EARTH and MOHC-HadGEM2-ES). In the following text, I refer to the climate scenarios as baseline climate scenario (BC), moderate climate change scenario (MC, RCP 4.5 ICHEC-EC-EARTH), hot climate change scenario (HC, RCP 8.5, ICHEC-EC-EARTH) and hot and wet climate change scenario (HWC, RCP 8.5, MOHC-HadGEM2-ES). Climate change time series were extended beyond 2099 by sampling with replacement from the years 2070 – 2099. All climate data were statistically downscaled to the study region at 100 m horizontal resolution. The occurrence of storm events was based on historically observed wind data, assuming no changes in future peak wind speeds and return intervals. To isolate the effect of disturbances on forest structure and composition, I simulated two different disturbance scenarios in each climate scenario. I used an *undisturbed* control scenario for which disturbances were omitted throughout the entire simulation period (referred hereafter as *undisturbed*) and a scenario in which disturbances (windthrow and bark beetle outbreaks) and their impacts on vegetation were dynamically simulated in iLand (referred hereafter as *disturbed*). All simulations were replicated 20 times to account for stochasticity.

Simulation design

The main aim of the simulation study was to investigate the long-term consequences of disturbances on forest development over a period of 600 years. Therefore, I hypothesized that disturbances result in increases in diversity and in order to test these assumptions I compared *undisturbed* simulation runs to *disturbed* runs. To quantify impacts on diversity I used two spatial scales (stand [100 m grid cells] and landscape) and two domains of diversity (forest structure and forest composition). In total, I derived eight indicators of diversity (see Appendix B Table 1) from the simulated data at 50-year time steps. To disentangle the effects of climate change, disturbances and the combined effect of climate change and disturbances, I compared diversity indicators among contrasting trajectories. The reference simulation was without climate change and without disturbances (i.e. BC and *undisturbed*). Contrast trajectories were simulations with climate change only (i.e. HWC and *undisturbed*), with disturbances only (i.e. BC and *disturbed*) and simulations with combined effects of climate change and disturbances (i.e. HWC and *disturbed*). I then used the simulation outputs to quantify the effects of disturbance-mediated changes in forest structure and composition on the resurgence of bark beetle disturbances.

Random forests (Breiman, 2001) were used on the simulation outcomes from the *disturbed* simulation series, using the amount of growing stock disturbed by bark beetles as response variable and the indicators of structural and compositional diversity as well as climate data as predictors. I then applied the trained random forest model to predict the amount of growing stock affected by bark beetles for forest structure and composition indicators of *undisturbed* simulation series. By using the same random forest model for *disturbed* and *undisturbed* trajectories I was able to quantify the potential of self-regulating feedbacks inherent in the disturbance regime.

3.2.3 Stand scale experimental study

For the field study on stand scale I used data from five study sites of a manipulated forest canopy and deadwood experiment. The study sides were set up using a randomized factorial block design. Each study side consisted of eight treated and one untreated study plot (i.e., 5 study sites × (8 treated plots + 1 untreated plot) = 45 plots in total). Plots were randomly distributed within each site, and consisted of squares of 50 m × 50 m. In October 2015, gaps were artificially created to mimic disturbances of individual trees and groups. For all treated plots, disturbance severity was held constant at approximately 25% of basal area removed. Trees were cut in two different spatial patterns, either in spatially *aggregated* groups (hereafter called *aggregated*) of 25 m x 25 m around the plot center or as individual trees *distributed* randomly (hereafter called *distributed*) across the plot. Each group of spatial disturbance pattern (i.e. *aggregated* and *distributed*) contained four different deadwood types: 1.) downed, 2.) standing, 3.) both downed and standing deadwood, as well as 4.) removed deadwood. Standing deadwood was created by cutting the stem below the first strong branch of the crown, which was on average at a height of 8.3 m.

The microclimate was here defined by temperature and vapor-pressure deficit. To quantify the effects of microclimatic changes I used data on temperature and relative humidity during summer (June - August) on an hourly basis from 2016 to 2019. I expected the modulation of the light regime to be the main process through which canopy openings influence forest microclimate. Light was measured as the total site factor (TSF) (i.e. total solar radiation including direct and diffuse light, relative to open conditions) at the same height as data loggers (1.3 m above surface) at four locations using hemispherical photography (Solariscope SOL 300B, Ing.-Büro Behling (2015)) in the first summer after implementing the treatments. Accounting for the theoretical path of the sun (depending on geographical orientation and latitude) the device obtained an accurate sub-canopy light estimate (Canham et al., 1990). Light measurements were taken at the four corners of a 10 m × 10 m square concentrated around the plot center and summarized to plot averages. Vapor-pressure deficit (VPD) was derived from temperature and relative humidity. VPD is the difference between saturated and actual vapor pressure and is representing the drying capacity of air. I used daily observations and extracted extreme values (maxima), and the variation (standard deviation, SD) of temperature and VPD. I assessed the dependencies among these microclimate parameters using Pearson's correlation coefficients. In particular, I was interested in the association between extremes and variations in the microclimate as they could cause compounding effects on plants with higher maxima and higher variation indicating particularly challenging conditions for the growth and survival of seedlings and saplings.

Treated and untreated plots were compared to derive disturbance-induced changes in the buffering capacity of temperature and VDP maxima, i.e. the differences between open and closed canopies. Interannual variation between plots was used to contrast between warm and dry years to cold and wet years. I tested annual differences in the buffering capacity of microclimate parameters for statistical significance using Tukey's Honest Significant Difference ($\alpha = 0.05$).

Statistical analyses

The effects of spatial disturbance patterns and deadwood type on light conditions were examined using a Bayesian analysis framework. By incorporating Markov Chain Monte Carlo sampling, I was able to assess my multi-hierarchical data without being restricted by the model's degrees of freedom (Rossi et al., 2006). After testing model performance, a multi-hierarchical Bayesian model with site as random effect and spatial disturbance pattern as the only fixed effect remained in my analysis. Surface light was log-transformed prior to the analysis to normalize the data distribution. The effects of light availability and deadwood type were tested using multi-hierarchical Bayesian models with both variables as fixed effects. Random effects for plot site and year allowed for variable intercepts and slopes of the response variables. Both VPD variables were square-root transformed to normalize their data distributions. As microclimate models were based on time-series data, I modelled the first-order autoregressive effects of residuals. All Bayesian models were evaluated with posterior predictive checks. The leave-one-out (LOO) adjusted R2 was calculated to avoid an overestimation of the variance explained by adding explanatory variables to the model, and residuals were tested for normality. Additionally, residuals of the microclimate parameter models were tested for temporal autocorrelation using generalized Durbin-Watson statistics.

4. Results

4.1 Global scale results

4.1.1 Global patterns of recent natural disturbances.

Disturbance dynamics varied strongly across the temperate forest biome 2001 - 2014. Unsupervised cluster analysis identified three distinct clusters (referred hereafter as *low*, *moderate* and *high* disturbance activity clusters). These clusters were composed of landscapes with similar characteristics in regard to the size and shape of disturbance patches (both patch-level metrics), the percentage of a landscape disturbed, and the average amount of edges (both landscape-level metrics). Landscapes in the *low* disturbance activity cluster were driven by a wide range of disturbance agents. In contrast, the cluster of *moderate* disturbance activity was dominated by bark beetle outbreaks and wildfires, while *high* disturbance activity was strongly driven by wildfire, often associated with bark beetle outbreaks and droughts. Landscapes experiencing *low* disturbance activity were dominantly composed of broadleaved tree species, while the *high* disturbance activity cluster in the northern hemisphere was dominantly composed of coniferous tree species. The *moderate* disturbance activity cluster was characterized by both broadleaved and coniferous tree species. Landscapes in the *high* disturbance clusters were not dominated a single tree species. On the contrary, landscapes with *high* disturbance activity showed less dominance compared to those landscapes in the *moderate* disturbance cluster.

4.1.2 Global disturbance differences inside and outside protected areas.

Disturbance patches inside protected areas were smaller and more complex than disturbance patches in surrounding areas affected by both human and natural disturbances in the *low* and *moderate* disturbance activity clusters. However, for landscapes in the *high* disturbance activity cluster, the distribution of patch sizes and perimeter-area-ratios did not differ significantly between protected areas and their surroundings. This means that the disturbances in regions of *high* disturbance activity were quite similar in protected and unprotected areas.

4.1.3 Global drivers of spatio-temporal disturbance dynamics

Climate variability among years was an important driver of disturbance dynamics in all disturbance activity clusters. The model comparison showed that the full model (with both climate variability and topographic complexity) was most strongly supported by the data. However, there was substantial variation in the direction and strength of topographic and climatic effects as well as in the lag time of climatic effects. Time lags for *low* and *moderate* disturbance activity were 2 to 3 years. In contrast, landscapes of *high* disturbance activity showed strongest effects using no lag time, meaning that climate had an immediate impact on disturbance activity. The strongest effects of climate were observed in the *high* disturbance activity cluster, where disturbance probability was high in years with high temperatures. This effect was strongly modulated by below average precipitation, indicating that warmer and drier years profoundly drove disturbance probability in high disturbance clusters. Topographic complexity also affected disturbance probability significantly, but the strongest effect was traceable in the *low* disturbance activity cluster. In those landscapes, were wind disturbances were strongly represented, more rugged terrain was associated with higher disturbance probability.

4.2 Landscape scale results

4.2.1 Future bark beetle dynamics in the Bavarian Forest landscape

Future bark beetle outbreaks in BFNP were strongly amplified by climate change. The growing stock affected by bark beetles increased by more than +200% (scenarios HWC and HC) compared to baseline climate. General sequences of disturbed growing stock were similar among climate scenarios. Most of the disturbed growing stock occurred within the first 200 years of the simulations, while bark beetle outbreaks subsided in the last centuries. Outbreak patterns differed according to the respective climate scenario with high and early peaks occurring in HWC and HC scenarios, while MC and BC scenarios showed lower and more prolonged peaks of disturbed growing stock. Essentially, all but one of the 80 replicate simulations (in a HWC setting) were well below the average recent disturbance observations of 1990 - 2010.

4.2.2 Effects of bark beetle disturbances on landscape diversity

Bark beetle outbreaks substantially increased compositional diversity within BFNP. Spruce dominance decreased under all climate scenarios, leading to an overall increase in species heterogeneity. Spruce shares were reduced from initially 60.5% down to 1.7% for the most severe climate scenario (HWC). The driver for spruce reduction was the interaction of climate change and disturbances, however spruce was replaced by beech and fir in the landscape. The effect of bark beetle outbreaks on structural diversity was less clear. While within-stand diversity (e.g. alpha diversity) decreased over the simulation period, among-stand diversity (e.g. beta diversity) increased over time, consistent for both height and dbh diversity. Similar to compositional diversity, the interaction of climate change and disturbances also drove effects on structural diversity.

4.2.3 Disturbance-mediated forest landscape development affects future disturbances

Bark beetle outbreaks showed strong signs of dampening feedbacks towards subsequent bark beetle disturbances. By using a random forest model, I was able to disentangle effects of forest composition, forest structure and climate, while explaining 96.0% of the variation within the simulation data. Disturbance effects on forest structure and composition accounted for up to 67.0% less affected growing stock by bark beetles compared to *undisturbed* simulations (HWC scenario). Structural effects had a similar strong damping feedback as compositional effects. The overall strength of dampening feedbacks increased with disturbance activity, resulting in considerably stronger feedbacks in HWC and HC scenarios compared to MC and BC scenarios. Although dampening feedbacks from disturbance-mediated changes were strong with these ones, they failed to fully compensate climate-related increases in disturbed growing stock.

4.3 Stand scale results

4.3.1 Climatic extremes, variation and microclimatic buffering

On the stand scale, extreme values in temperature and vapor-pressure deficit were positively associated with high variation in these values, meaning that days with high variation were also the hottest and driest days. The closed forest canopy was able to buffer climatic effects compared the disturbed forest canopies, and the strength of the buffering effect was highest in warmer and drier years. Closed canopy conditions accounted for 20.0% of temperature and 15.1% of vapor-pressure deficit differences in buffering capacity between cold and moist 2016 and warm and dry 2019.

4.3.2 Disturbance impacts on light regime and microclimate

Experimental disturbances drastically altered the amount of received sunlight above the forest floor. Undisturbed control plots showed on average 3.0% available light, whereas *distributed* and *aggregated* experimental plots have on average 9.8% (+ 226.7%) and 14.6% (+386.7%) of light relative to open conditions. Although disturbance treatments were standardized in terms of affected growing stock, light conditions varied considerably within each disturbance pattern, presumably due to diverse distribution, volume and numbers of trees within each plot. Spatial disturbance patterns alone explained 56.7% of the variation in light availability.

Higher light availability was consistently associated with warmer and drier microclimate. An increase of 10% available light on the forest floor increased maximum temperature by 0.42° C and maximum vapor-pressure deficit by 0.04 kPa.

4.3.3 Minor deadwood effects on microclimate

Effects of different types of deadwood on microclimate were in general weak and vague. Across all microclimatic parameters, there was no significant effect of the type of retained deadwood relative to the complete removal of deadwood. The data showed only a slight indication that retaining both downed and standing deadwood after disturbance might be more beneficial for the microclimate than all other treatments.

5. Discussion

5.1 Global patterns and drivers of forest disturbances

On the global level, disturbance activities in temperate forests were manifold. Severe and large disturbances were a major focus of research and lot of insights originated from these areas. However, my research showed that a large area of forests was subject to *low* and *moderate* disturbances. This finding emphasizes the need for a consistent and quantitative analysis across larger systems to avoid bias. The key to success was the usage of globally consistent remote sensing data, put into perspective with in-depth expert knowledge. This combination enabled an enormous spatial coverage while using the same methodology but yet integrating ecological knowledge that is not detectable from space. The variability in temperate biome was better explained by the main disturbance agents rather than geographic proximity of landscapes. For the northern hemisphere, I could also corroborated that landscapes with conifers tend to be associated with *high* disturbance activity (Loehle, 2000). However, I could not confirm that those landscapes with *high* disturbance activity are also dominated by fewer tree species as suggested by other studies (Perry, 2008). Regarding the differences between protected and unprotected areas, I found my expectations partially fulfilled as protected areas exhibit smaller and more complex disturbance patches in absence of human impacts. This finding alluded to pronounced influence of forest management (e.g. clear cutting), however other influences such as ecological legacies from former management or disturbance (Pan et al., 2011; Schurman et al., 2018) could not be excluded. Interestingly, this effect was overridden in landscapes of *high* disturbance activity, where protected and unprotected areas were equally large and complex. These landscapes, where disturbances strongly determined the shape of forest landscapes, were particular sensitive to climate. Thus, I found globally consistent evidence that landscapes of *high* disturbance activity were strongly driven by the joint occurrence of warmer and drier climate conditions. These global findings were in alignment with local studies (Allen et al., 2010; Anderegg et al., 2015; Collins & Stephens, 2010; Littell et al., 2009; Raffa et al., 2008; Westerling, 2016), particularly considering that the landscapes of *high* disturbance activity were dominated by disturbance agents whose mechanisms are directly linked to warm and dry climate conditions (e.g. wildfires, bark beetle outbreaks, and drought). In the face of a warming climate, my results indicated that the temperate forest biome is likely to experience elevated levels of large-scale disturbances in the future. Furthermore, as *high* disturbance activity was often associated with increased shares of conifers, managed forests with their higher shares of conifers and homogenous age class distribution might be at an elevated risk.

5.2 Feedbacks of bark beetle disturbances on future outbreaks on the landscape scale

On the landscape level, I was able to corroborate that bark beetle outbreaks were massively amplified by climate change. This finding in in line with numerous studies focusing on bark beetle-climate interactions (Bentz et al., 2010; DeRose et al., 2013; Dobor et al., 2020; Seidl et al., 2008, 2011), underlining that bark beetle disturbances were particular sensitive to warming temperatures and less precipitation. Despite the climate sensitivity, my results showed that disturbances in BFNP are not likely to reach similar levels of affected growing stock in future compared to those levels of recent outbreaks. Central tendencies of the simulations were well below recent levels of disturbed growing stock even under the most severe climatic scenarios (HWC and HC). This compensating effect of forest structure and composition was well documented in previous studies (DeRose et al., 2013; Hart et al., 2015; Temperli et al., 2015), partially even exceeding the amplifying effect of climate change.

Increased levels of structural and compositional diversity were results of the bark beetle outbreaks themselves. These finding are in line with several studies relating various disturbance agents to change in forest structure and composition (Janda et al., 2017; Kayes & Tinker, 2012; Panayotov et al., 2011). Bark beetle outbreaks had negative impacts on future bark beetle disturbances, by unfavorably changing the forest structure and composition, which they depend on. Evidence for such self-regulating feedbacks are well documented in fire-driven ecosystems, where burning depletes fuel, which hampers subsequent burning (Kulakowski et al., 2017). Similar mechanisms applied to some extent for host-specific disturbances, where disturbance agents deplete suitable hosts, hampering subsequent occurrences of the same agent (Hart et al., 2015; Temperli et al., 2015). However, my findings emphasized that structural diversity for itself exerts an important dampening feedback in host specific biotic disturbances. In fact, the effect size of increased structural diversity (e.g. beta diversity) was comparable to that of depleted host trees, indicating that landscapes with heterogeneous diameter and heights distributions among stands are important to mitigate large-scale bark beetle outbreaks.

My results suggested that disturbance-mediated forest development was less susceptible to large-scale bark beetle outbreaks. Therefore, preventing measures aiming to suppress all disturbance activities, such as trapping and timely removal of infested trees, might increase future risk. Previous studies documented this unintended risk increasing effect of preventing measures for fire and wind disturbances (Dobor et al., 2020; Stephens et al., 2014).

5.3 Effects of disturbance pattern and disturbance legacies on the microclimate

On the stand scale, I found closed canopies to be beneficial for buffering microclimatic extremes, especially in warmer and drier years. Increases in temperature and vapor-pressure deficits in warmer and drier years were partially mitigated by closed canopies. Given the changes within the global climate system, the mitigating potential might serve as a stand-scale lifebelt for forest ecosystems if canopies remain closed (Davis et al., 2019; De Frenne et al., 2013). However, climate change might also be able to diminish soil water storage which limits evaporative cooling and plant available water. The latter might directly lead to drought-induced mortality (Greenwood et al., 2017) or increased insect disturbances (Anderegg et al., 2015; Krams et al., 2012) which in turn opens up forest canopies and reduce their microclimatic buffering capacity. Nevertheless, it is important to note that I studied spatially small disturbances (0,25ha) with low severity (25% basal area removal). Forest ecosystems experiencing larger disturbances with higher severity showed temperature mitigating effects of closed canopies compared to disturbed canopies three times greater than in my example (e.g. 62% vs. 20%, Ewers & Banks-Leite (2013)).

Disturbances increased the transmission of light through the forest canopy prompting the microclimate towards a warmer and drier state. Even if disturbances were small in size and low in severity, they caused considerable changes within the microclimate. This is important because the disturbed area in Central Europe has at least doubled since the 1980s, mainly driven by low severity disturbances (Senf & Seidl, 2018). Disturbance activity is expected to increase further (Seidl et al., 2017), exposing the forest floor more frequently to the full force of climatic extremes without the buffering capacity of closed forest canopies. An average increase of 0.42°C temperature per 10% added light availability found here is similar to findings from other forest ecosystems (Hardwick et al., 2015; Schmidt et al., 2017). Additionally, other measures of disturbance impact and light availability such as forest gap diameters bolstered the claim that disturbances intensify summer temperatures (Ritter et al., 2005).

Spatial patterns of disturbances were strongly modulating the microclimate. Given similar severities (25% basal area removal), *aggregated* disturbances caused increased available light compared to spatially *distributed* disturbances. However, the impact of disturbances arise from the interaction of the elements size, severity and frequency disturbance (Turner, 2010). If disturbances manifest in larger extent and under higher severity then studied here, impacts on the microclimate will likely be much more profound (Baker et al., 2014; Davis et al., 2019).

The type of remaining deadwood did not show any important influence, neither on available light nor the microclimate. Moreover, my results did not support the hypothesis that standing deadwood buffer microclimatic extremes. In perspective, this experiment created deadwood by removing the entire tree crown. Increased shading might arise from dead but remaining twigs and branches if crowns were present, possibly limiting the light penetration. However, even if a dead crown effect potentially exists, branches and twigs remain attached to the tree only for a limited amount of time.

5.4 Need for comprehensive knowledge and protected areas

Climate-induced changes are likely to intensify forest disturbance regimes and therefore are able to dynamically diverge from recent historical disturbance conditions. In order to understand and address problems that arise from these changes we still need to gather insights about these complex systems. The field of regime shifts in terrestrial ecosystems is crucial for future forest dynamics but there is need of further research (Raffa et al., 2008). In order to enable advances we need to enhance our comprehensive knowledge base on various scales with linkages among scales (Peters et al., 2004; Raffa et al., 2008) and in different domains of research (e.g. fundamental research and applied research). An improved knowledge base would allow tracing changes, unraveling drivers, and identifying dynamic feedbacks. We still need more data on recent characteristics of disturbance regimes in order to detect changes now and in future. Also, we need do know that feedbacks and interactions might occur when dealing with complex and interrelated systems. Finally, we need to know how the microclimate within and below tree canopies is modulated by disturbances.

The studies I conducted for my thesis depended heavily on the existence of protected areas, especially the Bavarian Forest National Park. Protected areas in general fulfil an immense spectrum of tasks to ever-increasing societal expectations (Watson et al., 2014), ranging from the preservation of iconic landscapes and endangered wildlife up to bolstering economies through tourism revenues. For science in general, protected areas provide unimpeded reference conditions as a comparison to managed areas, feature ecosystem properties that are underrepresented or missing in managed areas and serve as nature “laboratories” (Nagel et al., 2013). For this thesis in particular, protected areas provided a reference of relative unaffected patterns and processes of forest disturbances. The bark beetle outbreak in BFNP from 1990 to 2010 was the largest unsuppressed bark beetle outbreak in Central Europe. Insights from this well documented outbreak helped the scientific community in Europe to better understand the dynamics of outbreaks (Kautz et al., 2018). This is of special importance in the light of unprecedented large outbreaks in managed forest from 2018 to at least 2021 in Germany, Czechia and Austria (Senf & Seidl, 2021). However, the transfer of knowledge from science and willingness of forest management to implement these insights are still in need of improvement.

5.5 Management implications

Forests across the globe fulfil important ecosystem services to meet the demands of human livelihood. In response to societal and environmental changes (e.g. human population growth, demand for non-provisioning forest services, climate change, anthropogenic nitrogen inputs) the demand for forest services is on the rise while the area for sustainable forest management is dwindling (Hansen et al., 2013). The aim of forest management is the constant provision of these services even under aggravated conditions. Forest disturbances are expected to increase with climate change (Seidl et al., 2017), disturbances generally exert a negative impact on forest ecosystem services (Thom & Seidl, 2016) and therefore must be taken explicitly into consideration by forest managers. However, my research confirms that merely suppressing disturbances might be counterproductive. Future risks of large-scale disturbances could be enhanced by a forest structure and composition (e.g. homogenous, even-aged stands of spruce) that is highly conductive for bark beetle outbreaks and above the possibilities of containment by management. However, the suppressing management principle is still an established sentiment in Central Europe's forest management. To overcome this sentiment, forest management should pursue a more nuanced way to foster processes of adaption of forests towards disturbances including risk mitigation and resilience of forests (Albrich et al., 2021).

Specifically, my research confirms the specific vulnerability of homogenous, even-aged conifer stands linked over large areas, often preferred by forest management (Lindenmayer et al., 2017). These "over-connected systems" (Peters et al., 2004) exhibit the highest probability of disturbance dynamics, whose spatial spread might increase in a nonlinear way. Spatial and temporal heterogeneity is an effective way to reduce the vulnerability of forest ecosystems to contagious processes such as bark beetle outbreaks (Turner et al., 1989). Potent risk dampening feedbacks such as the disturbance-mediated increases in diversity are immanent in forest ecosystems. Furthermore, the risk of disturbances within landscapes and the respective efficiency of management measures is highly uneven (Seidl et al., 2018). Countering measures to disturbance risk should utilize the local forest heterogeneity and amplify its mitigating potential by optimizing tree species choice, location, shape and timing of silvicultural interventions (Seidl et al., 2018). In general, forest management should support and possibly mimic processes of disturbance (North & Keeton, 2008) in order to foster the adaptation of forest ecosystems to changing forest disturbance regimes.

6. Conclusion

With my thesis I was able to contribute to the fundamental knowledge how disturbance patterns and processes affect the disturbance regime. I was able to attribute the variability of global disturbance patterns, highlighted dampening vegetation feedbacks on future disturbances on landscape-level, and showed the microclimatic implications of disturbed forest canopies at stand level. However, there is much more to learn about the disturbance system. On the global level, further studies should incorporate more biomes of Earth's biosphere, expand the study period, and include low severity disturbances as well as understorey tree mortality. Also, the effects of human activities and climatic extremes on disturbances should be invested further to increase our understanding of these important modulating factors. Research at the landscape level should aim to unravel existing dampening feedbacks within the forest ecosystem and inform forest management how to use these processes to adapt forest landscapes to changing disturbances regimes. At the stand level, more emphasis should be placed on effects of disturbance size and severity on the microclimate as they could be multiplicative and non-linear. Forest ecosystems face changes and unprecedented challenges in the future. Forest science and forest management must answer and adapt to those challenges ahead to guarantee that forest ecosystems, their services, and human livelihoods can be sustained in future.

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9. Appendix

A. Patterns and drivers of recent disturbances across the temperate forest biome

B. Do bark beetle outbreaks amplify or dampen future bark beetle disturbances in Central Europe?

C. Effects of disturbance patterns and deadwood on the microclimate in European beech forests

Appendix A

Patterns and drivers of recent disturbances across the temperate forest biome

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Patterns and drivers of recent disturbances across the temperate forest biome

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Increasing evidence indicates that forest disturbances are changing in response to global change, yet local variability in disturbance remains high. We quantified this considerable variability and analyzed whether recent disturbance episodes around the globe were consistently driven by climate, and if human influence modulates patterns of forest disturbance. We combined remote sensing data on recent (2001–2014) disturbances with in-depth local information for 50 protected landscapes and their surroundings across the temperate biome. Disturbance patterns are highly variable, and shaped by variation in disturbance agents and traits of prevailing tree species. However, high disturbance activity is consistently linked to warmer and drier than average conditions across the globe. Disturbances in protected areas are smaller and more complex in shape compared to their surroundings affected by human land use. This signal disappears in areas with high recent natural disturbance activity, underlining the potential of climate-mediated disturbance to transform forest landscapes.

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Natural disturbances are an essential component of forest ecosystems[1]. Yet, forest disturbance regimes are changing in response to global climate change[2]. Hotter and prolonged droughts[3], exceptional bark beetle outbreaks[4], and megafires[5] have been increasingly reported in recent years, and are impacting forest ecosystems across all forested continents[2]. Changes in disturbance dynamics can have substantial impacts on ecosystem services provided by forests, e.g., climate regulation[6,7], provisioning of drinking water[8,9], and protection from natural hazards[10], as well as affect conservation of biological diversity[11]. Quantifying disturbance patterns (i.e., the size, shape, and prevalence of disturbances in forest landscapes) and understanding their drivers is thus a key challenge for ecological research.

While the potential drivers of the ongoing disturbance change are global, the responses to these drivers vary considerably at the local scale. Insights from well-studied systems such as Yellowstone National Park in North America[1], the Bohemian Forest ecosystem in Europe[12], and the O'Shannassy water catchment in Australia[13] have provided important insights into the complex interactions between climate variability, disturbances, and forest development. While an in-depth understanding of disturbance dynamics exists for a growing number of landscapes (i.e., contiguous land areas of roughly between 10^3 and 10^6 ha) around the globe, their responses to global drivers have not consistently been compared to date. Questions such as whether recent bark beetle outbreaks in North America differ from those in Europe with regard to their climate sensitivity, or whether recent fires in Australia created similar patterns as those in the Americas remain largely unexplored. Comparing the variation in disturbance patterns and their relationship to climate variability among landscapes at subcontinental to global scales[14,15] has the potential to elucidate whether recent disturbance episodes were consistently driven by climate across continents, or whether climate sensitivities differ between systems. Furthermore, such a comparison can shed light on how regional- to continental-scale drivers such as climate variability interact with local factors such as the topographic template of a landscape[16] and the influence of human land use[17]. A better understanding of global disturbance patterns and their multi-scale drivers is also crucial for improving the representation of disturbances in global vegetation models[18,19], and can have important implications for policy decision making, e.g., in the context of climate change mitigation[20,21].

New opportunities for global forest disturbance research arise from recent advances in remote sensing. Increasingly available remotely sensed datasets on forest disturbance[22] offer high spatial resolution and are globally consistent, enabling large-scale comparative efforts. However, while the global mapping of forest disturbances is now feasible[23,24], attributing disturbance agents from remote sensing data and distinguishing between natural and anthropogenic disturbances remains challenging[25]. Furthermore, ecological context information such as the prevailing tree species composition cannot usually be gleaned from space, underlining the importance of terrestrial information and local ecosystem understanding for a meaningful interpretation of remotely sensed disturbance information. Integrating remote sensing analyses with in-depth knowledge on selected ecosystems across the globe can provide new insights by combining the consistent synoptic view of satellite analysis with the expertise and insights gained from decades of local forest disturbance research.

Our objective was to analyze patterns and drivers of recent disturbances across temperate forests at the global scale. We compiled a global network of 50 protected forest landscapes each with > 2000 ha contiguous forest area (Fig. 1) for which in-depth local systems knowledge exists. We jointly analyzed severe canopy disturbances (i.e., complete mortality of all trees taller 5 m within a 30 m grid cell) in these landscapes using Landsat-derived disturbance maps for 2001–2014[24]. Focusing our network of landscapes on protected areas and their surroundings allowed us to isolate patterns of natural disturbances (inside protected areas) from those of areas where natural and human disturbances

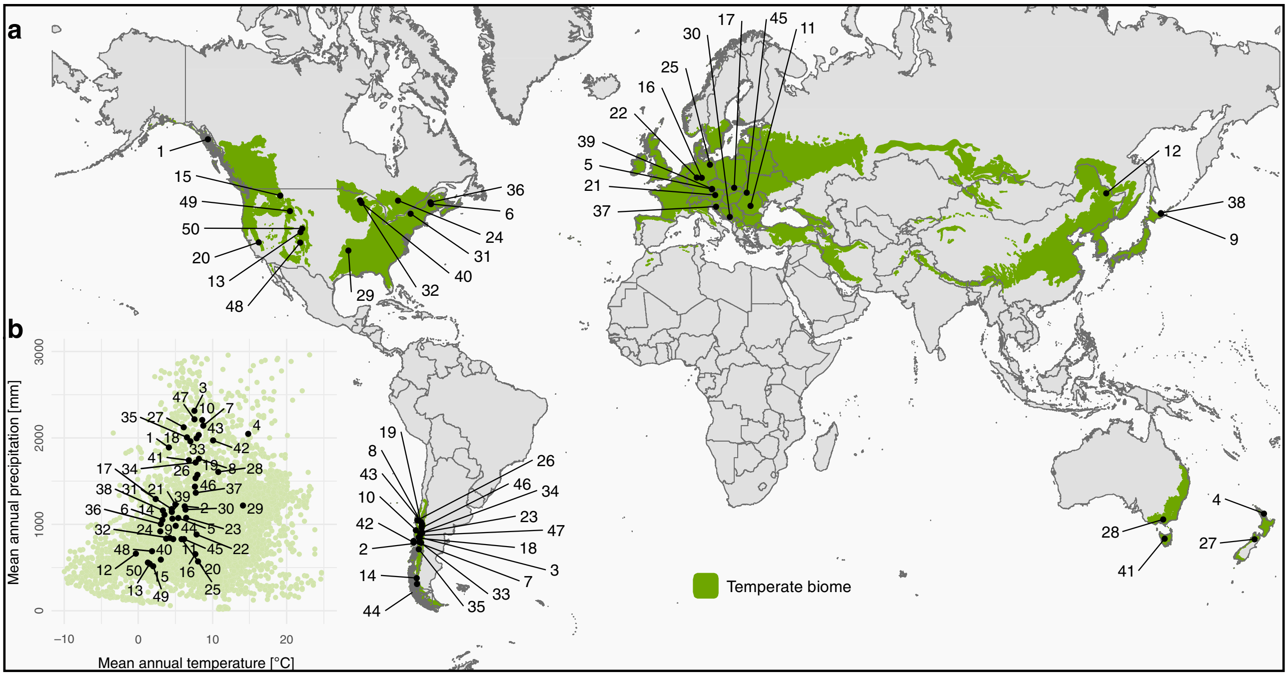

Fig. 1 A network of 50 protected landscapes to understand global patterns and drivers of temperate forest disturbances. **a** The geographic location of the landscapes, and **b** their location in climate space. The area of the temperate biome is indicated in green[47]. See Supplementary Table 1 for more detailed information on the individual landscapes. Note that the climatic envelope of the biome (green dots in **b**) is based on a sample of 10,000 4500 m×4500 m grid cells throughout the biome

Table 1 Characteristics of disturbance clusters

Cluster	Low	Moderate	High
Number of landscapes	18	23	9
Total forest area [ha]	788,986	1,216,364	1,965,572
Mean annual temperature [°C]	6.5 (5.6–7.5)	5.3 (4.4–6.2)	3.7 (2.8–4.6)
Mean annual precipitation [mm]	1393 (1241–1544)	1222 (1071–1374)	1197 (1046–1349)
Mean percent of forest area disturbed 2001–2014 [%]	0.31 (0.13–0.48)	4.61 (0.44–8.79)	21.50 (13.86–29.18)
Edge density [m/ha]	2.87 (1.24–4.50)	21.69 (2.80–40.58)	43.22 (25.53–60.91)
Area-weighted mean patch size [ha]	0.66 (0.46–0.85)	24.22 (6.96–41.47)	4451.04 (365.24–8536.84)
Area-weighted mean perimeter-area-ratio [m/ha]	960.09 (905.26–1014.92)	617.28 (560.74–673.82)	215.31 (150.15–280.74)

Characteristics of three global clusters of disturbance activity, determined based on satellite-derived disturbance metrics using Gaussian finite mixture models. Values in parentheses indicate the 95% confidence interval

interact (outside protected areas). We concentrated our analysis on a single biome as we were particularly interested in within-biome variation in disturbance patterns and drivers, rather than the comparatively well-studied between-biome differences. We selected temperate forests as the target of our study as they are affected by a wide variety of disturbance agents, frequently contain both angiosperm and gymnosperm species (i.e., high trait variability), and are represented in both the northern and southern hemisphere, spanning an extensive gradient in environmental conditions.

We hypothesized that differences in disturbance agents and tree species are the main determinants of among-landscape variation in disturbance patterns across the globe (H1). Specifically, we expected that areas predominately affected by fire as well as landscapes dominated by tree species with high general susceptibility (i.e., traits such as high maximum tree height and low wood density) are most affected by disturbances. Our alternative hypothesis was that spatial proximity of landscapes is a good indicator of similarities in disturbance patterns, with global differences in disturbances mainly explained by geographical location (e.g., on different continents or hemispheres). To test these hypotheses, we calculated four disturbance indicators, whereof two are landscape-level metrics (percent of landscape disturbed 2001–2014, edge density) and two are patch-level metrics (area-weighted mean patch size, area-weighted mean perimeter-area-ratio), and used cluster analysis to identify patterns among landscapes indicating differences in recent disturbance activity (with disturbance activity jointly referring to the prevalence, size, and shape of disturbances as characterized by our four focal indicators). Furthermore, we hypothesized that the patterns of natural disturbances (i.e., those observed in protected areas with only minimal direct human influence) differ from the combined natural and human disturbances outside protected areas (H2). We expected disturbances in protected areas to be generally smaller and more complex in shape (i.e., higher perimeter-area-ratio) compared to those outside of protected areas. This hypothesis is based on the insights that disturbances outside protected areas are the result of both natural and human disturbances (which can amplify each other, e.g., when strong winds uproot edge trees of freshly created clear-cuts), and that management-related biotic homogenization has the potential to increase forest susceptibility to disturbances relative to natural ecosystem development[26–28]. The alternative hypothesis was that high recent levels of natural disturbance activity supersede the signal of human land use, with similar disturbance patterns inside and outside protected areas. Finally, based on local and regional studies highlighting the importance of climate variability[29] and landscape structure[30] for disturbance dynamics, we tested for a consistent global relationship among climate variability, relative topographic complexity, and the spatio-temporal dynamics of forest disturbances. If recent disturbance episodes are responding consistently to climatic and topographic drivers, we would expect to find a non-random signal in a regression analysis across our set of globally distributed landscapes (H3). Alternatively, if responses vary among landscapes and cancel each other out at the global scale, the regression coefficients for these drivers would not differ significantly from zero.

Results

Patterns of recent natural disturbances. Disturbance dynamics between 2001 and 2014 varied strongly across the temperate forest biome. Unsupervised cluster analysis identified three distinct groups of landscapes based on their recent disturbance dynamics (Table 1; Supplementary Figure 1), which we in the following refer to as low, moderate, and high disturbance activity clusters. Each cluster comprises a group of landscapes of similar characteristics with regard to the size and shape of disturbance patches, the percentage of a landscape disturbed during the study period, and the average amount of edges created by these disturbances (Supplementary Figure 2). Approximately one-third of the landscapes studied (representing 19.9% of the forest area) fell within the low disturbance activity cluster. This group was characterized by small and complex disturbance patches (Table 1), with disturbances on average affecting only 0.31% of the landscape's forest area between 2001 and 2014. Examples of landscapes with low disturbance activity are the Te Paparahi Conservation Area (New Zealand), Shiretoko (Japan), Feng Lin (China), Five Ponds (USA), Hainich (Germany), and Hornopirén (Chile). The majority of the landscapes (23 landscapes, representing 30.6% of the forest area studied) fell within the moderate disturbance activity cluster. This group was characterized by a roughly 30 times larger area-weighted mean patch size than the landscapes in the low disturbance activity cluster (Table 1). Disturbance patches in the moderate cluster were less complex (i.e., had a lower area-weighted mean perimeter-area-ratio) but affected a larger forest area (on average 4.61% of the landscape) between 2001 and 2014. Examples of landscapes in this group are the Bavarian Forest (Germany), Baxter State Park (USA), Los Alerces (Argentina), and Nelson Lakes National Park (New Zealand). Although only 9 of the 50 landscapes analyzed fell within the high disturbance activity cluster, they accounted for 49.5% of the total forest area under study. Area-weighted mean patch size was two orders of magnitude larger than in the moderate disturbance activity cluster, and disturbance patches were considerably less complex (Table 1). On average, almost one quarter of the landscape's forested area was affected by disturbances between 2001 and 2014 in the high disturbance activity cluster, resulting in the highest edge density among all three

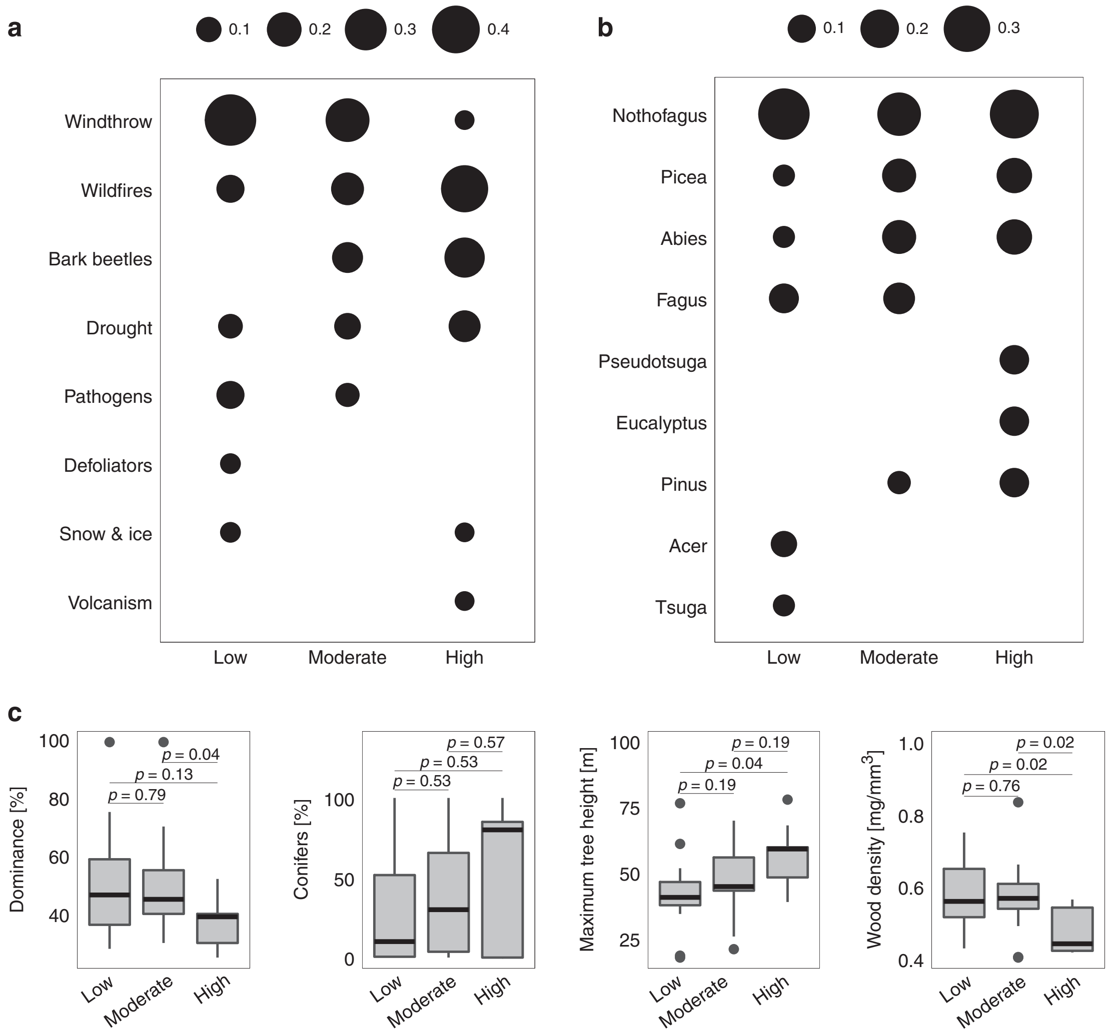

Fig. 2 Distribution of disturbance agents, tree genera, and tree species traits across three global clusters of disturbance activity (cf. Table 1). Bubbles are scaled relative to the occurrence of the two most important **a** disturbance agents and **b** tree genera within each cluster. **c** Dominance [%] indicates the share of the single most prevalent tree species on the overall tree species composition, while conifers [%] indicates the respective share of all conifer species. Maximum tree height and wood density indicate a weighted trait distribution across landscapes in the respective disturbance activity clusters. Boxplots denote the median (center line) and interquartile range (box), with whiskers extending to three times the interquartile range and points indicating values outside this range. Test statistics and *p*-values are based on approximate Kruskal-Wallis tests with 9999 permutations. For further information on statistical analyses see Supplementary Table 2

clusters. Examples for landscapes in this group are Yellowstone (USA), Puyehue (Chile), and O'Shannassy (Australia).

The clustering based on the four landscape metrics considered here did not reveal strong geographical patterns (Supplementary Figure 3a). Landscapes from at least three continents were present in each cluster, and all three disturbance activity clusters were represented in both the southern and northern hemispheres. Furthermore, no clear pattern emerged when comparing the clusters in climate space (Supplementary Figure 3b), although a tendency of cooler landscapes experiencing higher disturbance activity could be detected (Table 1).

Disturbance activity clusters were associated with different major disturbance agents and tree genera (Fig. 2a, b, Supplementary Figure 4). Agents differed significantly among disturbance activity clusters ($\chi^2 = 37.64$, $p < 0.01$). Landscapes in the low disturbance activity cluster were frequently affected by multiple disturbance agents, with windthrow being the most prevalent agent. Major bark beetle outbreaks were largely absent from this group of landscapes. In landscapes experiencing moderate disturbance activity in 2001–2014, fire and bark beetle outbreaks were more prevalent compared to the low cluster. High disturbance activity was predominately associated with wildfire, with bark beetle outbreaks and drought also being important agents in highly disturbed landscapes.

Dominant tree genera (i.e., the genera with the highest proportion of basal area) differed among disturbance activity clusters ($\chi^2 = 69.09$, $p < 0.001$). Low disturbance activity landscapes were largely dominated by broadleaved trees from the genera *Nothofagus*, *Fagus*, and *Acer*, i.e., species that have a relatively low maximum attainable height but higher wood density (Fig. 2c). The moderate disturbance activity cluster was characterized by both broadleaved and coniferous tree species, yet their average trait characteristics largely resembled those of the low disturbance activity landscapes. High disturbance activity landscapes in the northern hemisphere were dominated by the genera *Picea*, *Abies*, *Pseudotsuga*, and *Pinus*, which are

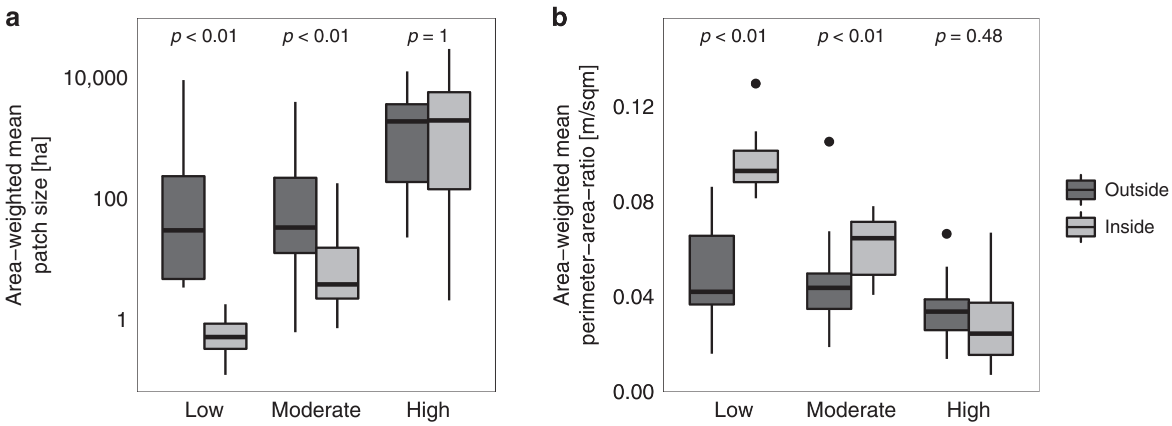

Fig. 3 Comparison of disturbance patterns inside and outside protected areas. **a** Area-weighted mean patch size and **b** area-weighted mean perimeter-area-ratio are compared for areas inside and outside protected areas for three global clusters of disturbance activity (cf. Table 1). Boxplots denote the median (center line) and interquartile range (box), with whiskers extending to three times the interquartile range and points indicating values outside this range. Test statistics and p-values are based on approximate Kruskal–Wallis tests with 9999 permutations

characterized by a higher maximum attainable tree height and lower wood density (see Supplementary Table 2 for test statistics on trait differences between clusters). Conversely, the high disturbance activity landscapes located in the southern hemisphere were mainly characterized by *Nothofagus*. The share of the single most dominant tree species on the overall species composition did not differ between landscapes in the low and moderate clusters. In high disturbance activity landscapes, however, the most important tree species was less dominant compared to landscapes in low and moderate clusters (Fig. 2c).

Disturbance differences inside and outside protected areas. Disturbance patches inside protected areas—almost exclusively influenced by natural disturbance agents (but see Supplementary Table 6)—were smaller and more complex than disturbance patches in surrounding areas affected by both human and natural disturbances in the low and moderate disturbance activity clusters (Fig. 3, Supplementary Table 3). For landscapes with high disturbance activity, however, the distribution of patch sizes and perimeter-area-ratios did not differ significantly between protected areas and their surroundings. Hence, there is a higher similarity between disturbances in protected and unprotected systems in areas that experienced high disturbance activity recently. Furthermore, patch size and patch complexity differed more strongly among disturbance activity clusters in protected systems compared to unprotected systems.

Drivers of spatio-temporal disturbance dynamics. Inter-annual climate variability was an important driver of temporal disturbance dynamics in all three disturbance activity clusters. The full model (including both temperature/precipitation anomalies and topographic complexity as predictors) was more strongly supported by the data than the spatial-only model (including only topographic complexity) and the Null model (likelihood-ratio tests; all p-values < 0.01; see Supplementary Table 4). However, the direction and strength of effects, as well as the lag time of climate effects, varied among clusters (Supplementary Figure 5; Fig. 4). A 2-year and 3-year lag was most strongly supported by the data for the low and moderate disturbance activity clusters, respectively. Conversely, climate variability had an immediate influence on disturbances (i.e., zero lag) in the high disturbance activity cluster (Supplementary Figure 5). For landscapes with low disturbance activity, we found a significant but moderately negative effect of temperature anomaly (GLMM; $\beta = -0.20$, std. error = 0.07, $p = 0.01$; see Supplementary Table 4). That is, warmer than average temperatures decreased the probability of disturbance in the following years (Fig. 4a). This effect of temperature was independent of variation in precipitation. Precipitation anomalies had a significant positive direct effect on disturbance probability (GLMM; $\beta = -0.33$, std. error = 0.07, $p <$ 0.01; Supplementary Table 4), with wetter conditions increasing disturbance probability in the low disturbance activity cluster (Fig. 4a). Conversely, for landscapes in the high disturbance activity cluster, we found a significant positive effect of temperature (GLMM; $\beta = 0.59$, std. error = 0.01, $p < 0.01$; Supplementary Table 4), with a higher disturbance probability in years with above average temperature (Fig. 4c). This effect was further modulated by precipitation, and was strongly amplified if warm years coincided with drier than average conditions (GLMM; $\beta =$ -0.43, std. error < 0.01, $p < 0.01$; Supplementary Table 4). While landscapes in the moderate disturbance activity cluster showed an overall negative effect of temperature on disturbance probability (GLMM; $\beta = -0.30$, std. error = 0.02, $p < 0.01$; Supplementary Table 4), the effect was also significantly influenced by precipitation (GLMM; $\beta = -0.17$, std. error = 0.03, $p < 0.01$; Supplementary Table 4). In addition, disturbance probability increased following years with above average temperature and below average precipitation (Fig. 4b).

Relative topographic complexity significantly affected spatial disturbance patterns, with different effects across disturbance activity clusters (Supplementary Table 4). In the predominately wind-influenced low disturbance activity landscapes, disturbance probability increased by ~7.5% with an increase in topographic complexity by one standard deviation (GLMM; $\beta = 0.30$, std. error = 0.04, $p < 0.01$; Supplementary Table 4). In contrast, disturbance probability decreased by ~1.25% (GLMM; $\beta =$ -0.05, std. error = 0.01, $p < 0.01$; Supplementary Table 4) and 2.5% (GLMM; $\beta = -0.10$, std. error < 0.01, $p < 0.01$; Supplementary Table 4) with the same amount of change in topographic complexity in the mainly beetle-driven and fire-driven landscapes of the moderate and high disturbance activity clusters.

Discussion

We present a quantitative analysis of recent disturbance dynamics across the temperate forest biome. Variation in recent forest disturbance activity across the globe was considerable, spanning a

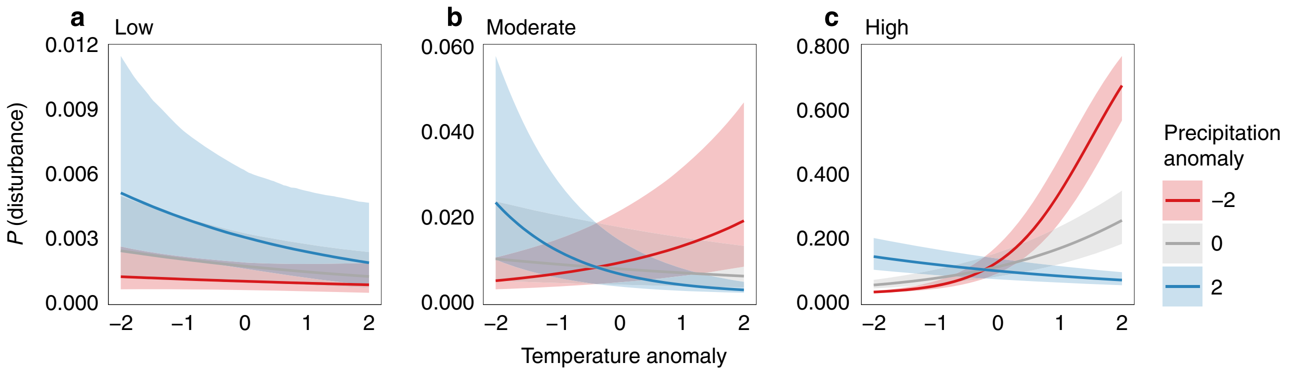

Fig. 4 Predicted response of disturbance probability to temperature anomaly, modulated by precipitation anomaly. **a**–**c** The climate sensitivity of disturbances separately for three global clusters of disturbance activity (cf. Table 1). Anomaly values are units of standard deviation with zero indicating the long-term mean. *Y*-axes are scaled differently across the three panels for clarity of presentation. Prediction uncertainty was estimated from 9999 model simulations, with the lower and upper limit representing the 2.5 and 97.5% quantile of all simulations. We note that prediction intervals include both parameter and model uncertainty, and overlapping prediction intervals can occur despite significant differences in parameter values. For parameter estimates and standard errors, see Supplementary Table 4. The number of experimental replicates equals the number of study sites per cluster (Low: 18, Moderate: 23, High: 9)

large gradient of patch sizes and landscape area affected by disturbance. Our results highlight that while extensive disturbances such as massive bark beetle outbreaks or severe large-scale fires have garnered considerable attention from researchers and the public recently, many temperate forests are dominated by small-scale disturbance events. This finding underscores the importance of a consistent quantification and analysis of disturbance dynamics across systems. The main disturbance agent affecting a system was more indicative of within-biome variation in disturbance activity than geographical proximity of landscapes or their location on the same continent or hemisphere (H1). Specifically, wind was an important agent responsible for small-scale disturbances in temperate forests[31]. Wildfires and bark beetle outbreaks, on the other hand, were the two most prominent agents associated with large and severe disturbances in recent years. However, the fact that both wind and wildfires occurred in all three clusters of disturbance activity highlights the considerable within-biome variability even within disturbance regimes characterized by the same agent.

Tree species composition was related to global differences in recent disturbances, with Northern Hemisphere temperate forests dominated by conifers experiencing elevated disturbance activity. This pattern can partly be explained by the general life-history strategy of conifers and their extensive coevolution with disturbances[32], as many conifers are well adapted to either tolerate disturbances or swiftly recolonize disturbed areas. An unexpected finding was that the dominance of the single most prevalent tree species was lower in landscapes with high disturbance activity compared to those with low and moderate disturbance activity. This contrasts with previous suggestions that disturbance risk increases if landscapes are dominated by a small number of tree species[33]. However, disturbances themselves can have a positive effect on tree species diversity[34,35]. Consequently, higher evenness in systems strongly affected by disturbances—as found here—could be a consequence of disturbances, rather than being causally related to them.

In large parts of the temperate forest biome, human disturbances dominate the landscape. Consequently, the disturbance patterns of unprotected systems differed from the natural disturbance regime observed in protected areas. In the majority of human-dominated landscapes outside protected areas, disturbance patches were larger and less complex than in protected areas, supporting our expectation (H2). In landscapes affected by large-scale disturbances, however, the patterns in protected areas and their surroundings were similar. This suggests that large natural disturbances can override the effect of human land use and dominate landscape patterns in forest ecosystems. As these events have been found to be particularly climate sensitive (Fig. 4c), future conditions could produce more coarse-grained landscape patterns (i.e., landscapes characterized by larger patch sizes) in temperate forests[36].

An important caveat associated with our analysis is that we could not consider vegetation structure and disturbance history as potential covariates in our analyses, resulting from the lack of a globally consistent data set on these variables. It therefore remains unclear whether the differences between protected and unprotected areas arise from a higher disturbance susceptibility of the latter systems, or whether they reflect management activities such as clearcutting in areas outside protected landscapes. Disturbance history and ecological legacies can exert an important influence on current disturbance activity[37,38]. This is important as most of our study landscapes have been protected only for a few decades, and legacies from former land use might still persist. Furthermore, although our 50 protected landscapes cover the climatic envelope of temperate forests well (Fig. 1b), they are not necessarily representative of the full range of ecological conditions of the entire temperate forest biome. Selecting areas with a long history of forest dynamics research enabled us to consistently compare patterns and responses across locally well-researched systems, but might also be a source of bias that should be considered in interpreting our results. The finding of similar disturbance patterns inside and outside of protected areas in the high disturbance activity cluster may, for instance, partly result from the generally remote location of these particular landscapes, with limited human activity in their surroundings. Future analyses explicitly contrasting disturbances inside and outside protected areas could help to better understand the effect of human activity on disturbances, and quantify the impact of anthropogenically altered disturbance regimes on biodiversity[25,39]. Furthermore, we here focused on severe canopy disturbances with complete canopy mortality of all trees taller 5 m within a 30 × 30 m grid cell[24]. Consequently, low severity disturbances and understory tree mortality were not considered, potentially leading to an underestimation of forest disturbance activity. However, the severe canopy disturbances examined here are generally well represented by the data set used: For example, Buma and Barrett[40] found an overall agreement of 91% when comparing the global disturbance data set used here to high-resolution imagery in southern Alaska. Furthermore, Borelli et al.[41] determined an overall accuracy of 81% in an independent evaluation of the data across Europe. We are thus confident that the data set used here is able to capture the variability in severe canopy disturbances across the temperate forest biome.

A remaining limitation of our analysis is the relatively short duration of our study period. The currently available disturbance time series from satellite data remain too short to characterize disturbance regimes[1] satisfactorily, and preclude the assessment of temporal trends in disturbance[7,42]. Consequently, we focused only on the effect of inter-annual climate variability rather than on long-term trends, using temperature and precipitation anomalies as predictors. Future work should also consider the effect of climatic extremes and intra-annual climate patterns for refining our understanding of climate—disturbance relationships[29]. In addition, process-based simulation modeling[43] could be employed to obtain a more dynamic and long-term perspective on global disturbance regimes and their responses to a changing climate.

Here we provide evidence that high recent disturbance activity in temperate forest ecosystems across the globe was strongly related to the joint occurrence of warmer and drier than average climate conditions (H3). These global scale findings are in general agreement with local studies[4,14,42,44,45], particularly considering that our high disturbance activity cluster was dominated by wildfires, bark beetle outbreaks, and drought. Our results therefore suggest that a warming climate could facilitate large-scale disturbances in temperate forest ecosystems in the future[2,46]. Our findings also show that climate sensitivity can, to some degree, be buffered by heterogeneous topography, which impedes the spread of disturbances and/ or increases the complexity of disturbed patches[25]. Interestingly, our analysis suggests that both the effect of climate and the effect of topography reversed for landscapes characterized by low disturbance activity, compared to those with high disturbance activity. For the former, which are predominately driven by wind disturbance, cooler and wetter conditions as well as higher relative topographic complexity increased disturbance probability[31], which is consistent with decreased tree anchorage (soil wetness) and increased wind susceptibility (exposed ridges, funnel effects) under such conditions. However, the signals detected for low disturbance activity areas were generally weak, underlining the highly stochastic nature of small-scale mortality events in forest ecosystems.

We conclude by emphasizing the importance of protected areas for understanding changes in forest landscapes in the absence of direct human influences. Furthermore, our work highlights the importance of consistent global information for characterizing patterns and identifying drivers of important ecological processes such as disturbances. Quantitative baselines acknowledging the substantial spatio-temporal variability in ecosystems are needed to identify, monitor, and attribute changes in ecological processes. The analyses presented here are an important step towards such an improved quantitative characterization of forest disturbances at the global scale, combining large-scale remote sensing data with ecological context information from local experts. An improved quantitative characterization of forest disturbances at the global scale can, for instance, inform the development and application of global vegetation models, which largely ignore the impacts of disturbances to date, or only consider a highly simplified representation of disturbance processes[18,19]. An improved consideration of disturbance processes in future projections is important as our results highlight the considerable sensitivity of disturbances to the ongoing changes in the climate system. We conclude that the resilience and adaptive capacity of ecosystems to disturbances remain important priorities of forest research and management.

Methods

A biome-wide network of protected forest landscapes. We compiled a network of study landscapes distributed throughout the temperate forest biome as defined by Olson et al.[47]. (see also Fig. 1). Selection criteria were that the landscapes are protected (i.e., IUCN Cat. I and Cat. II), and have a minimum of 2000 ha of contiguous forest area. Studying protected areas allowed us to largely control for anthropogenic disturbances and focus our main analyses on natural disturbances. We analyzed 50 landscapes distributed across 16 countries on five continents, representing a forest area of 3.9 Mill. ha (median landscape size: 30,889 ha; see Supplementary Table 1 for details). The study landscapes cover a wide climatic gradient of the temperate forest biome, with mean annual temperatures ranging from −0.3 °C to 14.8 °C, and mean annual precipitation sums between 517 mm and 2315 mm (Supplementary Table 1 and Fig. 1b).

Disturbance data and landscape pattern analysis. We acquired forest cover and annual disturbance maps (2001–2014) from Hansen et al.[24] (Version 1.2) at 30 m spatial resolution. A disturbance was defined as a severe canopy disturbance, meaning the complete mortality of all trees taller 5 m within a pixel[24]. Only disturbance events that occurred between 2001 and 2014 were considered. To characterize disturbance patterns, we calculated two landscape-level metrics and two patch-level metrics for each study landscape, using an eight-neighbor rule for defining adjacency and considering disturbances throughout the entire study period. The landscape-level metrics were: (i) percent of landscape disturbed 2001–2014, and (ii) edge density of all disturbed patches within the forest area of a landscape; with the patch-level metrics being (iii) area-weighted mean patch size, and (iv) area-weighted mean perimeter-area-ratio. To identify differences and similarities in recent disturbance patterns across the temperate forest biome, we used Gaussian finite mixture models, as implemented in the R package *mclust*[48] (version 5.4). Gaussian finite mixture models are an approach for unsupervised clustering, used here to identify groups of landscapes with similar disturbance patterns. The optimal number of cluster centers was determined by maximizing the Bayesian Information Criteria (BIC). Robust statistics for characterizing each cluster were derived by using parametric bootstrapping (9999 replications). Subsequently, the clusters were characterized with regard to their main disturbance agents and tree genera (i.e., the two most important agents and genera for a landscape during the period 2001–2014; see below for details). To describe potential functional differences between the clusters, we included plant traits in our analysis. After an initial screening and analysis of multicollinearity, we focused on two complementary plant traits corresponding to disturbance resistance and susceptibility, i.e., maximum potential tree height and mean wood density, extracted from the TRY database[49]. Plant height directly increases susceptibility to wind disturbance and is also a proxy for biomass accumulation potential, which is related to fuel load in the context of disturbances by wildfire. Wood density is positively correlated with the ability of trees to resist physical forces such as wind and drought. For each landscape, weighted trait means based on tree species shares were calculated. Differences in agents and tree genera among clusters were tested using approximate Pearson χ^2 tests of homogeneity with 9999 permutations. Differences in traits among clusters were tested using two-tailed pairwise approximate Kruskal–Wallis tests with 9999 permutations, applying false discovery rate correction. All test procedures were used as implemented in the *coin*[50] package (version 1.2-1) in R[51].

Expert-based information on local ecological context. Remote sensing provides a consistent estimate of disturbances across the biome, yet the ecological context of these disturbances, such as the dominant disturbance agents and the tree species affected, cannot be inferred from space. We thus consulted local experts for all 50 landscapes, collecting ecological context information via a questionnaire (see Supplementary Table 5). The questionnaire included four questions, two of which were multiple choice questions with the opportunity to add additional answers. They focused on determining the dominant tree species, the main disturbance agents affecting a landscape between 2001 and 2014, and the impact of disturbances on particular tree species. Values of tree species dominance in a given landscape were estimated as basal area shares. Local experts were identified via their publication record on the topic of forest dynamics for the selected areas. All consulted experts also contributed to the analysis and interpretation of the data, and are identified individually in Supplementary Table 1.

Difference inside and outside protected areas. After focusing on natural disturbance dynamics in protected areas in the previous analysis steps, we asked how protected areas differed from the disturbance dynamics in the unprotected systems surrounding our study landscapes. To compare spatial disturbance patterns inside vs. outside protected areas, we extracted all forest disturbances in a buffer surrounding the protected landscapes. The buffer size was selected proportional to the landscape size, and was set to the diagonal of the minimum bounding rectangle of each study landscape. We compared area-weighted mean patch size and area-weighted mean perimeter-area-ratio between strata (i.e., inside vs. outside protected areas) using boxplots, and tested differences using two-tailed approximate Kruskal–Wallis tests with 9999 permutations.

Drivers of spatio-temporal disturbance dynamics. We used generalized linear mixed effects models[52] (GLMMs) to test the influence of relative topographic complexity and climatic variability on spatial and temporal disturbance dynamics. Analyses were run separately for each disturbance activity cluster, modeling the annual probability of disturbance at the pixel level. As response variable we used annual binary disturbance maps indicating whether a pixel was disturbed in a given year or not. Consequently, the GLMMs were specified with a binomial error distribution and a logit link-function. As measure of topographic complexity we used the topographic ruggedness index[53] (TRI), which was calculated from a 30 m digital elevation model obtained from the Shuttle Radar Topographic Mission (SRTM). We calculated the TRI using a window size of 7 × 7 pixels, depicting the topographic complexity within a radius of ~100 m around a focal pixel. TRI values were subsequently scaled to zero mean and a standard deviation of one for each landscape, with negative values indicating a lower than average relative topographic complexity, and positive values indicating a higher than average relative topographic complexity. As a measure of climate variability we obtained time series of mean annual temperature and annual precipitation sum from *FetchClimate*[54], which are based on daily climate data from the NCEP/NCAR Reanalysis 1 database. We calculated climate anomalies by scaling the time series to zero mean and a standard deviation of one for each landscape, with negative values indicating colder/ dryer than average years, and positive values indicating hotter/ wetter than average years. As previous studies suggest variable lag times between climate anomalies and disturbance signals determined from remote sensing[12,16], we tested variable lags ranging from 0 years (i.e., relating the climate anomaly of the current year to the disturbance in the current year) to 3 years (i.e., relating the climate anomaly 3 years prior to the disturbance in the current year). The lag best supported by the data within each cluster was identified using Akaike's Information Criterion (AIC)[16,55]. Furthermore, we allowed for an interaction term between precipitation and temperature to account for potential modulating effects between these two variables[56]. Using GLMMs enabled us to incorporate factors on different hierarchical levels into a combined modeling framework. In particular, TRI values were available at the pixel level, but remain constant across years. In contrast, the temperature and precipitation anomalies varied among years, but did not differ spatially in a study landscape. Hence, we used relative topographic complexity to explain the spatial variation in disturbance probability, while climate variability was related to temporal variation of disturbances in our model. In addition, the GLMM framework allowed us to account for random variation in the model intercept among study landscapes within a cluster. As sample sizes were very large (several millions of 30 m pixels), we randomly sampled 10% of the pixels per landscape. As disturbances were rare in many landscapes, we employed a case-control sampling design[57], that is we randomly down-sampled the absence class (no disturbance) to approximately the same size of the presence class (disturbance). This design has the advantage that model estimates are unbiased (with the exception of the intercept), and the intercept can easily be corrected using the known true proportion of disturbance presence/absence in the population. Finally, we compared three candidate models per cluster: a full model containing predictors of spatial (TRI) and temporal (precipitation and temperature anomalies as well as their interaction) variation, a model containing TRI only (spatial-only model), and a null model (containing only an intercept while maintaining the random effects structure of the GLMMs). Model comparison was done using the AIC and log- likelihood tests. For the model most strongly supported by the data we created response curves by drawing 9999 random simulation from the model (i.e., accounting for parameter and model uncertainty), as suggested by Gelman and Hill[58]. All models and calculations were implemented using the *lme4* package[59] (version 1.1-14) in R.

Data availability

Data on forest disturbances were derived from the global forest change data set[24], available at https://earthenginepartners.appspot.com/science-2013-global-forest. Data on tree species traits were derived from the plant trait database TRY[49], available at https://www.try-db.org/TryWeb/Home.php (doi: 10.17871/TRY.3). Landscape-level data on ecological context variables was derived by means of a questionnaire (see Supplementary Table 5), and is published in full in Supplementary Table 1.

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Author contributions

A.S., C.S., and R.S. designed the study, analyzed the data and wrote the paper. B.B., A.W. D., T.D., I.D.-H., S.F., L.E.F., Á.G.G., S.J.H., B.J.H., H.S.H., T.H., A.H., T.K., D.K., D.L., A. S.M., J.M., J.P., G.L.W.P, S.L.S., M.S., M.G.T., and T.T.V. contributed data and commented on the manuscript.

Additional information

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Supplementary material

Patterns and drivers of recent disturbances across the temperate forest biome

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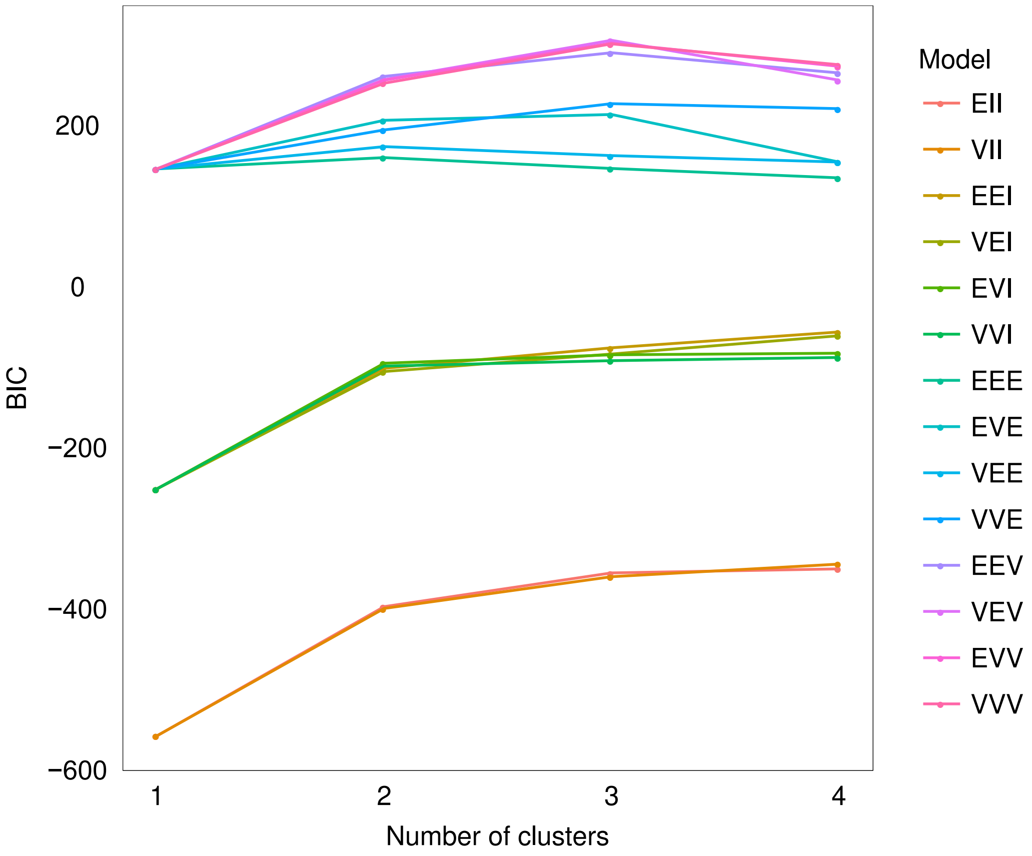
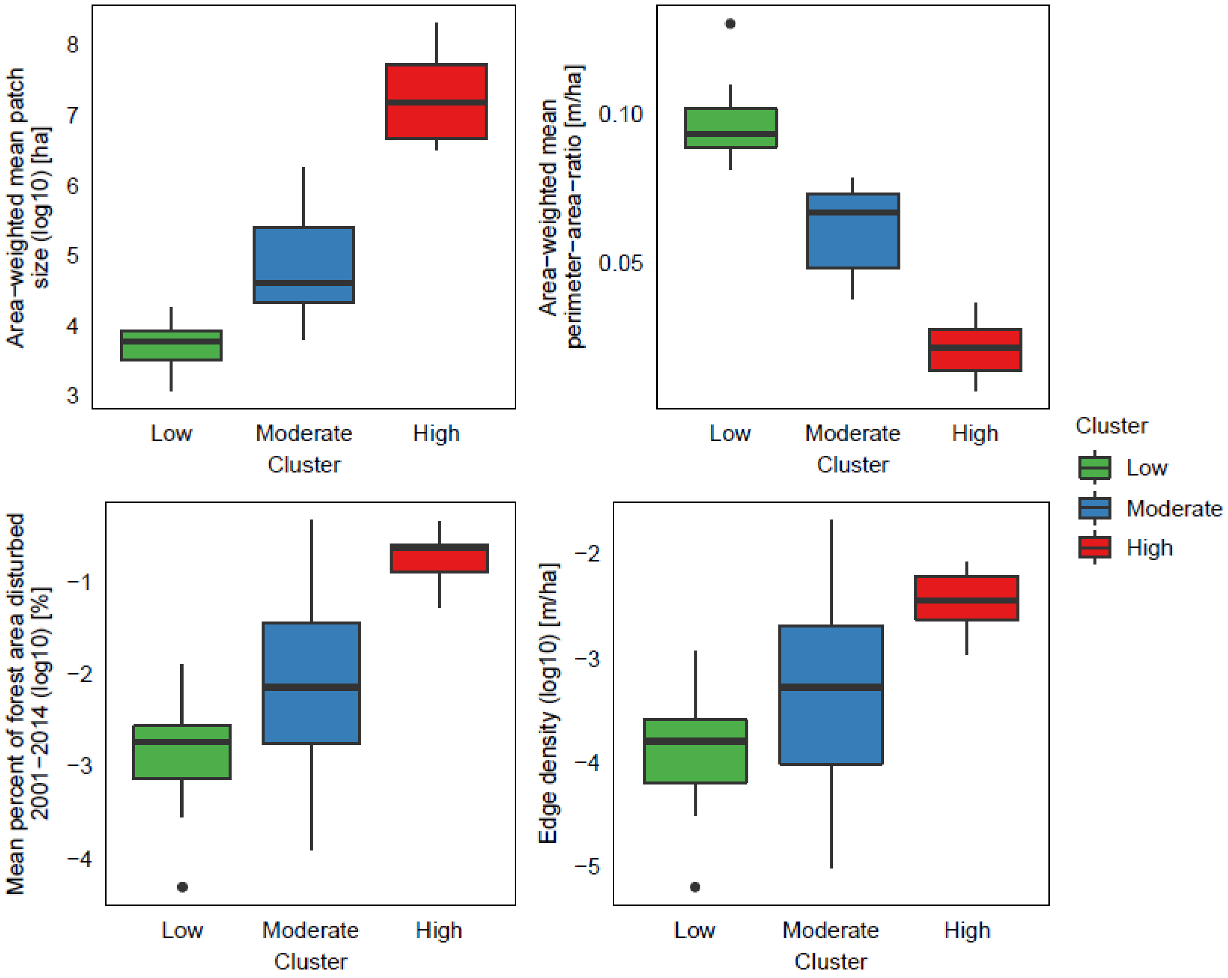
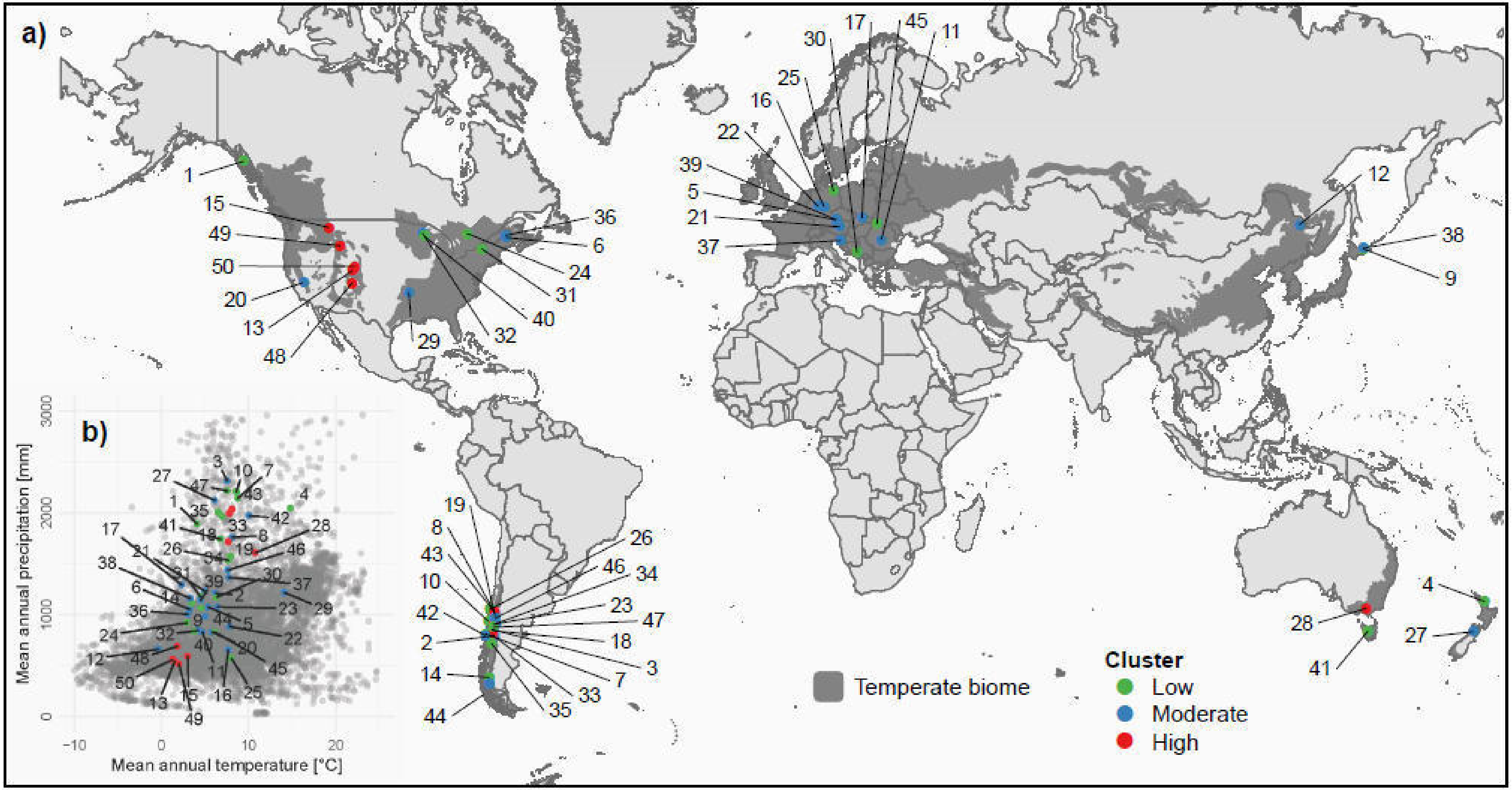
Supplementary Figures



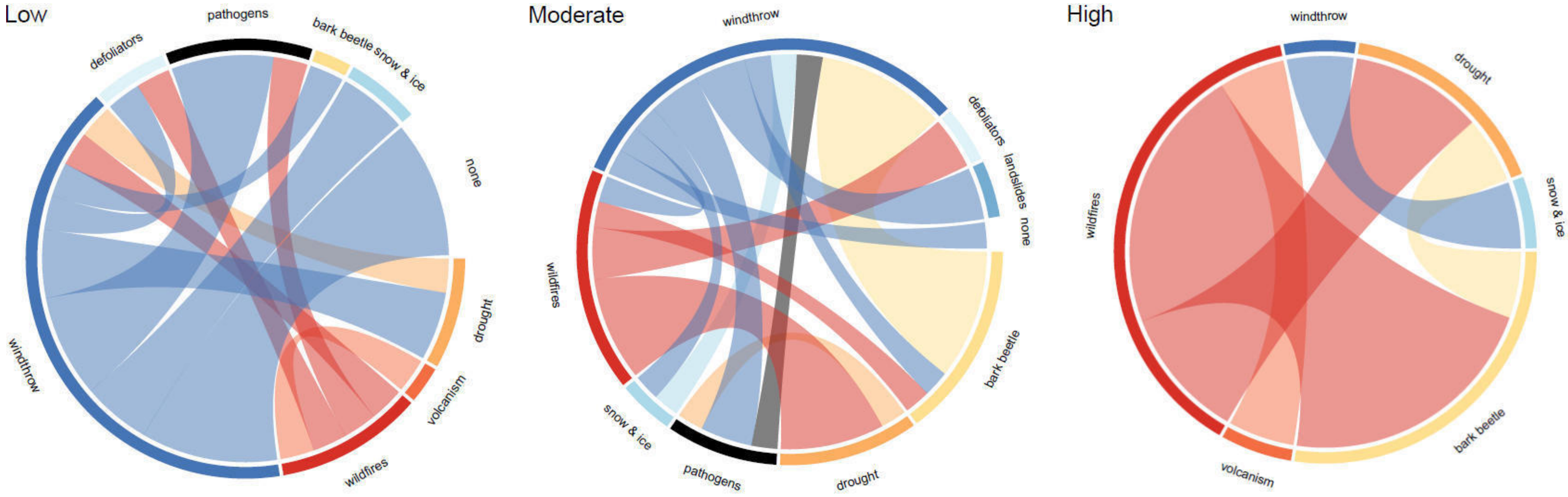
Supplementary Figure 1: Comparison of different clustering models (colors) and number of clusters using the Bayes Information Criterion (BIC). Models are identified using three letter codes describing the geometric characteristics of the approach, namely volume, shape, and orientation. E means equal and V means varying across components or clusters, while I refers to the identity matrix in specifying shape or orientation and is a special case of E. For details we refer to Fraley et al. [1].



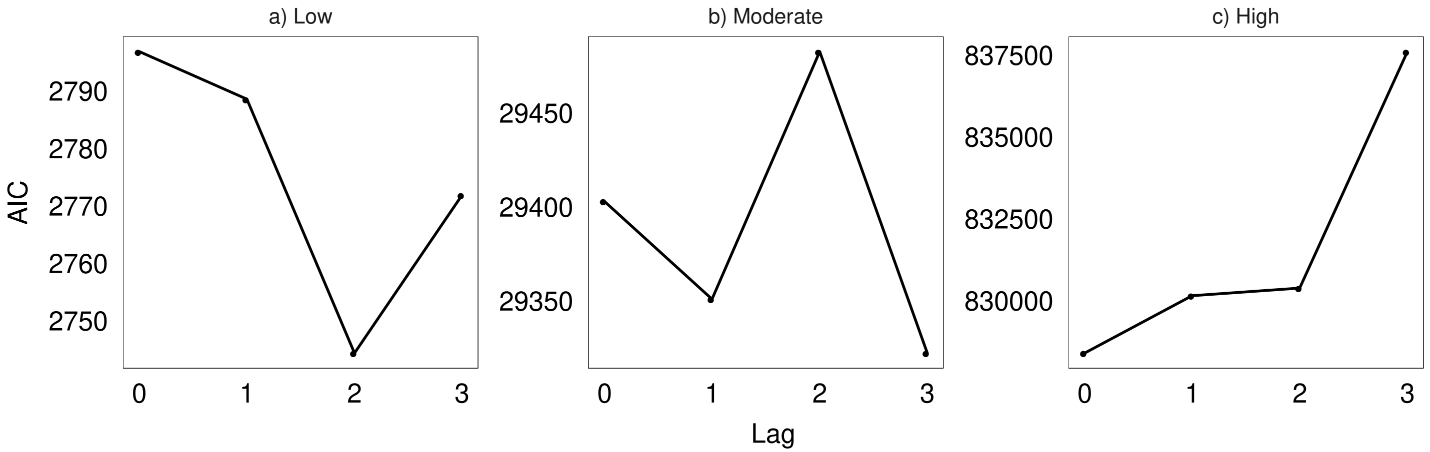
Supplementary Figure 2: Boxplots showing the distribution of the four disturbance metrics in the three clusters of disturbance activity. See also Table 1. Boxplots denote the median (center line) and interquartile range (box), with whiskers extending to three times the interquartile range and points indicating values outside this range. The number of experimental replicates equals the number of study sites per cluster (*Low:* 18, *Moderate:* 23, *High:* 9)



Supplementary Figure 3: A network of 50 protected landscapes across the temperate biome (biome area indicated in dark grey[2]). The panels show a) the geographic location, and b) the location of the landscapes in climate space. Study sites are colored according to their respective cluster, with green, blue and red representing clusters of *low*, *moderate* and *high* disturbance activity. Note that the climatic envelope of the biome (dark grey dots in panel b) is based on a sample of 10,000 4500 m × 4500 m grid cells throughout the biome.



Supplementary Figure 4: Co-occurrences of the two most important disturbance agents per landscape in clusters with *low*, *moderate*, and *high* disturbance activity. The sector size in the outer circle indicates the relative prevalence of a disturbance agent in a respective cluster, while the links denote co-occurrence.



Supplementary Figure 5: Variable lag times (years) between climate anomaly and disturbance response, compared using the Akaike Information Criterion (AIC) of the respective GLMM. The lag with the lowest AIC was chosen in the final model.

Supplementary Tables

Supplementary Table 1: Summary of the 50 study sites. Disturbance characteristics (area-weighted mean patch size, area-weighted perimeter-area ratio, percent of area disturbed, and edge density) pertain to the years 2001 to 2014.

#	Landscape name	Country	Local experts	Total area disturbed [ha]	Forest-cover [ha]	Main disturbance agents	Dominant tree species	Percent of area disturbed [%]	Edge density [m/ha]	Area-weighted mean patch size [ha]	Area-weighted perimeter-area ratio [m/ha]	Cluster
1	Admirality Island	USA	B. Buma	192	367853	windthrow, pathogens, snow & ice, landslides, lack of snow	*Tsuga heterophylla, Picea sitchensis, Tsuga mertensiana, Callitropsis nootkatensis, Pinus contorta*	0.05	0.53	0.85	1011	*Low*
2	Alerces	Argentina	A. Holz & J. Paritsis	1338	154313	wildfires, defoliators, snow & ice, drought	*Nothofagus pumilio, Nothofagus antarctica, Nothofagus dombeyi, Austrocedrus chilensis, Fitzroya cupressoides*	0.87	6.53	4.39	754	*Moderate*
3	Alerce Andino	Chile	Á. G. Gutiérrez & I. Díaz-Hormazábal	38	36009	windthrow, landslides	*Fitzroya cupressoides, Nothofagus betuloides, Nothofagus nitida, Nothofagus pumilio, Nothofagus dombeyi*	0.11	0.71	2.07	670	*Moderate*
4	Te Paparahi Conservation Area	New Zealand	G. L. W. Perry	23	12378	windthrow, herbivory, drought, landslides	*Kunzea robusta, Agathis australis, Beilschmiedia tarairi, Vitex lucens, Dysoxylum spectabile*	0.19	1.55	1.15	821	*Low*
5	Bavarian Forest	Germany	J. Müller	1694	7271	bark beetles, windthrow, pathogens	*Picea abies, Fagus sylvatica, Abies alba, Sorbus aucuparia, Acer pseudoplatanus*	23.3	103.65	56.89	445	*Moderate*
6	Baxter State Park	USA	S. Fraver	169	69939	windthrow, pathogens	*Picea rubens, Abies balsamea, Acer saccharum, Betula alleghaniensis, Fagus grandifolia*	0.24	1.03	48.87	427	*Moderate*

#	Landscape name	Country	Local experts	Total area disturbed [ha]	Forest-cover [ha]	Main disturbance agents	Dominant tree species	Percent of area disturbed [%]	Edge density [m/ha]	Area-weighted mean patch size [ha]	Area-weighted perimeter-area ratio [m/ha]	Cluster
7	Chiloé	Chile	Á. G. Gutiérrez & I. Díaz-Hormazábal	2	34827	windthrow	*Nothofagus nitida, Tepualia stipularis, Aextoxicon punctatum, Fitzroya cupressoides, Eucryphia cordifolia*	0	0.06	0.12	1298	*Low*
8	Conguillío	Chile	Á. G. Gutiérrez & I. Díaz-Hormazábal	104	20885	wildfires, drought, windthrow, snow & ice, landslides	*Nothofagus dombeyi, Nothofagus antarctica, Nothofagus pumilio, Araucaria araucana, Nothofagus alpina*	0.5	2.93	4.07	587	*Moderate*
9	Shiretoko Cool temperate	Japan	A. S. Mori	9	7029	windthrow, browsing, defoliators, snow & ice, landslides	*Picea jezoensis, Abies sachalinensis, Quercus crispula, Betula ermanii, Kalopanax septemlobus*	0.13	1.06	0.62	810	*Low*
10	Alerce Costero	Chile	Á. G. Gutiérrez & I. Díaz-Hormazábal	15	22858	windthrow	*Laureliopsis philippiana, Nothofagus nitida, Nothofagus dombeyi, Drimys winteri, Fitzroya cupressoides*	0.06	0.55	0.57	860	*Low*
11	Fagaras	Romania	M. Svoboda	241	7736	bark beetles, windthrow	*Fagus sylvatica, Abies alba, Picea abies*	3.11	13.15	19.16	423	*Moderate*
12	Feng Lin	China (PRC)	H. S. He	243	17571	wildfires, bark beetles, windthrow, defoliators, drought	*Pinus koraiensis, Abies nephrolepis, Betula costata, Picea koraiensis, Tilia amurensis*	1.38	10.78	2.13	781	*Moderate*
13	Flattops	USA	D. Kulakowski, T. T. Veblen & S. J. Hart	5516	44540	wildfires, bark beetles, drought	*Picea engelmannii, Abies lasiocarpa, Populus tremuloides, Pinus contorta, Pseudotsuga menziesii*	12.38	17.16	1511.41	139	*High*

#	Landscape name	Country	Local experts	Total area disturbed [ha]	Forest-cover [ha]	Main disturbance agents	Dominant tree species	Percent of area disturbed [%]	Edge density [m/ha]	Area-weighted mean patch size [ha]	Area-weighted perimeter-area ratio [m/ha]	Cluster
14	Glaciares	Argentina	A. Holz & J. Paritsis	733	61828	wildfires, defoliators, snow & ice (avalanches, ice storms, etc.)	*Nothofagus pumilio, Nothofagus antarctica, Nothofagus betuloides*	1.19	11.66	0.65	984	*Low*
15	Glacier	USA	B. J. Harvey & M. G. Turner	153393	642334	wildfires, bark beetles	*Pinus contorta, Pseudotsuga menziesii, Picea engelmannii, Abies lasiocarpa, Larix occidentalis*	23.88	35.37	5882.1	148	*High*
16	Hainich	Germany	J. Müller	40	4458	pathogens, windthrow, snow & ice	*Fagus sylvatica, Acer pseudoplatanus, Fraxinus excelsior, Quercus robur, Carpinus betulus*	0.91	6.47	2.6	714	*Moderate*
17	High Tatra	Slovakia	T. Hlasny	388	4695	bark beetles, windthrow, pathogens	*Pinus mugo, Picea abies, Sorbus aucuparia, Larix decidua, Betula sp*	8.26	31.53	80.48	382	*Moderate*
18	Hornopirén	Chile	Á. G. Gutiérrez & I. Díaz-Hormazábal	23	19961	windthrow, snow & ice	*Nothofagus betuloides, Nothofagus pumilio, Nothofagus nitida, Fitzroya cupressoides, Nothofagus dombeyi*	0.12	1.17	0.41	1016	*Low*
19	Huerquehue	Chile	Á. G. Gutiérrez & I. Díaz-Hormazábal	12	9527	drought, windthrow, snow & ice, landslides	*Nothofagus dombeyi, Nothofagus pumilio, Nothofagus obliqua, Nothofagus antarctica, Araucaria araucana*	0.13	1.18	0.76	930	*Low*
20	Illilouette Creek/ Yosemite	USA	S. L. Stephens	1903	23221	wildfires, drought, bark beetles, pathogens	*Abies concolor, Abies magnifica, Pinus contorta, Pinus jeffreyi*	8.19	33.19	175.8	405	*Moderate*

#	Landscape name	Country	Local experts	Total area disturbed [ha]	Forest-cover [ha]	Main disturbance agents	Dominant tree species	Percent of area disturbed [%]	Edge density [m/ha]	Area-weighted mean patch size [ha]	Area-weighted perimeter-area ratio [m/ha]	Cluster
21	Kalkalpen	Austria	R. Seidl	492	13465	windthrow, bark beetles, snow & ice, wildfires	*Picea abies, Fagus sylvatica, Larix decidua, Abies alba, Acer pseudoplatanus*	3.65	19.32	4.6	529	*Moderate*
22	Kellerwald	Germany	J. Müller	241	5048	bark beetles, windthrow, snow & ice, drought, pathogens	*Fagus sylvatica, Picea abies, Quercus robur, Larix europaea, Pinus sylvestris*	4.78	24.32	5.53	509	*Moderate*
23	Nahuel Lanin	Argentina	T. Kitzberger	4506	628938	wildfires, drought, volcanism, defoliators, snow & ice	*Nothofagus pumilio, Nothofagus antarctica, Nothofagus dombeyi, Austrocedrus chilensis, others*	0.72	5.24	33.15	731	*Moderate*
24	Malakisis	Canada	T.Després	8	2861	windthrow, bark beetles	*Acer saccharum, Betula alleghaniensis, Tsuga canadensis, Abies balsamea, Betula papyrifera*	0.28	2.5	0.39	902	*Low*
25	Müritz	Germany	J. Müller	51	4077	wildfires, windthrow	*Pinus sylvestris, Fagus sylvatica, Betula pendula, Alnus glutinosa, Quercus robur*	1.26	11.43	0.87	906	*Low*
26	Nahuelbuta	Chile	Á. G. Gutiérrez & I. Díaz-Hormazábal	26	6065	windthrow, drought, pathogens	*Araucaria araucana, Nothofagus dombeyi, Nothofagus obliqua, Nothofagus antarctica*	0.43	3.81	1.36	882	*Low*

#	Landscape name	Country	Local experts	Total area disturbed [ha]	Forest-cover [ha]	Main disturbance agents	Dominant tree species	Percent of area disturbed [%]	Edge density [m/ha]	Area-weighted mean patch size [ha]	Area-weighted perimeter-area ratio [m/ha]	Cluster
27	Nelson Lakes National Park	New Zealand	G. L. W. Perry	204	52503	windthrow, landslides, herbivory	*Lophonzonia menziesii, Fuscaspora fuscaspora, Fuscaspora cliffortioides, others*	0.39	2.33	3.93	598	*Moderate*
28	O'Shannassy	Australia	D. Lindenmayer	5845	13241	wildfires, drought	*Eucalyptus regnans, Eucalyptus delegatensis, Eucalyptus nitens, Eucalyptus obliqua, others*	44.14	60.32	5304.76	137	*High*
29	Ozarks	USA	H. S. He	9	7264	drought, pathogens, bark beetles, defoliators, snow & ice	*Quercus alba, Pinus echinata, Quercus rubra, Quercus veltutina, Carya tomentosa*	0.12	0.86	2.2	722	*Moderate*
30	Perućica	Bosnia and Herzegowina	M. Svoboda	3	1408	windthrow, pathogens, landslides, snow & ice, bark beetles	*Fagus sylvatica, Abies alba, Picea abies*	0.23	2.26	0.28	981	*Low*
31	Five Ponds	USA	A. D'Amato	6	12574	windthrow, pathogens, defoliators, snow & ice, drought	*Acer saccharum, Fagus grandifolia, Picea rubens, Tsuga canadensis, Betula alleghaniensis*	0.05	0.51	0.27	1071	*Low*
32	Porcupine	USA	L. E. Frelich	30	24006	windthrow, wildfires, defoliators, drought	*Acer saccharum, Tsuga canadensis, Betula alleghaniensis, Tilia americana, Acer rubrum*	0.12	0.9	3.14	732	*Moderate*
33	Pumalín	Chile	Á. G. Gutiérrez & I. Díaz-Hormazábal	8728	169220	windthrow, snow & ice	*Nothofagus nitida, Nothofagus dombeyi, Nothofagus pumilio, Nothofagus betuloides, Laureliopsis philippiana*	5.16	11.07	4659.35	215	*High*

#	Landscape name	Country	Local experts	Total area disturbed [ha]	Forest-cover [ha]	Main disturbance agents	Dominant tree species	Percent of area disturbed [%]	Edge density [m/ha]	Area-weighted mean patch size [ha]	Area-weighted perimeter-area ratio [m/ha]	Cluster
34	Puyehue	Chile	Á. G. Gutiérrez & I. Díaz-Hormazábal	21531	67012	volcanism, wildfires, windthrow, snow & ice	*Nothofagus pumilio, Nothofagus dombeyi, Laureliopsis philippiana, Nothofagus betuloides, Nothofagus antarctica*	32.13	23.35	20045.21	73	*High*
35	Queulat	Chile	Á. G. Gutiérrez & I. Díaz-Hormazábal	82	11082	windthrow, snow & ice	*Nothofagus betuloides, Nothofagus pumilio, Nothofagus dombeyi, Nothofagus nitida, Laureliopsis philippiana*	0.74	6.93	0.68	932	*Low*
36	Big Reed	USA	S. Fraver	6	1929	windthrow, pathogens	*Picea rubens, Abies balsamea, Thuja occidentalis, Acer saccharum, Fagus gradifolia*	0.32	2.43	0.69	754	*Moderate*
37	Risnjak	Croatia	M. Svoboda	4	3224	snow & ice, windthrow, bark beetles	*Fagus sylvatica, Abies alba, Picea abies*	0.12	0.89	0.65	744	*Moderate*
38	Shiretoko subalpine	Japan	A. S. Mori	6	44069	windthrow, snow & ice, defoliators, browsing, landslides	*Betula ermanii, Sorbus commixta, Sorbus matsumurana, Alnus maximowiczii, Acer tschonoskii*	0.01	0.1	1.67	774	*Moderate*
39	Sumava	Czech	M. Svoboda	1095	2422	bark beetles, windthrow	*Picea abies, Sorbus aucuparia*	45.22	207.68	89.04	459	*Moderate*
40	Sylvania	USA	L. E. Frelich	11	6006	windthrow, drought, defoliators	*Tsuga canadensis, Acer saccharum, Betula alleghaniensis, Tilia americana, Acer rubrum*	0.18	1.63	0.51	929	*Low*

#	Landscape name	Country	Local experts	Total area disturbed [ha]	Forest-cover [ha]	Main disturbance agents	Dominant tree species	Percent of area disturbed [%]	Edge density [m/ha]	Area-weighted mean patch size [ha]	Area-weighted perimeter-area ratio [m/ha]	Cluster
41	Tasmania	Australia	A. Holz	13	45078	wildfires, pathogens, drought	*Athrotaxis cupressoides, Eucalyptus coccifera*	0.03	0.31	0.24	1096	*Low*
42	Tepuhueico	Chile	Á. G. Gutiérrez & I. Díaz-Hormazábal	72	19779	windthrow	*Tepualia stipularis, Nothofagus nitida, Drymis winteri, Amomyrtus luma, Aextoxicon punctatum*	0.37	2.63	2.11	719	*Moderate*
43	Tolhuaca	Chile	Á. G. Gutiérrez & I. Díaz-Hormazábal	668	4169	wildfires, drought, windthrow, snow & ice, landslides	*Nothofagus obliqua, Nothofagus dombeyi, Nothofagus alpina, Nothofagus pumilio, Araucaria araucana*	16.02	44.2	407.81	276	*High*
44	Torres del Paine	Chile	A. Holz & J. Paritsis	1456	43475	wildfires, defoliators, snow & ice (avalanches, ice storms, etc.)	*Nothofagus pumilio, Nothofagus antarctica, Nothofagus betuloides*	3.35	21.6	12.1	645	*Moderate*
45	Uholka	Ukraine	M. Svoboda	14	5489	windthrow	*Fagus sylvatica, others*	0.25	2.6	0.3	1024	*Low*
46	Villarrica	Chile	Á. G. Gutiérrez & I. Díaz-Hormazábal	19	24145	wildfires, drought, windthrow, snow & ice, landslides	*Nothofagus pumilio, Nothofagus dombeyi, Nothofagus antarctica, Nothofagus obliqua, Araucaria araucana*	0.08	0.54	1.71	695	*Moderate*
47	Vicente Pérez Rosales	Chile	Á. G. Gutiérrez & I. Díaz-Hormazábal	365	158085	volcanism, wildfires, windthrow, snow & ice	*Nothofagus dombeyi, Nothofagus pumilio, Nothofagus betuloides, Nothofagus nitida, Eucryphia cordifolia*	0.23	1.92	1.75	831	*Low*

#	Landscape name	Country	Local experts	Total area disturbed [ha]	Forest-cover [ha]	Main disturbance agents	Dominant tree species	Percent of area disturbed [%]	Edge density [m/ha]	Area-weighted mean patch size [ha]	Area-weighted perimeter-area ratio [m/ha]	Cluster
48	Weminuche	USA	T. T. Veblen & S. J. Hart	17666	77444	bark beetles, drought, wildfires, defoliators	*Picea engelmannii, Abies lasiocarpa, Pinus contorta, Pinus flexilis, Populus tremuloides*	22.81	82.84	316.74	363	*High*
49	Yellowstone	USA	B. J. Harvey & M. G. Turner	113924	915221	wildfires, bark beetles, defoliators, pathogens	*Pinus contorta, Pseudotsuga menziesii, Picea engelmannii, Abies lasiocarpa, Pinus albicaulis*	12.45	30.55	1469.1	245	*High*
50	Mount Zirkel	USA	D. Kulakowski & B. Buma	7953	32392	wildfires, bark beetles	*Picea engelmanii, Abies latifolia, Populus tremuloides, Pinus contorta, Pseudotsuga menziesii*	24.55	84.12	462.86	343	*High*

Supplementary Table 2: Multiple comparisons of species composition and weighted mean trait values among clusters of disturbance activity. Test statistics and p-values are based on approximate Kruskal-Wallis tests with 9,999 permutations. P-values were adjusted for multiple comparisons using false discovery rate (FDR) correction.

Trait	Comparison of clusters	Statistic (H)	p-value	p-value (FDR-corrected)
Dominance	Low – Moderate	0.0699	0.7936	0.7936
	Low – High	2.9120	0.0880	0.1320
	Moderate – High	5.9930	0.0133	0.0399
Conifers	Low – Moderate	1.1780	0.2809	0.5320
	Low – High	0.9316	0.3547	0.5320
	Moderate – High	0.3500	0.5722	0.5722
Height	Low – Moderate	1.7950	0.1879	0.1879
	Low – High	5.8440	0.0147	0.0441
	Moderate – High	2.2140	0.1476	0.1879
Wood density	Low – Moderate	0.0994	0.7645	0.7645
	Low – High	5.5980	0.0154	0.0231
	Moderate - High	6.6440	0.0079	0.0231

Supplementary Table 3: Comparison of area-weighted mean patch size and area-weighted mean perimeter-area-ratio inside and outside of protected areas. Test statistics and p-values are based on approximate Kruskal-Wallis tests with 9,999 permutations.

Metric	Cluster	Statistic (H)	p-value
Area-weighted mean patch size	Low	26.2703	< 0.0001
	Moderate	12.5885	0.0002
	High	0.0020	1.0000
Area-weighted mean perimeter-area-ratio	Low	24.9922	< 0.0001
	Moderate	12.7448	0.0005
	High	0.5634	0.4777

Supplementary Table 4: Summary of the GLMMs testing the effect of temperature and precipitation anomalies as well as relative topographic ruggedness on disturbance probability. Values in parentheses are standard errors estimated from the GLMMs. Asterisks indicate the level of significance (*** P < 0.001, ** P < 0.01, * P < 0.05). Results of likelihood-ratio-tests comparing the full model to a spatial-only and a Null-model are also indicated.

Cluster	Model	Intercept	Topographic Ruggedness Index	Precipitation anomaly	Temperature anomaly	Precipitation × temperature anomaly	AIC	Log-likelihood	χ^2 (DF)	*P*
Low	Full	0.02 (±0.36)	0.30 (±0.04)***	0.33 (±0.07)***	-0.20 (±0.07)**	-0.04 (±0.06)	2744.36	-1365.18	63.07 (3)	< 0.001
	Spatial-only	0.08 (±0.35)	0.29 (±0.04)***	-	-	-	2801.42	-1396.71	47.67 (1)	< 0.001
	Null	0.08 (±0.35)	-	-	-	-	2847.09	-1420.55	-	-
Moderate	Full	-0.50 (±0.50)	-0.05 (±0.01)***	-0.11 (±0.02)***	-0.17 (±0.03)***	-0.03 (±0.02)***	29322.28	-14654.14	255.94 (3)	< 0.001
	Spatial-only	-0.41 (±0.50)	-0.05 (±0.01)***	-	-	-	29572.22	-14782.11	12.36 (1)	< 0.001
	Null	-0.41 (±0.50)	-	-	-	-	29582.58	-14788.29	-	-
High	Full	-0.65 (±0.24)**	-0.10 (±0.00)***	-0.09 (±0.01)***	0.59 (±0.01)***	-0.43 (±0.00)***	828401.56	-414193.78	18073.93 (3)	< 0.001
	Spatial-only	0.07 (0.28)	-0.11 (±0.00)***	-	-	-	846469.48	-423230.74	1670.36 (1)	< 0.001
	Null	0.07 (0.28)	-	-	-	-	848137.85	-424065.92	-	

Supplementary Table 5: Questionnaire to compile expert-based information on tree species, disturbance agents, and potential human interventions for the 50 protected landscapes. See Table S1 for the names of the local experts contacted.

#	Question
1	What are the five most important tree species (in terms of basal area share) occurring on the landscape? Please give scientific names and approximate percentages.
2	List the major disturbance agents that were active on the landscape during 2001-2014 (in decreasing order of importance).
3	Which tree species where affected by these disturbance agents?
4	Were any human interventions undertaken during or after disturbance (e.g., fire suppression, salvage logging)? If so, please list them in decreasing order of their intensity.

Supplementary Table 6: Known direct human interventions within the studied protected landscapes (see Supplementary Table 1 for more details on landscapes).

#	Landscape name	Country	Main disturbance agents	Direct human interventions
2	Alerces	Argentina	wildfires, defoliators, snow & ice, drought	fire suppression
8	Conguillio	Chile	wildfires, drought, windthrow, snow & ice, landslides	fire suppression, irrigation
11	Fargaras	Romania	bark beetles, windthrow	sanitary cuts, salvage logging
12	Feng Lin	China (PRC)	wildfires, bark beetles, windthrow, defoliators, drought	fire & defoliator suppression, salvage logging
13	Flattops	USA	wildfires, bark beetles, drought	fire suppression
14	Glaciares	Argentina	wildfires, defoliators, snow & ice	fire suppression
23	Nahuel Lanin	Argentina	wildfires, drought, volcanism, defoliators, snow & ice	fire suppression
28	O’Shannassy	Australia	wildfires, drought	fire suppression
29	Ozarks	USA	drought, pathogens, bark beetles, defoliators, snow & ice	pathogen & defoliator suppression
32	Porcupine	USA	windthrow, wildfires, defoliators, drought	fire suppression
34	Puyehue	Chile	volcanism, wildfires, windthrow, snow & ice	fire suppression
37	Risnjak	Croatia	snow & ice, windthrow, bark beetles	sanitary cuts, salvage logging
39	Sumava	Czech	bark beetles, windthrow	sanitary cuts, salvage logging
43	Tolhuaca	Chile	wildfires, drought, windthrow, snow & ice, landslides	fire suppression, irrigation
44	Torres del Paine	Chile	wildfires, defoliators, snow & ice	fire suppression
46	Villarrica	Chile	wildfires, drought, windthrow, snow & ice, landslides	fire suppression, irrigation
48	Weminuche	USA	bark beetles, drought, wildfires, defoliators	fire suppression, salvage logging

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Appendix B

Do bark beetle outbreaks amplify or dampen future bark beetle disturbances in Central Europe?

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RESEARCH ARTICLE

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Do bark beetle outbreaks amplify or dampen future bark beetle disturbances in Central Europe?

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Abstract

1. Bark beetle outbreaks have intensified in many forests around the globe in recent years. Yet, the legacy of these disturbances for future forest development remains unclear. Bark beetle disturbances are expected to increase further because of climate change. Consequently, feedbacks within the disturbance regime are of growing interest, for example, whether bark beetle outbreaks are amplifying future bark beetle activity (through the initiation of an even-aged cohort of trees) or dampening it (through increased structural and compositional diversity).
2. We studied bark beetle–vegetation–climate interactions in the Bavarian Forest National Park (Germany), an area characterised by unprecedented bark beetle activity in the recent past. We simulated the effect of future bark beetle outbreaks on forest structure and composition and analysed how disturbance-mediated forest dynamics influence future bark beetle activity under different scenarios of climate change. We used process-based simulation modelling in combination with machine learning to disentangle the long-term interactions between vegetation, climate and bark beetles at the landscape scale.
3. Disturbances by the European spruce bark beetle were strongly amplified by climate change, increasing between 59% and 221% compared to reference climate. Bark beetle outbreaks reduced the dominance of Norway spruce (*Picea abies* (L.) Karst.) on the landscape, increasing compositional diversity. Disturbances decreased structural diversity within stands (α diversity) and increased structural diversity between stands (β diversity). Overall, disturbance-mediated changes in forest structure and composition dampened future disturbance activity (a reduction of up to −67%), but were not able to fully compensate for the amplifying effect of climate change.
4. *Synthesis*. Our findings indicate that the recent disturbance episode at the Bavarian Forest National Park was caused by a convergence of highly susceptible

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forest structures with climatic conditions favourable for bark beetle outbreaks. While future climate is increasingly conducive to massive outbreaks, the emerging landscape structure is less and less likely to support them. This study improves our understanding of the long-term legacies of ongoing bark beetle disturbances in Central Europe. It indicates that increased diversity provides an important dampening feedback, and suggests that preventing disturbances or homogenizing post-disturbance forests could elevate the future susceptibility to large-scale bark beetle outbreaks.

KEYWORDS
climate change, disturbance interactions, diversity, forest composition, forest structure, iLand

1 | INTRODUCTION

Disturbances are key drivers of the structure, composition and functioning of forest ecosystems (Turner, 2010). Disturbance regimes are strongly driven by climatic conditions, and are thus sensitive to ongoing global climate change (Seidl et al., 2017). Due to increasing disturbances, the interactions and feedbacks within disturbance regimes are also of increasing importance (Buma, 2015). Insect outbreaks are biotic disturbances of major importance in forests around the globe (Anderegg et al., 2015). In the temperate and boreal biome, bark beetles are the most important insect disturbance agents (Netherer & Schopf, 2010; Raffa, Grégoire, & Lindgren, 2015). Bark beetle outbreaks are particularly affected by climate change due to the ectothermic physiology of the beetles (Jakoby, Lischke, & Wermelinger, 2019) and the drought sensitivity of the defence system of trees (Huang et al., 2020). Consequently, bark beetle outbreaks are intensifying in many forests globally (Hicke, Meddens, & Kolden, 2016; Marini et al., 2017).

The European spruce bark beetle (*Ips typographus* L., hereafter referred to as 'bark beetle' for brevity) is the economically most important bark beetle species in conifer forests of Europe, primarily attacking Norway spruce (*Picea abies* (L.) Karst., hereafter referred to as 'spruce') trees. At low population levels, bark beetles preferentially colonize weakened trees. Favourable conditions, like drought that weakens tree defences, high temperatures that accelerate bark beetle population growth and major windthrows that provide large amounts of breeding material, can trigger large-scale outbreaks, resulting in widespread mortality of healthy spruce trees (Biedermann et al., 2019; Kausrud et al., 2011; Marini et al., 2017). Spruce is a tree species of major economic interest in Europe (Grégoire, Raffa, & Lindgren, 2015), and growth in monocultures was promoted by foresters in the past (Hlásny et al., 2019), which further increases the susceptibility of the current vegetation to bark beetle outbreaks. On average, 14.5 Mill. m^3 of timber were affected by bark beetle disturbance annually between 2002 and 2010 in Europe (Seidl, Schelhaas, Rammer, & Verkerk, 2014), and bark beetles were an important driver of the recent doubling in canopy mortality across Central Europe (Senf et al., 2018).

Post-disturbance forest development of areas affected by bark beetles is receiving increasing attention as bark beetle outbreaks in forest landscapes of Central Europe increase in frequency and severity. Most of the recently disturbed forests regenerate vigorously even in the absence of human intervention, with several thousand saplings colonizing post-outbreak areas one to two decades after disturbance (Senf, Müller, & Seidl, 2019; Wild et al., 2014; Zeppenfeld et al., 2015). Interestingly, recent studies show that spruce, which is a mid- to late-seral species adopted to cool climate, dominates the regenerating cohort in subalpine forests, while pioneer species and warm-adapted species are largely missing (Macek et al., 2017). This suggests that recent disturbances have not catalysed tree species change (cf. Thom, Rammer, & Seidl, 2017a, 2017b), and that forests will likely recover to a species composition that is similar to the pre-disturbance state. Given the expectation of continued warming in coming decades (Stocker et al., 2013) and the large, even-aged, spruce-dominated cohort regenerating on the landscape, it has been hypothesized that the recent wave of disturbances will increase forest susceptibility to future disturbances. This is supported by the observation that past waves of disturbance also contribute to current disturbance activity in Europe's forests (Schurman et al., 2018). An alternative hypothesis is that forests regenerating following natural disturbances are *born complex* (Donato, Campbell, & Franklin, 2012), that is, they have high structural diversity despite being of similar age. Complexity can arise from the many biological legacies left after natural disturbances (e.g. remnant live trees, standing and downed woody debris, advanced tree regeneration not affected by disturbance, heterogeneous seed bank) and their influence on post-disturbance forest development (Diskin, Rocca, Nelson, Aoki, & Romme, 2011; Johnstone et al., 2016; Kayes & Tinker, 2012; Seidl, Rammer, & Spies, 2014). This complexity can result in multiple successional pathways (Meigs et al., 2017; Tepley, Swanson, & Spies, 2013) creating diversity on the landscape, which, in turn, dampens future forest susceptibility to spreading disturbances, such as bark beetles (Hart, Veblen, Mietkiewicz, & Kulakowski, 2015; Honkaniemi, Rammer, & Seidl, 2020; Seidl, Donato, Raffa, & Turner, 2016). Empirical findings and simulation studies from North America suggest that past bark beetle outbreaks exert strong negative feedbacks on subsequent outbreaks (Hart et al., 2015; Kashian, Jackson, & Lyons, 2011; Temperli, Veblen, Hart, Kulakowski, & Tepley, 2015). These negative feedbacks emerge mainly due to shifts in tree species composition and subsequent reduction in host availability as well as increased structural diversity (Kayes & Tinker, 2012; Temperli et al., 2015). Recent analyses for Central Europe show that natural forests are characterized by higher structural diversity than managed forests in the first decades after disturbance (Senf et al., 2019). Yet, it remains unclear whether such a disturbance-mediated increase in diversity will persist as forests mature and develop through a stem exclusion stage. Furthermore, whether elevated diversity is able to counteract the increasing disturbance pressure caused by climate change remains unclear (Dobor et al., 2020; Temperli, Bugmann, & Elkin, 2013; Thom et al., 2017b).

Testing hypotheses on the long-term development of forest landscapes under future climate change relies on the use of simulation models. Dynamic process-based simulation models represent key biological processes of forest dynamics (e.g. competition, growth, regeneration, mortality, seed dispersal, disturbance) based on first principles of ecology (Gustafson, 2013), and are thus able to make robust projections of future vegetation development. Process-based simulation models can investigate the complex interdependencies of interacting disturbance agents, disturbance legacies and the compositional and structural diversity of forest landscapes under past and future climatic conditions. Analysing the feedbacks of disturbances on vegetation development and their implications for future disturbances particularly relies on the use of simulation models, due to the need to consider time horizons of multiple centuries (Temperli et al., 2013; Thom, Rammer, Garstenauer, & Seidl, 2018). A further advantage of using simulation modelling is the ability to derive dynamic reference trajectories (e.g. simulations of undisturbed forest development) in order to isolate the effects of focal processes such as disturbances (Dobor et al., 2018). Additionally, while the investigation of disturbances necessitates analyses across landscapes, field experimentation with sufficient replication is not possible at this spatial scale (Phillips, 2007), a problem that can be overcome by conducting experiments in silico.

Here we used landscape-scale simulation modelling to investigate how bark beetle outbreaks influence structural and compositional diversity, and how they affect future bark beetle dynamics under climate change. We hypothesized that bark beetle disturbances will increase under future climate conditions (H1). Specifically, we expected that higher temperatures will accelerate the development of bark beetles and that associated increases in water demand will increase the susceptibility of host trees (Huang et al., 2020; Netherer & Schopf, 2010; Seidl & Rammer, 2017). Furthermore, we hypothesized that future bark beetle disturbances will increase compositional and structural diversity of forest landscapes (H2). We expected compositional diversity to increase due to disturbances creating niches for the establishment of new tree species, and due to reduction in the competitive strength of spruce (Hilmers et al., 2019; Thom et al., 2017a). Furthermore, we expected forest structure to increase in diversity due to the effect of disturbance legacies as well as spatially heterogeneous regeneration and stand development (Donato et al., 2012; Meigs et al., 2017). Finally, we quantified the feedbacks of disturbance-mediated compositional and structural diversity on future bark beetle outbreaks, hypothesizing a dampening (self-regulating) effect of forest dynamics under disturbance (H3). We expected that more diverse forests will dampen future bark beetle disturbances due to the presence of fewer host trees and decreased host connectivity (Seidl, Müller, et al., 2016; Temperli et al., 2013).

2 | MATERIALS AND METHODS

2.1 | Study landscape

The Bavarian Forest National Park (BFNP) is a forested landscape in Southeastern Germany (Figure 1). The area is characterized by moderate topography, with an elevation range from 655 to 1,420 m a.s.l. Mean annual temperature ranges from 3.5 to 7.0°C and decreases with elevation, and annual precipitation ranges from 1,000 to 1,900 mm, increasing with elevation. Dominant tree species include Norway spruce at mid- to high elevations as well as silver fir (*Abies alba* Mill.) and European beech (*Fagus sylvatica* L.) mixed with spruce at lower elevations. Natural tree species composition was heavily affected by humans at least since 500 BC, which has reduced the proportion of silver fir (van der Knaap et al., 2020). The cultivation of spruce was expanded in the 16th century due to an increasing wood demand for manufacturing, and in the 19th century due to the emergence of commercial forestry. Founded in 1970, the BFNP is Germany's oldest national park. The 24,000 ha landscape was protected in two phases, with an extension of the initial protected area in 1997. We here focus on the 13,985 ha designated as national park in 1970 due to data availability issues. The BFNP saw the largest unsuppressed bark beetle outbreak in Central Europe in recent history, characterized by two distinct outbreak waves (1996–2000 and 2005–2009) affecting close to 50% of the study area.

2.2 | Simulation model

We used the individual-based forest landscape and disturbance model iLand (Seidl, Rammer, Scheller, & Spies, 2012) to study the effects of future climate and disturbance regimes. Specifically, we applied the model to quantify the interactions between structural and compositional diversity at BFNP and the development of bark beetle populations. iLand dynamically simulates the regeneration, growth and mortality of individual trees, influenced by climate, soil, initial legacies of vegetation and disturbance. The spatial grain of the simulations is 2 m × 2 m for the calculation of the light regime, while ecosystem processes (e.g. water and carbon cycles) are tracked at a grain of 100 m × 100 m; the spatial extent of the simulations is 13,985 ha of BFNP. We simulated disturbances by

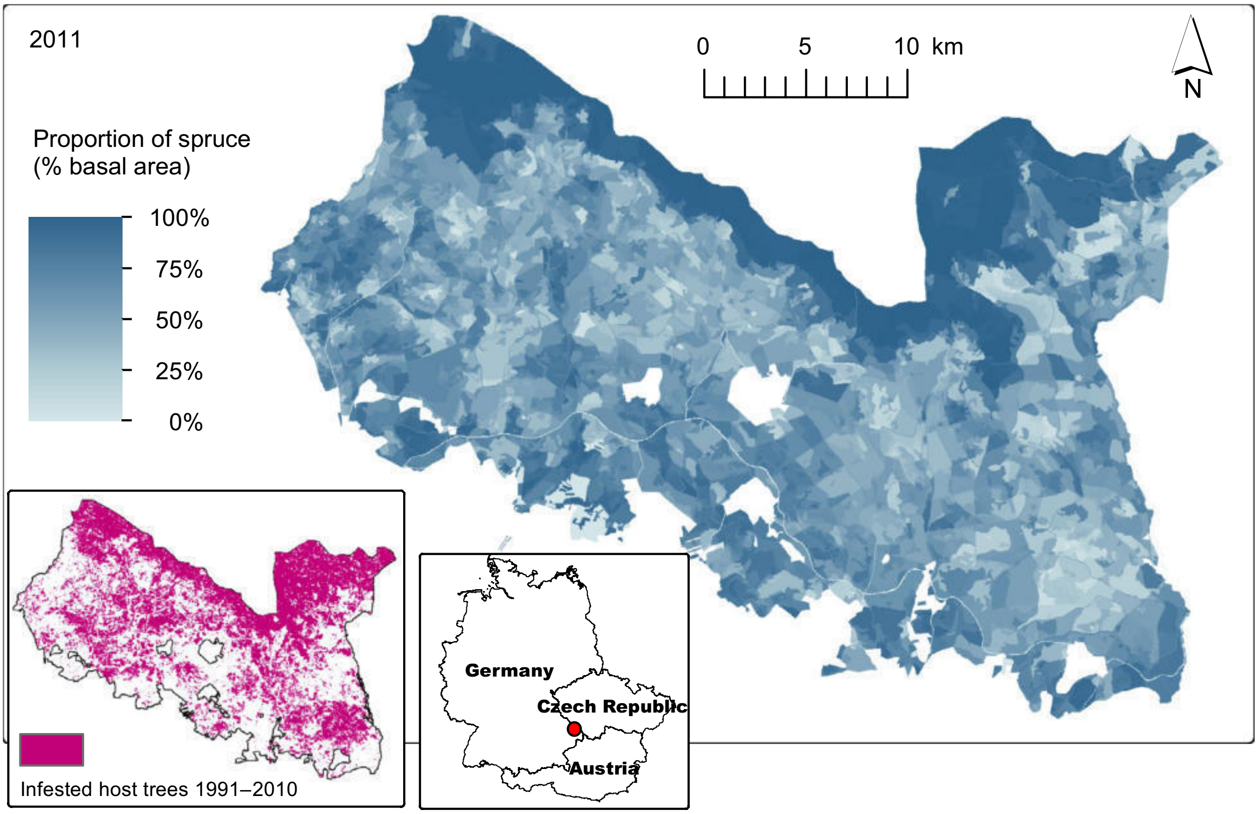

FIGURE 1 The Bavarian Forest National Park landscape, depicting the proportion of Norway spruce (i.e. the host tree of the European spruce bark beetle) on total basal area in the year 2011 (i.e. the initial year of this study). The lower left panel shows bark beetle infested host trees between 1991 and 2010 and the lower right panel indicates the location of the landscape in Central Europe

bark beetle outbreaks and windthrow, the two most important disturbance agents in the region, explicitly. Simulated bark beetle population dynamics accounts for beetle development and phenology and models beetle dispersal in a spatially explicit manner. The processes of host colonization, tree defence and temperature-dependent winter mortality are also considered (Seidl & Rammer, 2017). As the ability to realistically simulate bark beetle outbreaks is crucial for the current study, we extensively tested spatial and temporal patterns of simulated bark beetle infestations against independent data (Kautz, Dworschak, Gruppe, & Schopf, 2011; Figures S1–S3). In addition, we examined model performance in a pattern-oriented modelling approach (Grimm et al., 2005), comparing simulated data against independent empirical observations of tree growth and potential natural vegetation (PNV) development (Figures S4–S8). A more detailed description of iLand can be found in Seidl, Spies, et al. (2012) and Thom et al. (2017b). The model code and executable as well as an extensive online documentation are available at http://iLand.boku.ac.at.

2.3 | Initial conditions and climate scenarios

Simulation runs were initiated with the state of the vegetation in 2011, that is, after the most recent bark beetle outbreak waves of the years 1996–2010. We initialized the model based on the latest available plot-level forest inventory data regarding tree species, basal area, tree height and stand age (year 1992), and prescribed bark beetle disturbances as observed from aerial surveys (Kautz et al., 2011) to obtain the initial vegetation state (year 2011) from dynamic simulations. Data on soils and climate were available at a 100 m × 100 m grid. Soil properties required in the simulation (i.e. effective soil depth, the relative proportion of sand, silt and clay, as well as plant-available nitrogen and the initial carbon stocks in litter and soil organic matter layers) were derived by combining the wall-to-wall site classification system of BFNP with quantitative soil profile data.

We ran simulations under four different climate scenarios. Historical climate data from 1980 to 2015 was used as a reference period for constructing a baseline climate scenario by randomly drawing years with replacement. In addition, we simulated three different climate change scenarios, representing different combinations of representative concentration pathways (RCP 4.5 and 8.5) and climate models (ICHEC-EC-EARTH and MOHC-HadGEM2-ES). The temperature and precipitation changes resulting from these scenarios in our study region are detailed in Table S1. In the following text, we refer to the climate scenarios as baseline climate scenario (BC), moderate climate change scenario (MC, RCP 4.5 ICHEC-EC-EARTH), hot climate change scenario (HC, RCP 8.5, ICHEC-EC-EARTH) and hot and wet climate change scenario (HWC, RCP 8.5, MOHC-HadGEM2-ES). Climate change time series were extended beyond 2099 by sampling with replacement from the years 2070–2099. The dependency of our simulation results on this particular approach of generating a long-term climate time series was tested in a sensitivity analysis (see Figure S8). All climate data were statistically downscaled to the study region at 100 m horizontal resolution (see Seidl et al., 2019 for details). As the current generation of climate models is not yet able to capture extreme local wind events well, the occurrence of storm events was based on historically observed wind data, assuming no changes in future peak wind speeds and return intervals. To isolate the effect of disturbances on forest structure and composition, we simulated two different disturbance scenarios in each climate scenario, that is, an undisturbed control scenario for which disturbances were omitted throughout the entire simulation period (referred hereafter as *undisturbed*) and a scenario in which disturbances and their impacts on vegetation were dynamically simulated in iLand (referred hereafter as *disturbed*). All simulations were replicated 20 times to account for stochasticity.

2.4 | Analyses

In order to assess the long-term consequences of disturbances we simulated forest development over a period of 600 years. First, to test our hypothesis of increased future bark beetle disturbances (H1), we evaluated the amount of growing stock disturbed by beetles in the different simulation scenarios. To put simulated future trajectories into context, values were compared to reference data for the outbreaks of the period 1996–2010.

Second, to address our hypothesis on disturbance-mediated increases in diversity (H2), we compared *undisturbed* simulations to those simulating wind and bark beetle disturbances dynamically (*disturbed*). We here characterized diversity at two spatial scales (stand [100 m grid cells], landscape) and for two domains (structure, composition), deriving a total of eight indicators of diversity (see Table 1) from the simulated data at 50-year time steps. For landscape-level analyses, an eight-neighbour rule was used to define neighbourhood. To attribute individual effects of climate change, disturbances and the combined effect of climate change and disturbances, we compared diversity indicators between contrasting trajectories. Our reference simulations without climate change and disturbances (i.e. BC and *undisturbed*) were contrasted to simulations with climate change only (e.g. HWC and *undisturbed*), with disturbances only (i.e. BC and *disturbed*) and to simulations with combined effects of climate change and disturbances (e.g. HWC and *disturbed*). We used principle component analyses (PCA), as implemented in the R package *factoextra* (version 1.0.5; Kassambara & Mundt, 2017), to reduce the dimensions of our dataset and visualize differences in forest development trajectories between *disturbed* and *undisturbed* simulations.

Third, we used simulation outputs in combination with machine learning to quantify the effect of differences in diversity on simulated bark beetle outbreaks (H3). Specifically, we trained a random forest model (Breiman, 2001) using the R package RANDOMFOREST (version 4.6-14; Liaw & Wiener, 2002), on the simulation outcomes from the *disturbed* simulation series, using the amount of growing stock disturbed by bark beetles as the response variable and the indicators of structural and compositional diversity (cf. Table 1) as well as climate data (e.g. mean annual temperature, mean annual precipitation)

TABLE 1 Overview of the indicators analysed

Attribute	Scale	Indicator (abbreviation)	Unit	Description
Structure	Stand	α-diversity of tree height (AlpHei)	Dim.	Shannon–Wiener index of height classes (4 m class width) within forest stands
	Stand	α-diversity of tree diameter (AlpDbh)	Dim.	Shannon–Wiener index of dbh classes (4 cm class width) within forest stands
	Landscape	Canopy cover (CanCov)	Dim.	Horizontal structure and distribution of canopy, described by the proportion of the ground surface that is covered by tree crowns
	Landscape	Rumple index (RumInd)	Dim.	Vertical structure and distribution of canopy, described by the ratio of the canopy surface area to the ground surface area
	Landscape	β-diversity of tree height (BetHei)	Dim.	Shannon–Wiener index of height classes (4 m class width) among forest stands, multiplicative beta diversity (β-div. = γ-div./α-div.)
	Landscape	β-diversity of tree diameter (BetDbh)	Dim.	Shannon–Wiener index of dbh classes (4 cm classes) among forest stands, multiplicative beta diversity (β-div. = γ-div./α-div.)
Composition	Landscape	Proportion of spruce (ProSpr)	%	Per cent of Norway spruce on the total basal area of all trees
	Landscape	Aggregation index of potential host trees for bark beetle attack (AggInd)	%	Percentage of the landscape with contiguous raster cells hosting spruce trees above 15 cm dbh

Abbreviations: Dbh, diameter at breast height; Dim., dimensionless.

as predictors. To quantify the effect of disturbance-mediated changes in forest structure and composition on bark beetle dynamics, we predicted the amount of growing stock affected by bark beetles using the random forest model. Specifically, predictions were made for (a) the forest structure and composition simulated in the *disturbed* series and (b) the forest structure and composition simulated in the *undisturbed* series, using the same random forest model. This approach allowed us to disentangle the effects of disturbance-mediated changes in forest structure and composition on the propensity of bark beetle disturbances, effectively quantifying potential self-regulating feedbacks within the disturbance regime. We used the R software for statistical computing (version 3.5.1; R Core Development Team, 2018) for data preparation, analyses of simulation data and visualization.

3 | RESULTS

3.1 | Future bark beetle dynamics

Climate change had a strong amplifying effect on future bark beetle dynamics. The cumulative growing stock affected by bark beetles was 59.0% higher under moderate climate change scenario, and 204.8% and 221.1% higher in the hot and hot and wet climate change scenarios, respectively, compared to baseline climate. These cumulative differences between climate scenarios mainly accrued in the first half of the 600-year simulation period, while differences among climate scenarios diminished in the last century of the simulation. The general pattern of future bark beetle dynamics over time was similar in all climate scenarios. Bark beetle activity was low in the first years of the analysis, and peaked between years 50 and 200 of the simulation. Of the cumulative growing stock affected by bark beetle over the 600-year study period, between 57.6% (scenario MC) and 85.6% (scenario HWC) accrued in the first 200 years of the simulation (Figure 2). Outbreak patterns within this period differed strongly with climate scenario. Under the HWC scenario, bark beetle outbreaks peaked early and showed the highest peaks (10-year moving average of up to 3.71 m^3 of growing stock disturbed per ha and year). The hot climate scenario resulted in a lower and more prolonged peak (maximum 10-year moving average of 2.30 m^3 ha^{-1} $year^{-1}$). While the central tendency in both of these scenarios was thus below the bark beetle impact observed for the outbreaks of 1990–2010 (10.73 m^3 ha^{-1} $year^{-1}$), beetle activity in one of the 20 replicate simulations under the hot and wet climate scenario exceeded recent observations (Figure 2). Under moderate climate change, future outbreaks led to a distinctly different pattern over time, with more frequent yet much smaller outbreak waves (maximum 10-year moving average of 1.07 m^3 ha^{-1} $year^{-1}$) occurring in the simulations.

3.2 | Effects of bark beetle disturbances on diversity

Bark beetle disturbances increased compositional diversity within the landscape (Figure 3). Specifically, they reduced spruce dominance and increased the spatial heterogeneity of species composition. Spruce proportion decreased dramatically under all climate scenarios, even under baseline climate it declined by more than 50% (from an initial value of 60.5% to 28.9% at the end of the simulation period, Figure S10). Spruce virtually disappeared under the hot climate scenarios (only 1.7% of spruce basal area remained under HWC at the end of the simulation period). The most important factor

TABLE 2 Response of forest structure and composition to climate change and disturbances. Results are shown as differences in indicator values averaged over the entire simulation period, relative to the mean value of simulations with baseline climate and no disturbances. Shown are results for the hot and wet climate scenario, which is the scenario with the highest disturbance activity in terms of timber volume disturbed (cf. Figure 2). For results of all other climate scenarios see Tables S2–S4. See Table 1 for a detailed description of the indicators used

Indicator	Attribute	Scale	Effect of climate change (*undisturbed simulations*)	Effect of disturbances (*disturbed simulations under BC climate*)	Effect of disturbances and climate change
α-diversity height	Structure	Stand	−0.8%	−2.0%	−25.5%
α-diversity dbh		Stand	+2.4%	−2.8%	−20.5%
Canopy cover		Landscape	+2.4%	−0.2%	+7.1%
Rumple index		Landscape	+0.8%	+1.2%	+2.4%
β-diversity height		Landscape	+2.0%	+1.3%	+42.1%
β-diversity dbh		Landscape	+1.3%	+1.4%	+35.2%
Proportion of spruce	Composition	Landscape	−8.2%	−9.4%	−58.9%
Aggregation index		Landscape	+1.7%	−5.3%	−11.6%

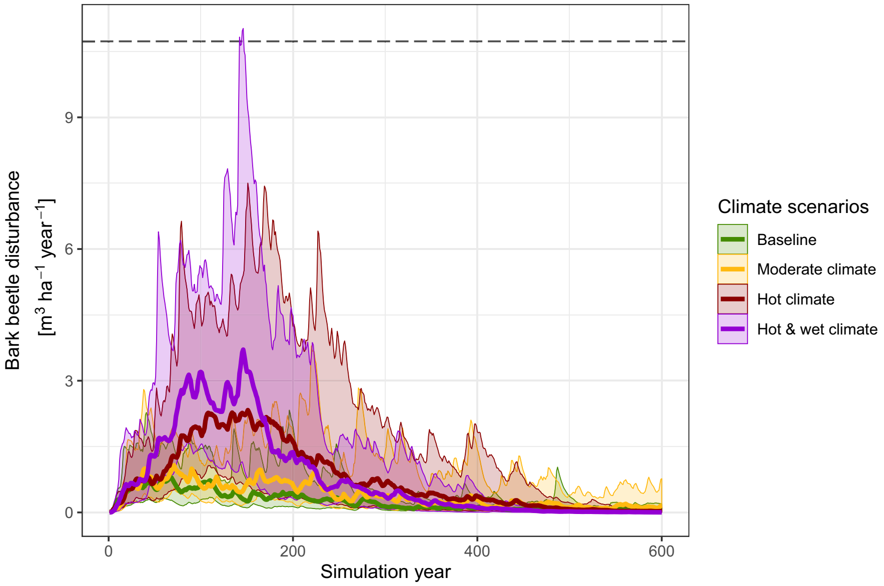

FIGURE 2 Projected growing stock affected by bark beetles in different climate scenarios. The figure shows the exponential moving average of bark beetle disturbance (averaging window = 10 years with reduction factor of 1/10). Bold lines are mean values and envelopes indicate the range of values derived from 20 replicated simulations per scenario. The horizontal dashed line at $y = 10.73$ indicates the 10-year exponential moving average of bark beetle activity in the recent past (1990–2010)

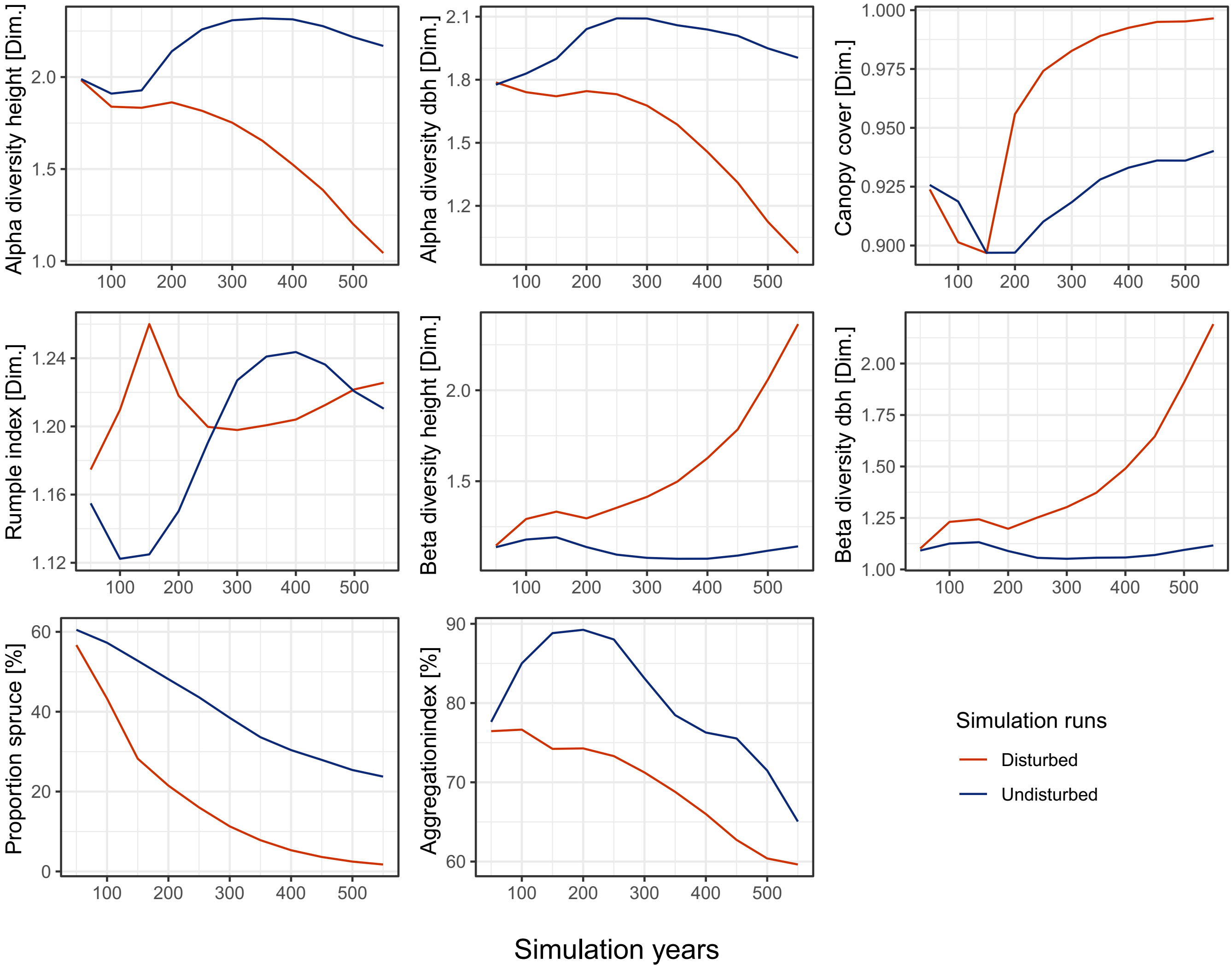

FIGURE 3 Effect of disturbances on forest structure and composition. Shown are the mean effects for the hot and wet climate scenario, which is the scenario with the highest disturbance activity in terms of timber volume disturbed (cf. Figure 2). For results of all other climate scenarios see Figures S10–S12. We refer to Table 1 for a detailed description of the indicators used

contributing to spruce decline was the amplifying interactions between climate change and bark beetle disturbances. European beech and silver fir were the main tree species replacing spruce on the landscape (Figure S9).

The response of structural diversity to bark beetle disturbances was less clear and differed with scale. Beta diversity increased and alpha diversity decreased in *disturbed* compared to *undisturbed* simulations. This pattern was consistent for both diameter and height diversity. Among-stand diversity doubled in simulations under the climate scenario with the most intense bark beetle impacts (HWC), while within-stand diversity halved over the simulation period compared to *undisturbed* simulations. Similar to the decline of spruce, these changes were primarily driven by the combined effects of climate change and disturbances (Table 2). Principle component analysis suggests that *disturbed* scenarios followed a distinctly different trajectory of forest development compared to *undisturbed* simulations (Figure 4a). The first two principle components explained 90.2% of the total variation in our data (PCA axis 1 = 63.5% and PCA axis 2 = 26.7%). Factor loadings (Figure 4b) showed that variables of forest composition and structure were largely orthogonal, while indicators of α and β diversity were inversely related. In early years of the simulation, the development trajectories mainly differed in composition (i.e. along the PCA axis 2 in the Figure 4a,b), while in later years divergent structural development (i.e. differences along PCA axis 1) add to increasingly diverging trajectories.

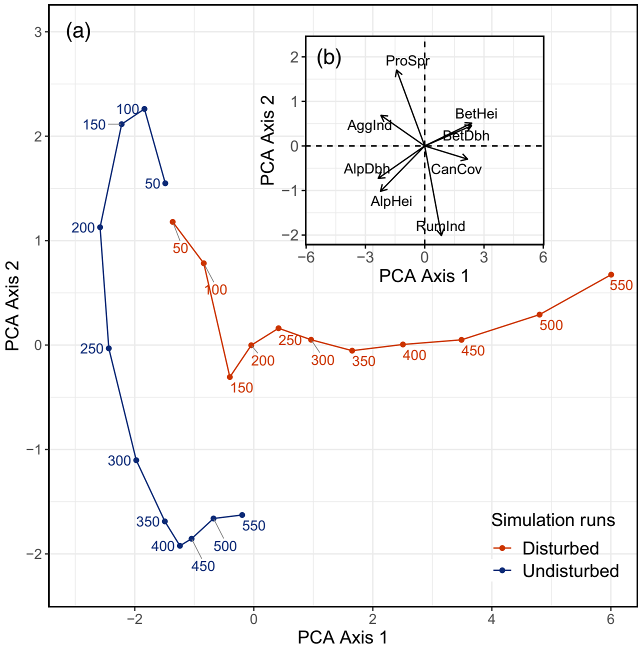

FIGURE 4 Principle component analysis showing forest development trajectories in *disturbed* and *undisturbed* simulation runs (Panel a). The disturbed trajectory shows the hot and wet climate scenario, which is the scenario with the highest disturbance activity in terms of timber volume disturbed (cf. Figure 2), with numbers indicating simulation years. Panel (b) shows the loadings of individual variables contributing to the PCA (for abbreviations we refer to Table 1)

3.3 | Disturbance-mediated forest development affects future disturbances

We found strong evidence for dampening feedbacks within the disturbance regime, with disturbance-mediated changes in forest structure and composition decreasing future disturbance activity. The random forest model used to disentangle the effects of forest structure, composition and climate on disturbance activity was well able to describe the simulated data, explaining 96.0% of its variance. Sensitivity analyses using this random forest model showed that due to the disturbance effects on forest structure and composition, the amount of growing stock affected by bark beetles was 67.4% lower than under *undisturbed* forest structure and composition (scenario HWC). Structural effects—although more ambiguous across the indicators investigated (see Figure 3)—had a similar dampening impact as compositional effects (Figure 5). The strength of dampening feedbacks in the disturbance regime increased with disturbance activity and was considerably higher in the hot as well as in the hot and wet climate scenarios compared to moderate and baseline climate. However, dampening feedbacks from disturbance-mediated changes in forest structure and composition could not fully compensate the disturbance increases caused by climate change.

4 | DISCUSSION

Natural disturbances from both abiotic and biotic agents have increased strongly in recent decades in many parts of the world (Kautz, Meddens, Hall, & Arneth, 2017; Senf et al., 2018; Westerling, 2016), with unprecedented disturbance episodes affecting landscapes throughout the globe. Given that climate change is an important driver of shifting disturbance regimes (Dale et al., 2001; Marini et al., 2017; Seidl et al., 2017), it is important to quantify potential future trajectories of natural disturbances considering the range of possible future climate conditions. Here we show that climate change has an amplifying effect on future bark beetle outbreaks in Central Europe, supporting our initial hypothesis (H1). This finding is in line with previous analyses for different forest ecosystems in the northern hemisphere (Bentz et al., 2010; DeRose, Bentz, Long, & Shaw, 2013; Dobor et al., 2020; Seidl, Rammer, Jäger, & Lexer, 2008; Seidl, Schelhaas, Lindner, & Lexer, 2009; Temperli et al., 2013; Thom et al., 2017b), emphasizing that bark beetle disturbances are among the most climate-sensitive processes in temperate forest ecosystems. What makes our study unique is that it focused on the landscape that experienced the largest unmanaged bark beetle outbreak recorded throughout Europe in the recent history. Despite the high climate sensitivity of bark beetle outbreaks, our results suggest that future outbreaks of bark beetles in the BFNP are unlikely to reach similar intensities as those that have occurred in the recent past. While individual simulation trajectories reached previously observed levels of bark beetle activity, the central tendency remained considerably below these levels even under severe climate change (scenarios

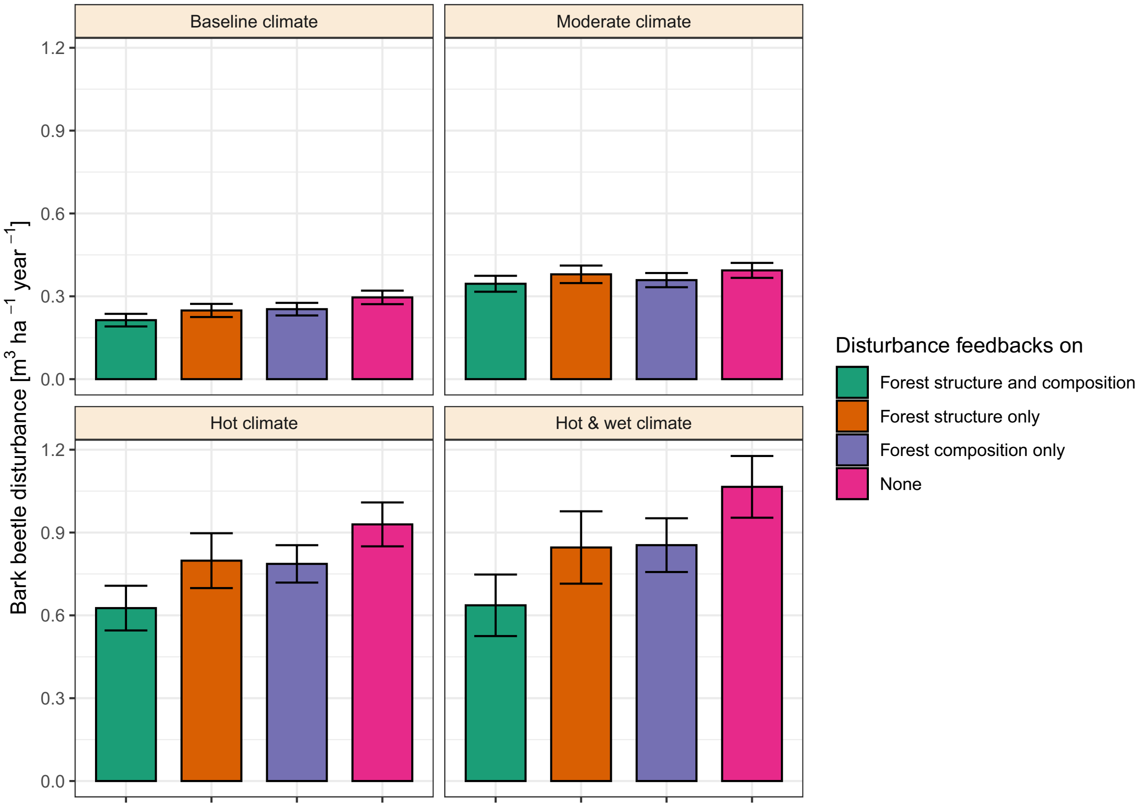

FIGURE 5 Effects of disturbance-mediated feedbacks of forest structure and composition on bark beetle activity, summarized over the entire 600-year simulation period. Disturbance feedbacks were isolated using a random forest model trained on simulation data. Bars indicate mean values and whiskers give the 95% confidence interval over all replicates per climate scenario

HC & HWC). This suggests that future climate is increasingly conducive to such massive outbreaks, but the emerging landscape structure is unlikely to support them. Our results thus indicate that the BFNP bark beetle outbreaks of the recent past resulted from the convergence of favourable climate and highly susceptible forest conditions (Aukema et al., 2006; Duan, Taylor, & Fuester, 2011; Seidl, Schelhaas, & Lexer, 2011). These two factors are unlikely to coincide again in the future at BFNP because compositional and structural diversity is increasing relative to the low values of the past, which were largely the result of past land-use. More broadly the importance of forest structure and composition for bark beetle outbreaks found here is in line with insights from ecosystems in Northern America, where the dampening effects of structure and composition can even exceed the amplifying effect of climate (DeRose et al., 2013; Hart et al., 2015; Temperli et al., 2015).

We showed that the BFNP landscape is dynamically changing away from its recent historical condition of structurally homogeneous and highly spruce-dominated forests. European beech and silver fir expanded in our simulations, which is in line with previous projections of future forest development (Cailleret, Heurich, & Bugmann, 2014; Hanewinkel, Cullmann, Schelhaas, Nabuurs, & Zimmermann, 2013; Temperli et al., 2013; Thom et al., 2017b). In this context, it is important to note that we did not explicitly consider disturbance agents that target specific tree species other than Norway spruce. Future work should aim to capture the biotic disturbance regime more comprehensively, as other agents could impede the expansion of fir and beech in the future. For bark beetle outbreaks, we show that climate change has both positive (amplifying) and negative (dampening) impacts, fostering beetle development and increasing host susceptibility (direct effect, short-term), while at the same time, shifting the competitive balance towards non-host trees (indirect effect, mid- to long-term; Seidl et al., 2017). A second important trend in future forest development was an increase in structural diversity between stands (β-diversity). This suggests that the heterogeneity in diameters and tree heights at a grain of 100 m will considerably increase in the future BFNP landscape (cf. Schall et al., 2018). In contrast to the change in tree species composition—which was primarily driven by climate change—the increase in beta diversity was mainly the result of increasing disturbances. Simultaneously, structural diversity within 100 m grid cells decreased in our simulations. It is important to note that we used Whitaker's multiplicative definition of beta diversity (Jost, 2007), which means that the values for both levels are not independent of each other. The patterns identified here, however, are ecologically realistic, given that most bark beetles only disperse several tens of meters (resulting in spatially clustered mortality; Kautz et al., 2011), and that the mean size of disturbance patches in Central Europe is roughly 1 ha (Senf, Pflugmacher, Hostert, & Seidl, 2017; Sommerfeld et al., 2018).

Overall, bark beetle outbreaks increased the structural and compositional diversity of forest ecosystems in our simulation, supporting our initial hypothesis (H2). These findings are in line with previous studies relating forest composition and structure to disturbances. Panayotov, Kulakowski, Laranjeiro Dos Santos, and Bebi (2011), for instance, using empirical data and remote sensing, related large variation in tree heights and diameters to prior wind disturbances. Janda et al. (2017) documented that past disturbance severity is a strong driver of current stand structure, using a combination of dendroecology and historical data sources. Kayes and Tinker (2012) and Veblen, Hadley, Reid, and Rebertus (1991) found that bark beetles increase the structural and compositional diversity by releasing advanced regeneration and small-diameter trees. Likewise, Kashian et al. (2011) report increases in stand structural diversity as a result of prior bark beetle outbreaks. Silva Pedro, Rammer, and Seidl (2016) found that disturbances have positive effects on forest composition at both alpha and beta levels even under high disturbance frequencies. The fact that they did not study highly spatially aggregated disturbance agents such as bark beetles might account for the different response of alpha diversity compared to our study. Overall, we show that bark beetle disturbances can substantially alter forest development trajectories. It is thus essential to consider them explicitly in models that aim to project the future of forest ecosystems (Huang et al., 2020).

We documented important dampening feedbacks within the natural disturbance regime of Central Europe's forests. Specifically, we showed that bark beetle disturbances have a negative influence on future bark beetle activity via modifying the structure and composition of forest ecosystems. Dampening feedbacks are well-documented for many fire-driven systems, where burning consumes fuel, limiting subsequent fire activity (Bigler, Kulakowski, & Veblen, 2005; Harvey, Donato, & Turner, 2016; Parks, Holsinger, Miller, & Nelson, 2015). By analogy, studies for biotic disturbances have shown dampening feedbacks due to depletion of suitable hosts on the landscape (Cruickshank, Jaquish, & Nemec, 2010; Temperli et al., 2013; Thom et al., 2017b). Engelmann spruce *Picea engelmannii* – spruce beetle *Dendroctonus rufipennis* systems in Northern America, for instance, have reduced susceptibility to large-scale outbreaks after disturbance due to the paucity of large-diameter host trees (Hart et al., 2015; Temperli et al., 2015). We highlight how structural diversity can serve as another critical dampening feedback mechanism within biotic disturbance regimes. Our simulations suggest that disturbance-mediated beta diversity inhibits the spread of future bark beetle outbreaks (see also Honkaniemi et al., 2020). This is in line with recent findings of dampening feedbacks between wildfires and bark beetle outbreaks (Seidl, Donato, et al., 2016). Based on our simulations, the effect size of increased structural diversity was comparable to that of depleted host trees (cf. Figure 5), suggesting that a diverse vertical and horizontal structure between stands is an important factor mitigating bark beetle outbreaks.

Our results indicate that disturbance-mediated forest development trajectories are less prone to very large-scale bark beetle outbreaks compared to those in which natural disturbances are absent for a long time. This finding suggests that preventing bark beetle disturbances via technical measures (e.g. trapping, chemicals, timely remove of infested trees) could in fact increase the risk for future, large-scale bark beetle outbreaks. This result is in line with findings regarding the effect of fire prevention (Stephens et al., 2013), and with recent analyses showing that a management-induced reduction in bark beetle disturbances can lead to increased disturbances from wind (Dobor et al., 2020). It furthermore supports broader conceptual arguments that suggest preventing natural disturbances is only successful under a limited set of conditions and can lead to unintended consequences (Holling & Meffe, 1996; Seidl, 2014).

We conclude that while future climate change will intensify forest disturbance regimes, potent dampening feedbacks such as disturbance-mediated increases in diversity exist in the forest ecosystems of Central Europe. Management should aim to support and—where possible—mimic these processes to foster the adaptation of forest ecosystems to changing forest disturbance regimes.

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AUTHORS' CONTRIBUTIONS

A.S., W.R., and R.S. designed the study, analysed the data and wrote the paper; M.H., T.H. and J.M. contributed data and commented on the manuscript. All authors contributed critically to earlier drafts and gave final approval for publication.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

Data are available from the figshare repository: https://doi.org/10.6084/m9.figshare.12885200.v1 (Sommerfeld et al., 2020).

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SUPPORTING INFORMATION

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

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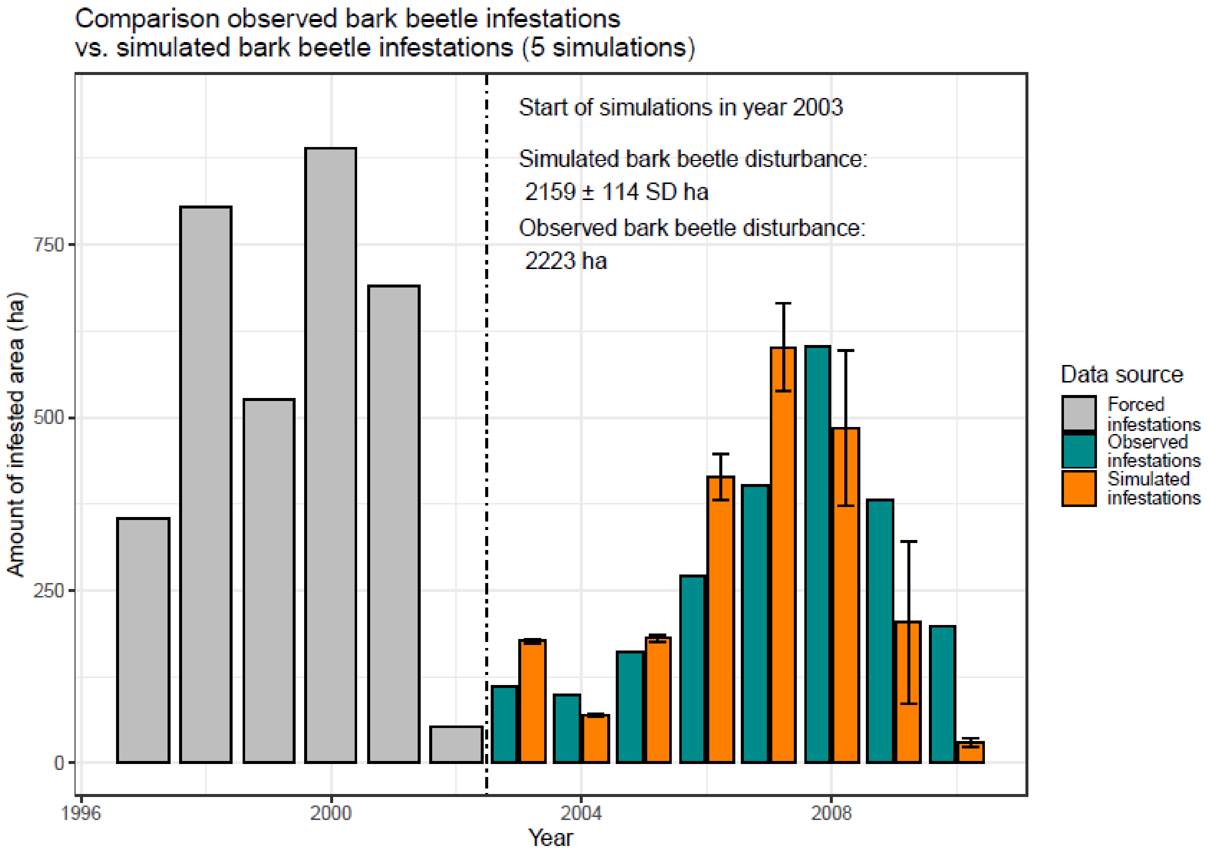
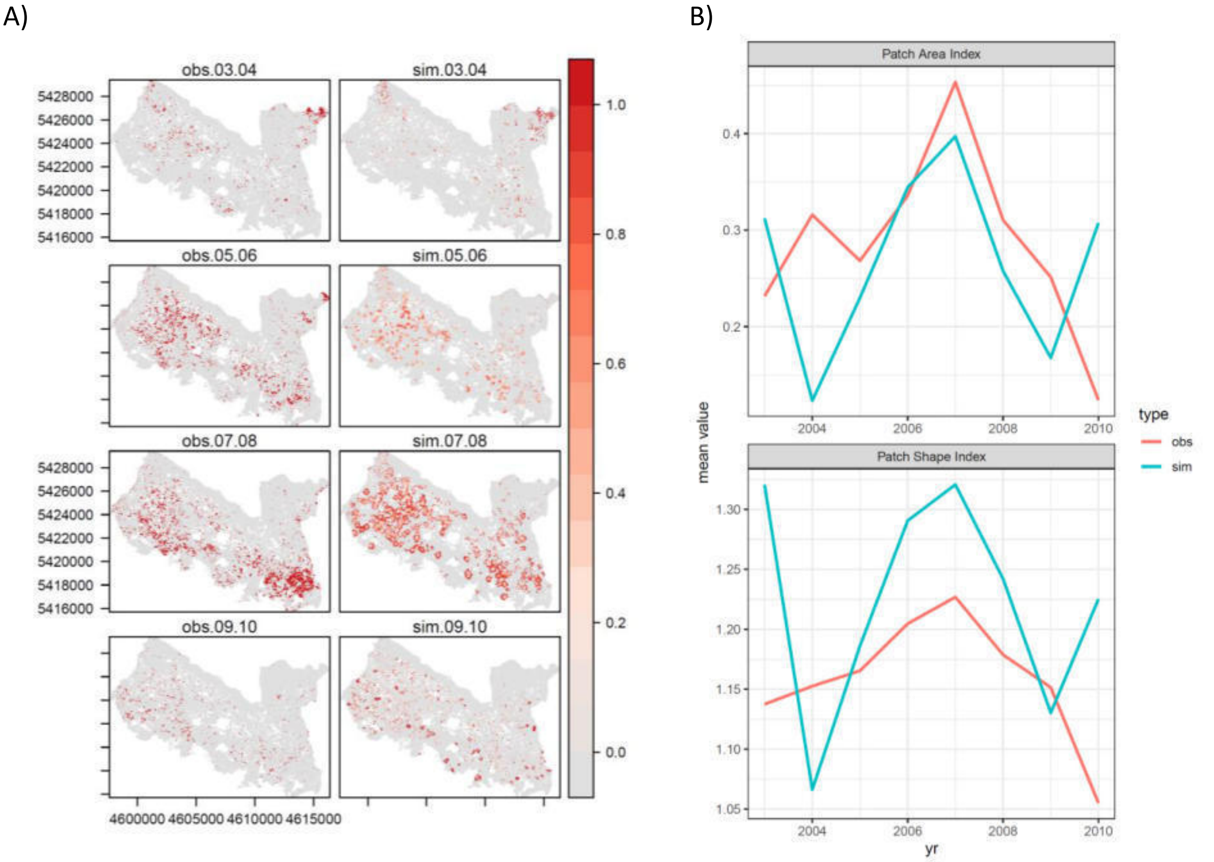
Supplement: Do bark beetle outbreaks amplify or dampen future bark beetle disturbances in Central Europe?

Andreas Sommerfeld, Werner Rammer, Marco Heurich, Torben Hilmers, Jörg Müller, Rupert Seidl

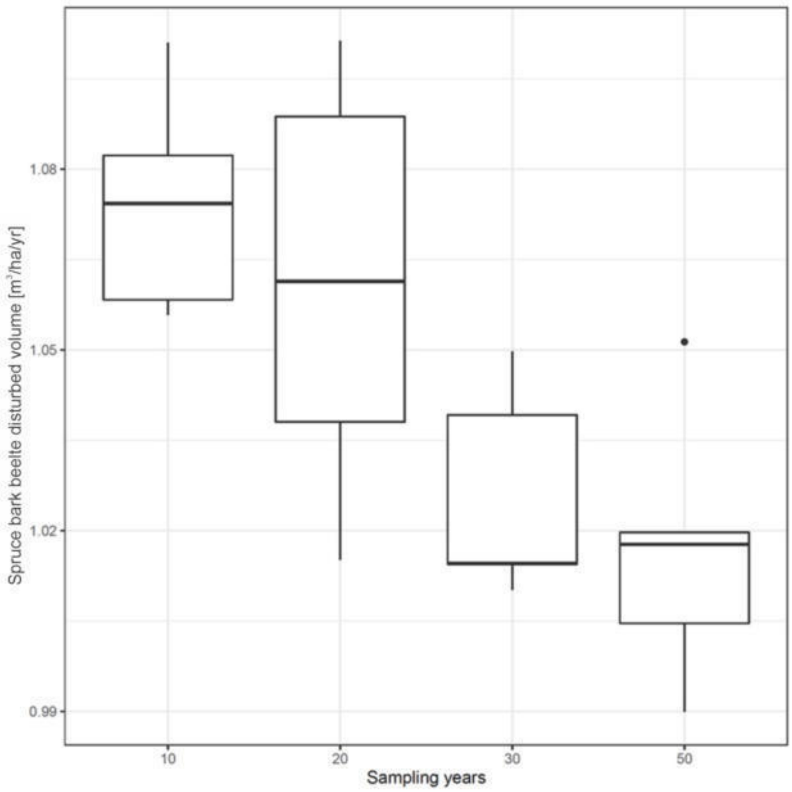
1. Bark beetle tests



Supplemental Figure 1: Comparison of observed and simulated temporal pattern of bark beetle infestations. Simulated bark beetle infestations were forced to follow observed infestation until year 2002 in order to initialize bark beetle population levels. From 2003 onwards bark beetle dynamics was simulated as an emergent property in iLand. Simulated values are the annual mean area of bark beetle infestations derived from 5 replicated simulations, with error bars indicating their standard deviation.

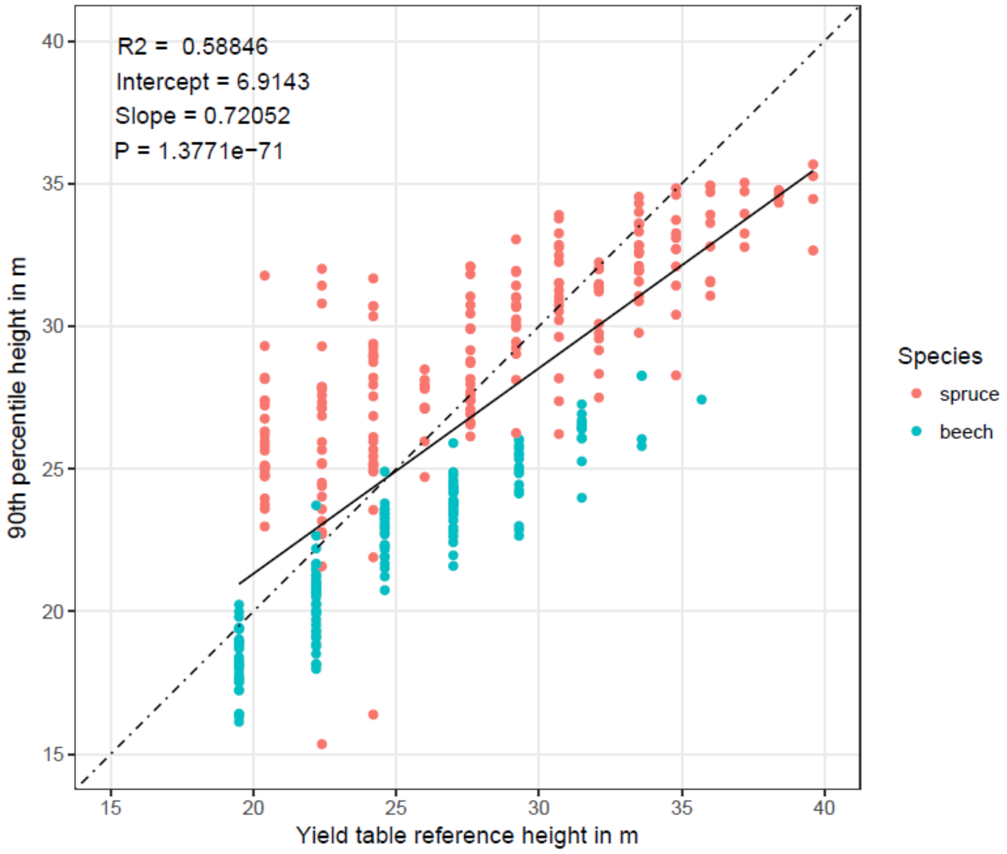


Supplementary Figure 2: A) Observed spatial patterns of bark beetle infestation (left) and simulated infestation probability based on five replicated simulations (right), aggregated in bins of two years for the period 2003 to 2010. The mean contiguity index over all years (± sd) was 0.124 ±0.035 for the observed outbreak and 0.094 ±0.032 for the simulated outbreak. B) Landscape metrics of the observed (obs) and simulated (sim) bark beetle outbreak, showing the mean patch area (ha) and the mean shape index (i.e., the ratio of actual perimeter to the hypothetical minimum perimeter of a disturbance of the same size) per year.

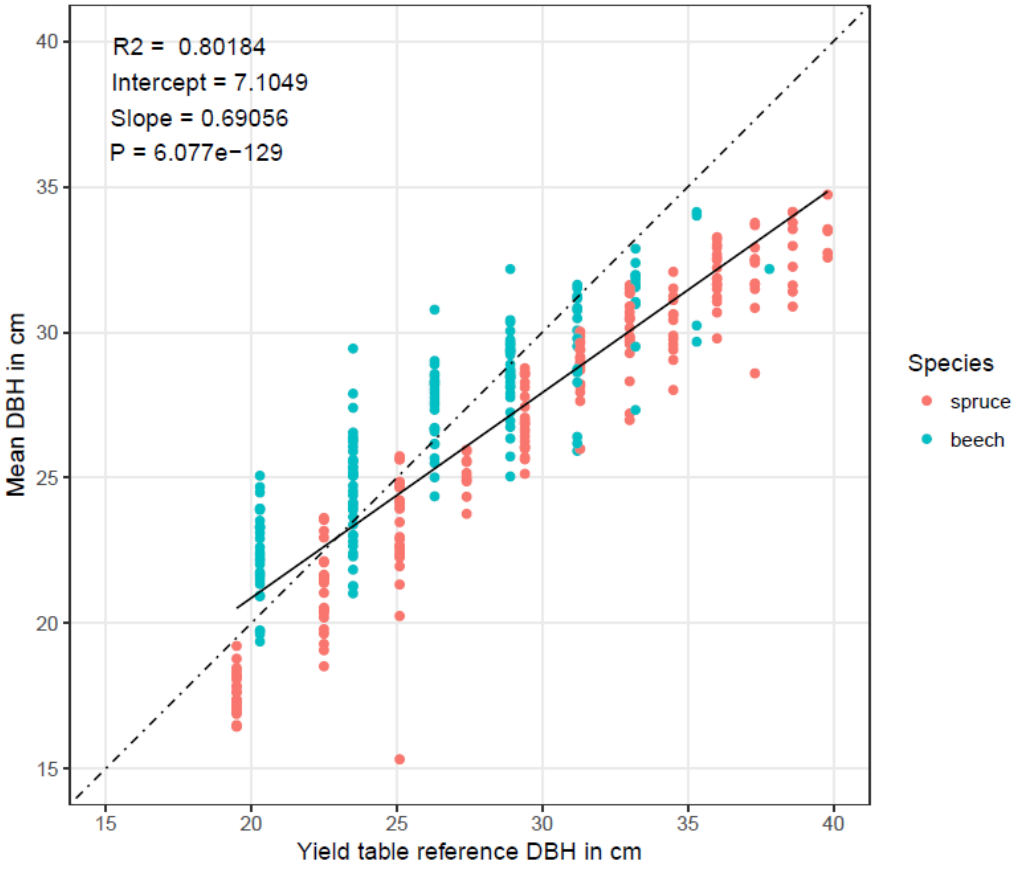


Supplementary Figure 3: Sensitivity of simulated bark beetle disturbances over the 600 year simulation period to different sampling periods used for extending the climate time series beyond the year 2100. The default value used in the main text is 30 years (i.e., sampling from the years 2070 – 2099 with replacement), and all values pertain to the HC scenario (RCP 8.5, ICHEC-EC-EARTH). Sampling from the last 10 and 20 years of the 21st century respectively increases simulated bark beetle disturbances by on average 3.9% and 2.9%, respectively. Sampling from the last 50 years of the century decreased simulated bark beetle disturbances by on average 1.0%. Boxes and whiskers give the variation from five replicated simulations with different years sampled.

2. Productivity tests

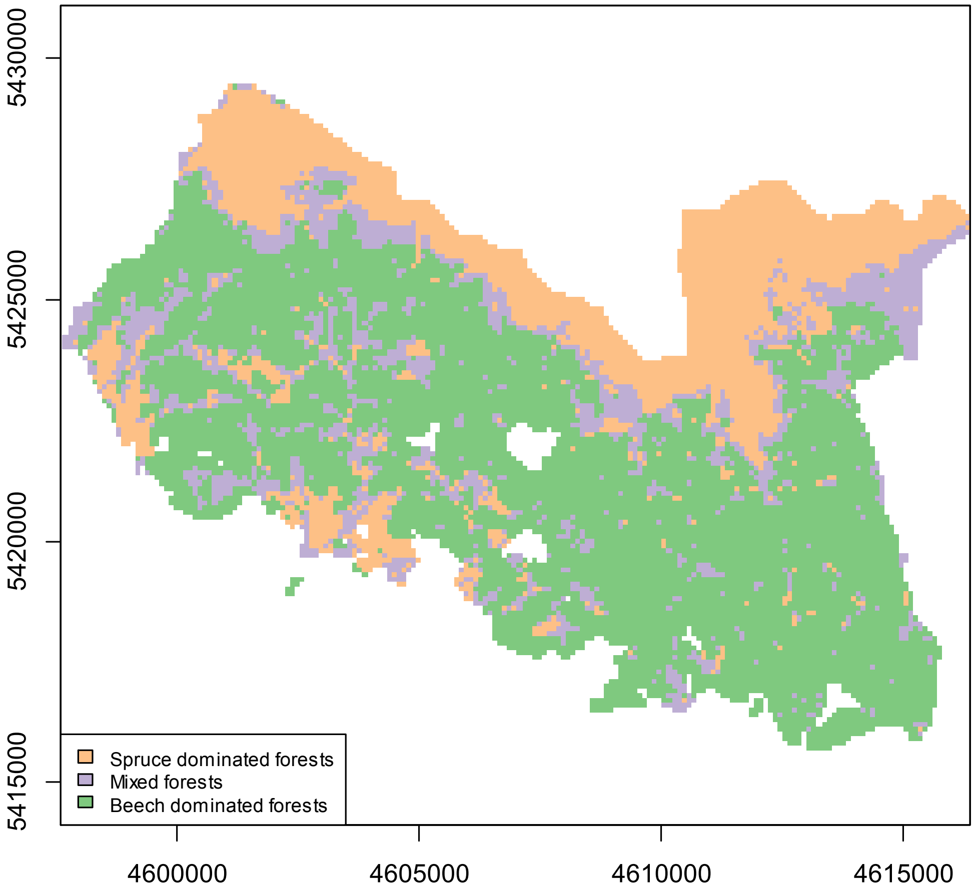


Supplemental Figure 4: Productivity comparison between the 90th percentile of predicted tree heights (y-axis) and reference dominant heights from suitable yield tables (x-axis). Tests were conducted in 401 single species stands at the age of 100 years. Samples were randomly selected from an elevation stratified subset of the two major tree species in Bavarian Forest National Park.

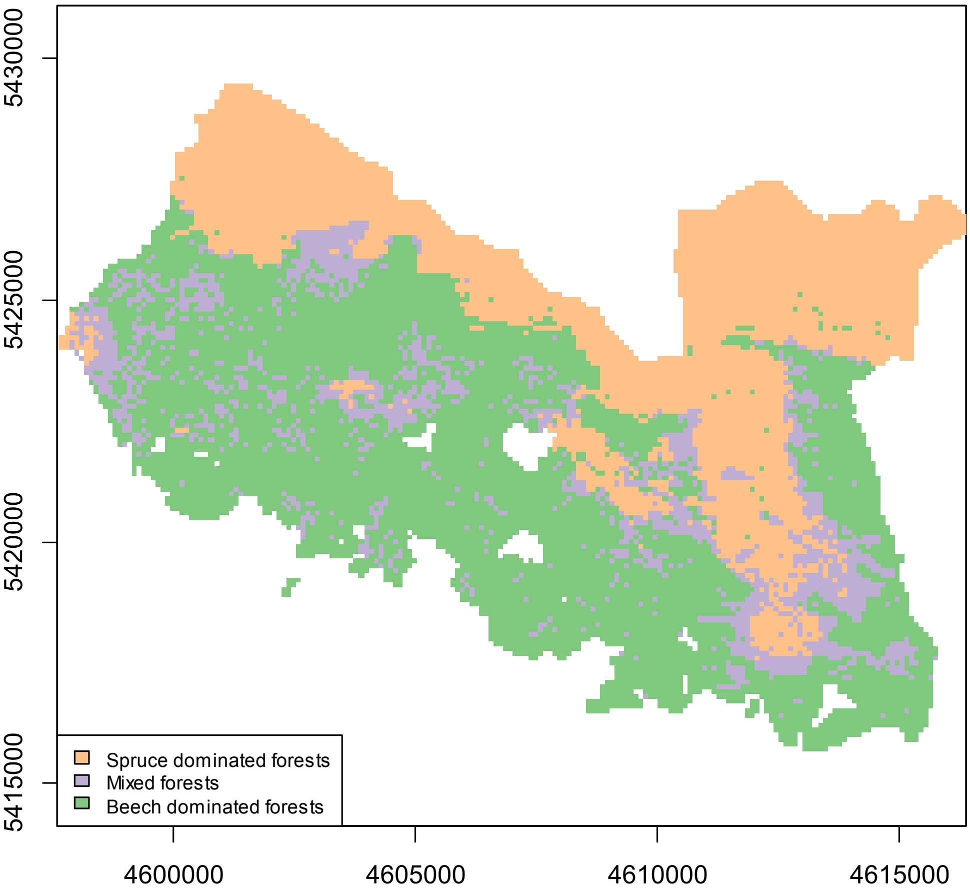


Supplemental Figure 5: Productivity comparison between predicted diameter at breast height (DBH) values (y-axis) and reference DBH values from suitable yield tables (x-axis). Tests were conducted in 401 single species stands at the age of 100 years. Samples were randomly selected from an elevation stratified subset of the two major tree species in Bavarian Forest National Park.

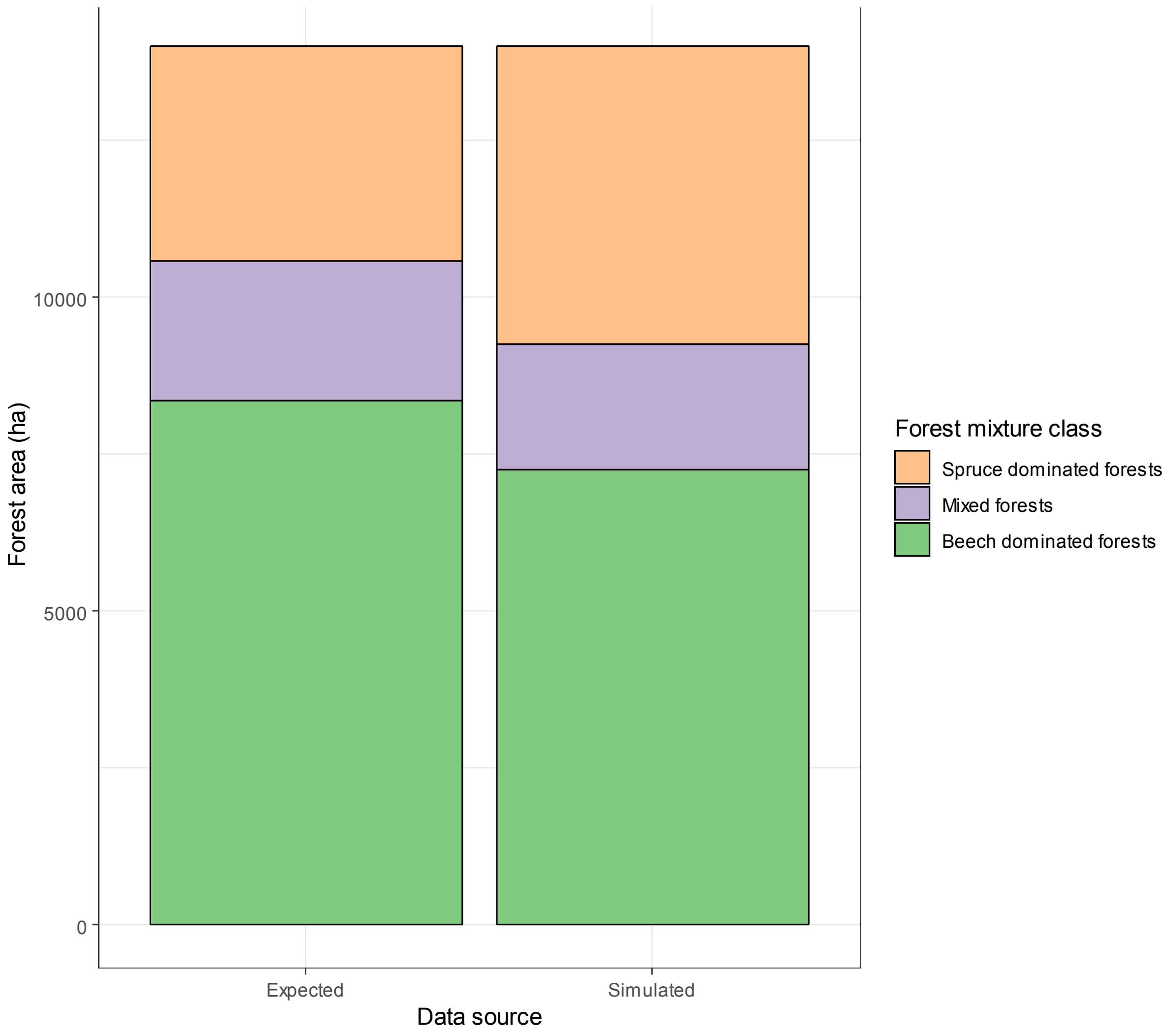
3. Potential natural vegetation (PNV) tests



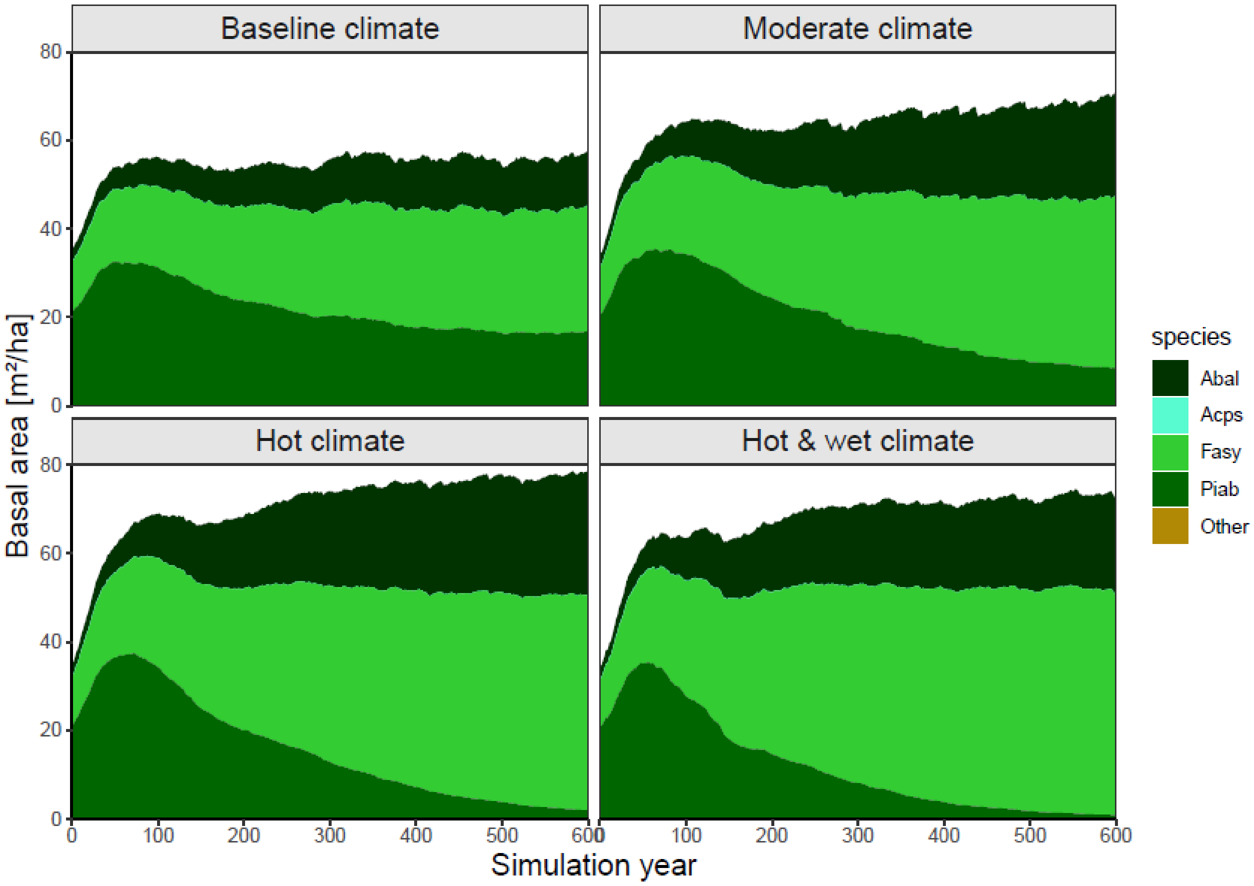
Supplemental Figure 6: Expected potential natural vegetation based on plant sociological assessments. Forests with 60% or more spruce or beech on total stand basal area were categorized as spruce or beech dominated forests.



Supplemental Figure 7: Simulated potential natural vegetation after 2000 simulated years. The simulation was started from bare ground and was run under baseline climate conditions and in the absence of disturbances. Forests with 60% or more spruce or beech on stand basal area were categorized as spruce or beech dominated forests.



Supplemental Figure 8: Comparison of forest area shares of different forest types between expected and simulated potential natural vegetation. Forests with 60% or more spruce or beech were categorized as spruce or beech dominated forests.



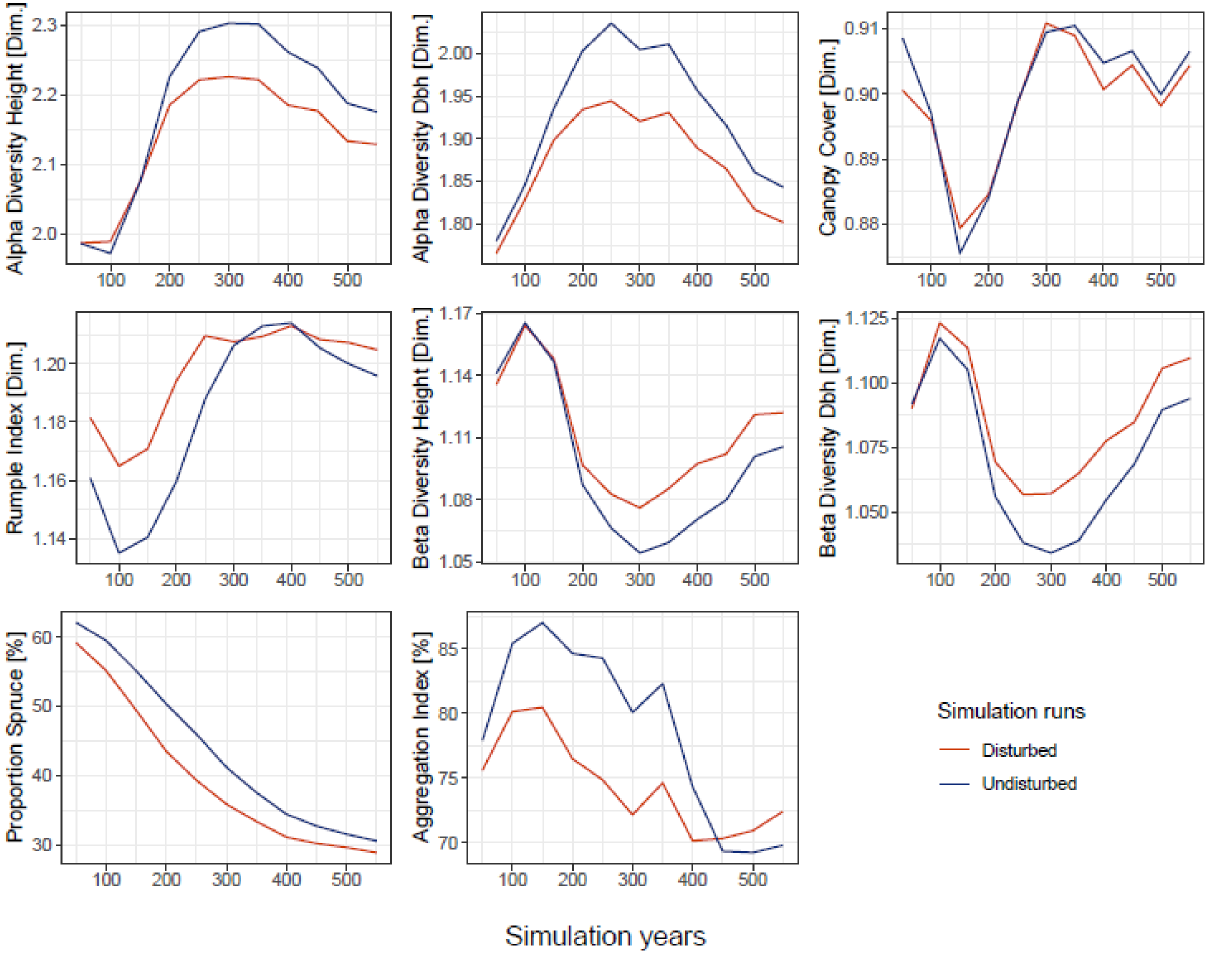
Supplemental Figure 9: Species shares under different scenarios of climate change (species: Abal = Abies alba, Acps = Acer pseudoplatanus, Fasy = Fagus sylvatica, Piab = Picea abies, Other = remaining species).

Climate scenarios

Supplemental Table 1: Description of simulated climate scenarios and their mean annual temperature and mean annual precipitation.

Climate scenario name	Representative concentration pathway	Climate model	Mean annual temperature	Mean annual precipitation
Base climate	Historic	Historic	6.2 ° C	1403 mm
Moderate climate change scenarios	4.5	ICHEC-EC-EARTH	7.9 ° C	1494 mm
Hot climate change scenario	8.5	ICHEC-EC-EARTH	9.6 ° C	1595 mm
Hot and wet climate change scenario	8.5	MOHC-HadGEM2-ES	10.9 ° C	1731 mm

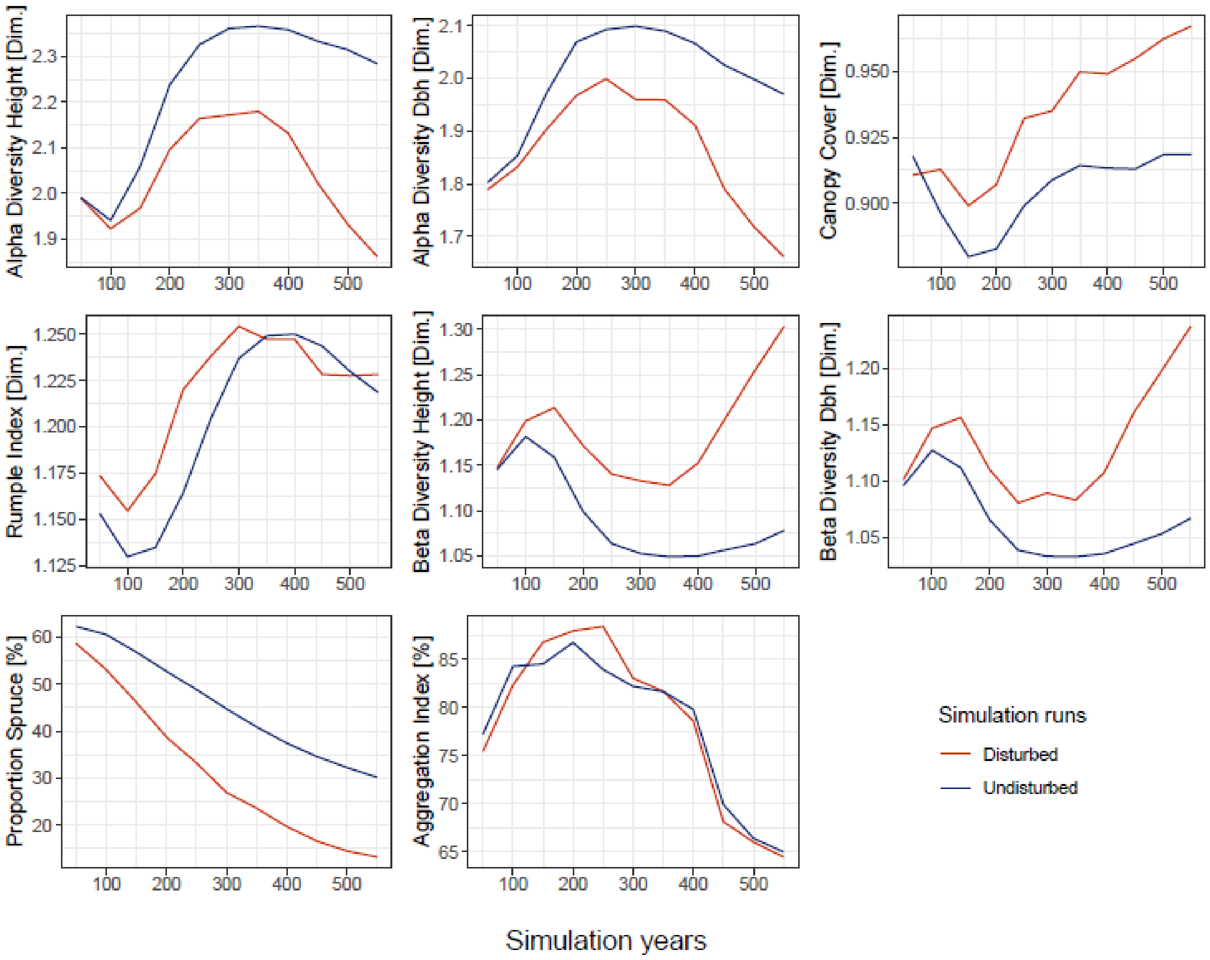
Forest indicator changes for different climate scenarios



Supplemental Fig. 10: Effect of forest disturbance on forest structure and composition. Shown are the mean effects over all replicates under the baseline climate scenarios (BC). We refer to Table 1 for a detailed description of the indicators used.

Supplemental Table 2: Response of forest structure and composition to climate change and disturbances. Results are shown for the baseline climate scenarios (BC).

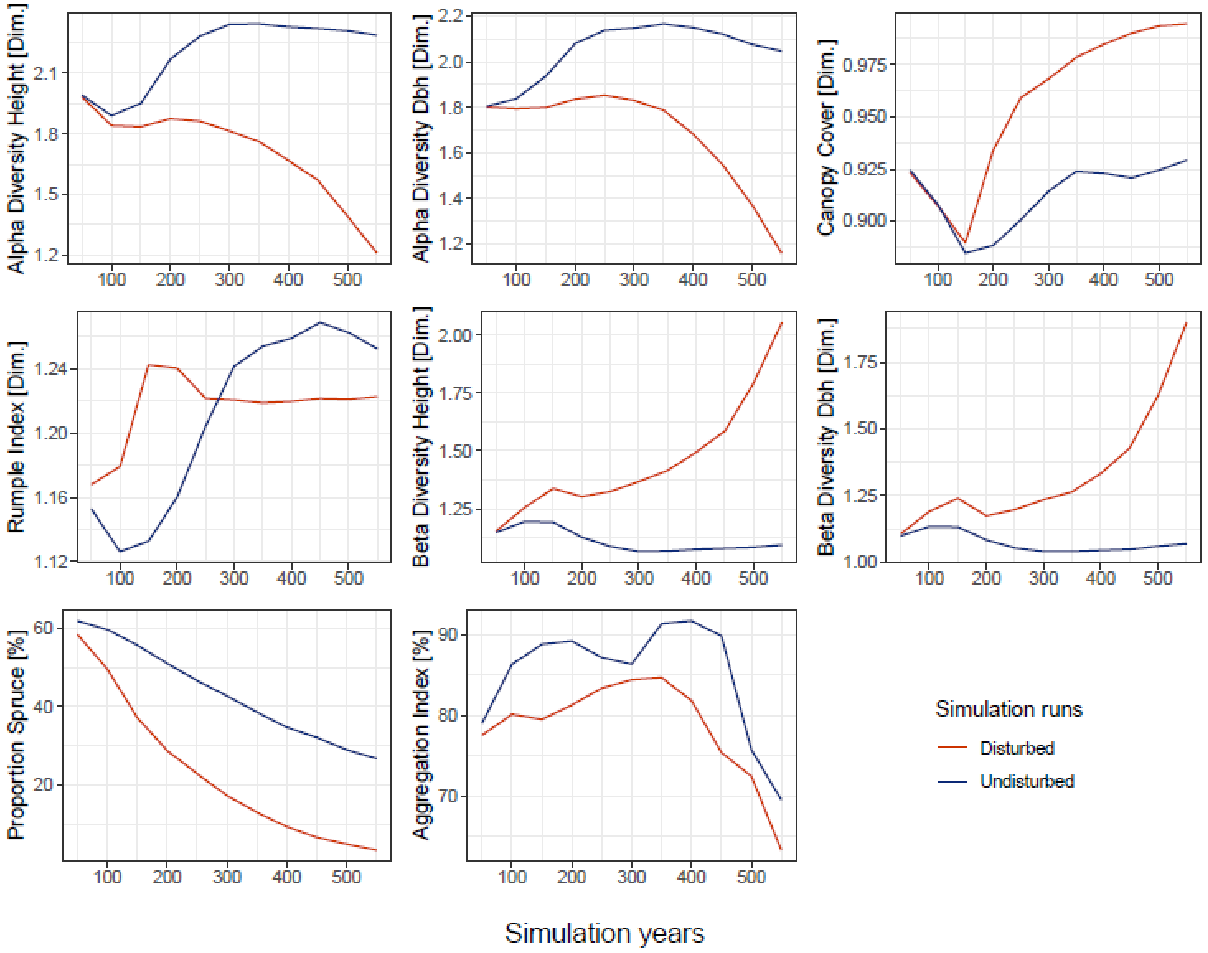
Indicator	Attribute	Scale	Effect of climate change (*undisturbed simulations)*	Effect of disturbances (*disturbed simulations under BC climate*)	Effect of disturbances and climate change
α-diversity height	Structure	Stand	-	- 2.0 %	-
α-diversity dbh		Stand	-	- 2.8 %	-
Canopy cover		Landscape	-	- 0.2 %	-
Rumple index		Landscape	-	+ 1.2 %	-
β-diversity height		Landscape	-	+ 1.3 %	-
β-diversity dbh		Landscape	-	+ 1.4 %	-
Proportion of spruce	Composition	Landscape	-	- 9.4 %	-
Aggregation index		Landscape	-	- 5.3 %	-



Supplemental Fig. 11: Effect of forest disturbance on forest structure and composition. Shown are the mean effects over all replicates under the moderate climate change scenarios (MC). We refer to Table 1 for a detailed description of the indicators used.

Supplemental Table 3: Response of forest structure and composition to climate change and disturbances. Results are shown for the moderate climate change scenario (MC).

Indicator	Attribute	Scale	Effect of climate change (*undisturbed simulations)*	Effect of disturbances (*disturbed simulations under BC climate*)	Effect of disturbances and climate change
α-diversity height	Structure	Stand	+ 2.3 %	- 2.0 %	- 6.6 %
α-diversity dbh		Stand	+ 4.0 %	- 2.8 %	- 3.3 %
Canopy cover		Landscape	+ 0.6 %	- 0.2 %	+ 3.8 %
Rumple index		Landscape	+ 1.5 %	+ 1.2 %	+ 2.9 %
β-diversity height		Landscape	- 0.7 %	+ 1.3 %	+ 8.0 %
β-diversity dbh		Landscape	- 0.7 %	+ 1.4 %	+ 5.8 %
Proportion of spruce	Composition	Landscape	+ 4.1 %	- 9.4 %	- 28.5 %
Aggregation index		Landscape	- 0.3 %	- 5.3 %	- 0.1 %



Supplemental Fig. 12: Effect of forest disturbance on forest structure and composition. Shown are the mean effects over all replicates for the hot climate change scenario (HC). We refer to Table 1 for a detailed description of the indicators used.

Supplemental Table 4: Response of forest structure and composition to climate change and disturbances. Results are shown for the hot climate change scenarios (HC).

Indicator	Attribute	Scale	Effect of climate change (*undisturbed simulations)*	Effect of disturbances (*disturbed simulations under BC climate*)	Effect of disturbances and climate change
α-diversity height	Structure	Stand	+ 0.8 %	- 2.0 %	- 21.7 %
α-diversity dbh		Stand	+ 6.2 %	- 2.8 %	- 12.9 %
Canopy cover		Landscape	+ 1.4 %	- 0.2 %	+ 6.3 %
Rumple index		Landscape	+ 2.3 %	+ 1.2 %	+ 2.8 %
β-diversity height		Landscape	+ 1.1 %	+ 1.3 %	+ 33.2 %
β-diversity dbh		Landscape	+ 0.0 %	+ 1.4 %	+ 24.5 %
Proportion of spruce	Composition	Landscape	- 0.6 %	- 9.4 %	- 47.8 %
Aggregation index		Landscape	+ 8.2 %	- 5.3 %	± 0.0 %

Appendix C

Effects of disturbance patterns and deadwood on the microclimate in European beech forests

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Effects of disturbance patterns and deadwood on the microclimate in European beech forests

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Latent heat
Microclimate

ABSTRACT

More frequent and severe disturbances increasingly open the forest canopy and initiate tree regeneration. Simultaneously, increasing weather extremes, such as drought and heat, are threatening species adapted to cool and moist climate. The magnitude of the microclimatic buffering capacity of forest canopies to mitigate hot and dry weather conditions and its disturbance-induced reduction remains poorly quantified. Also, the influence of disturbance legacies (e.g., deadwood) on forest microclimate is unresolved. In a unique manipulation experiment we investigated (i) the microclimatic buffering capacity of forest canopies in years with different climatic conditions; (ii) the impacts of spatial disturbance patterns on surface light and microclimate; and (iii) the effect of deadwood presence and type on microclimate.

Treatments included two disturbance patterns (i.e., aggregated and distributed), four deadwood types (i.e., standing, downed, standing and downed, removed), and one untreated control (i.e., nine treatments in total), replicated at five sites dominated by European beech (*Fagus sylvatica* L.) in southeastern Germany. We measured forest floor light conditions and derived diurnal extremes and variation in temperature (T) and vapor pressure deficit (VPD) during four consecutive summer seasons (2016 – 2019).

The buffering capacity of intact forest canopies was higher in warm and dry years. Surface light was significantly higher in spatially aggregated disturbance gaps compared to distributed disturbances of similar severity. An increase in surface light by 10 % relative to closed canopies elevated T_{max} and VPD_{max} by 0.42°C and 0.04 kPa, respectively. Deadwood presence and type did not affect the forest microclimate significantly.

Microclimatic buffering under forest canopies can dampen the effects of climate change. However, increasing canopy disturbances result in more light penetrating the canopy, reducing the microclimatic buffering capacity of forests. We conclude that forest management should foster microclimatic buffering in forests as one element of a multi-pronged strategy to counter climate change.

1. Introduction

Climate change is increasingly impacting forest ecosystems, with negative consequences for plant growth, regeneration, and survival (Anderson-Teixeira et al., 2013; D'Orangeville et al., 2018; McDowell et al., 2020). If climate change continues unabated, drought-induced stress may exceed everything that plants experienced over the past 1000 years by 2050 (Williams et al., 2013). Such extreme droughts will have dramatic consequences for biodiversity and ecosystem services supply (Choat et al., 2012). Forest canopies have the potential to buffer climate change effects through the specific microclimate they create, e.g. by providing shelter from direct insolation and increasing evaporative cooling (Bonan, 2008; De Frenne et al., 2019; Thom et al., 2017). However, climate change is also expected to decrease forest

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canopy cover through increases in natural disturbance activity (Seidl et al., 2017). To date, it remains uncertain how strong the climate buffering capacity (i.e., the mitigation of hot and dry weather conditions) of undisturbed forests is, and how different disturbance patterns and processes alter microclimatic conditions.

Climate change has direct and indirect effects on plants. Direct effects include extreme heat damaging plant tissue (Guha et al., 2018) as well as water stress through the combination of heat, low humidity, and infrequent rainfall (Davis et al., 2019). Increasing activity of natural disturbances (Seidl et al., 2017) constitute an indirect effect of climate change on environmental conditions. Disturbances create canopy openings which affect the local microclimate (Schmidt et al., 2017). Previous studies have shown that the microclimate becomes warmer and drier with increasing distance from intact forests (Baker et al., 2014; Davies-Colley et al., 2000; Ewers and Banks-Leite, 2013; Wright et al., 2010). Hence, increasing disturbances will likely add to climate-induced plant stress, with consequences for future forest development. For instance, regeneration failure of the currently prevailing tree species may accelerate thermophilization (i.e., a change in the forest composition towards warm-adapted species) (De Frenne et al., 2013; Stevens et al., 2015; Zellweger et al., 2020) or in extreme cases cause a regime shift from forests to grass- or shrub-dominated ecosystems (Anderson-Teixeira et al., 2013). These transitions could have dramatic consequences for forest-dwelling species (Laurance and Bruce Williamson, 2001) and could negatively affect the services provided for human well-being (Nelson et al., 2013).

Droughts have increased over the past decades, and initiated major waves of tree mortality in Central European forests (Senf and Seidl, 2018). While droughts, often in combination with bark beetle infestations, have primarily affected Norway spruce (*Picea abies* [Karst.]) in the past, recent events have shown that also other tree species are increasingly susceptible to global change-type droughts (Breshears et al., 2009) in Central Europe. European beech (*Fagus sylvatica* [L.]) is one of the species promoted as being fairly robust to future climatic conditions (Paul et al., 2019). Furthermore, European beech is the most abundant and economically important broadleaved tree species in Central Europe, and harbors numerous forest-dwelling species (Brunet et al., 2010; Grebenc et al., 2009; Hanewinkel et al., 2012). For instance, about 70% of central European saproxylic beetles can be found in beech-dominated forests (Müller et al., 2013). With the goal to adapt forests to climate change, practitioners have intensified their efforts to convert spruce-dominated forests to beech forests. However, the high beech mortality rates of two consecutive drought years in 2018 and 2019 (Buras et al., 2019; Schuldt et al, 2020) challenge the expectation that beech will be able to cope with future climate change. A crucial element is the question of how to best mitigate the impact of severe droughts in the future. While scientists and forest managers have mainly focused on species conversion (e.g., Temperli et al., 2012; Vitali et al., 2017) and stand density regulation (e.g., D'Amato et al., 2013; Gebhardt et al., 2014) to maintain forests and their services, microclimatic conditions have received comparably little attention.

Forest canopies have a cooling effect on the local environment. The phase change from liquid water transpired by forests to water vapor causes an energy flux from the surface to the atmosphere (i.e., latent heat flux) resulting in an evaporative cooling effect (Bonan, 2008). Given sufficient water supply, an intact forest's evapotranspiration (and thus its cooling effect) increases under higher temperatures (Thom et al., 2017). However, resulting from an intense forest management history and increasing natural disturbances, large landscapes with continuous forest canopy have become rare in Central Europe (McGrath et al., 2015). Instead, landscapes are mosaics of different land-use systems and forest canopies are fragmented by management practices such as gap and shelterwood cutting as well as by natural disturbances. Thus the resultant forest edges are exposed to stronger winds, lower humidity and higher air temperatures than the interior of undisturbed forests (Magnago et al., 2015). These conditions will likely amplify climate-induced stress for trees. Forest regeneration will be most strongly affected, as their root systems do not yet reach deep into the soil (E Silva et al., 2012) while, at the same time, regeneration density is usually highest in canopy gaps (Vodde et al., 2015).

Despite the importance of microclimate for future forest development, the number of studies investigating disturbance impacts on microclimatic conditions remains limited. Previous studies have analyzed the spatial extent of forest effects on microclimate from edges into open (disturbed) areas (Aragón et al., 2015; Baker et al., 2014; Pinto et al., 2010; Wright et al., 2010) or from open areas into the forest (Chen et al., 1999; Davies-Colley et al., 2000; Ewers and Banks-Leite, 2013). Others have tested the correlation between canopy closure and microclimate (Brown, 1993; Davis et al., 2019; Hardwick et al., 2015). However, to our knowledge, no study has yet assessed the effects of different spatial patterns of disturbance on microclimate. Most disturbances in Central European forests are characterized by mortality at the level of individuals or small groups of individuals, while stand-replacing disturbances happen only infrequently (Nagel et al., 2017; Panayotov et al., 2015; Splechtna et al., 2005; Standovár and Kenderes, 2003). Whether disturbance patterns are distributed (i.e., with several spatially segregated individual trees being affected by the disturbance) or aggregated (i.e., clusters of trees affected) within a stand can potentially lead to different microclimatic outcomes.

Disturbances not only cause variable openings in the canopy but also create important biological legacies. An important disturbance legacy is standing and downed deadwood. Deadwood is an important pool of carbon in natural forests (Jacob et al., 2013), and is crucial for the occurrence of a large number of saproxylic organisms (Seibold et al., 2016). However, the potential deadwood effect on forest microclimate has received little attention to date (Kovács et al., 2017). For instance, moisture stored in deadwood within the first few years after a disturbance could induce an evaporative cooling effect. Further, standing deadwood can still shield the ground from insolation, and thus reduce energy input, potentially modifying local temperature and moisture conditions. Understanding the role of deadwood on microclimate is important because management frequently removes disturbance-killed trees by salvage logging (Thorn et al., 2018).

Here, we conducted a replicated manipulation experiment with a factorial design of nine treatments. Previous microclimate studies have rarely been based on manipulation experiments, despite the fact that controlled experiments are best suited to control for the noise that is introduced by the inherent heterogeneity in ecosystems (Hurlbert, 1984). Our treatments were specifically designed to assess the effects of different disturbance patterns and deadwood types on microclimate. Disturbance sizes and severities were chosen to reflect patterns that are characteristic for the natural disturbance regime of forests dominated by European beech (Drößler and Von Lüpke, 2005; Kenderes et al., 2008). They also span a typical management gradient from single-tree to group-selection harvesting, in effect, management systems that are frequently used to initialize regeneration in Central European forests (Lorenz et al., 2018). We investigated (i) the climatic buffering capacity of forest canopies in years with different climatic conditions, (ii) the effects of different spatial patterns of disturbance on surface light and microclimate, and (iii) the effect of deadwood presence and type on microclimate. We expected a higher microclimatic buffering capacity of undisturbed forests in warm and dry years due to increases in evapotranspiration causing additional cooling and wetting of the air (de Frenne et al., 2019). We also expected a change towards warmer and drier conditions with disturbances that more strongly increase surface light (i.e., aggregated > distributed disturbances), as openings are more exposed to direct solar radiation, warming and drying the surface (Ritter et al., 2005). Finally, we hypothesized deadwood retention to mitigate the effects of increasing surface light on the forest microclimate as the evaporation of moisture stored in deadwood increases evaporative cooling, and as standing deadwood

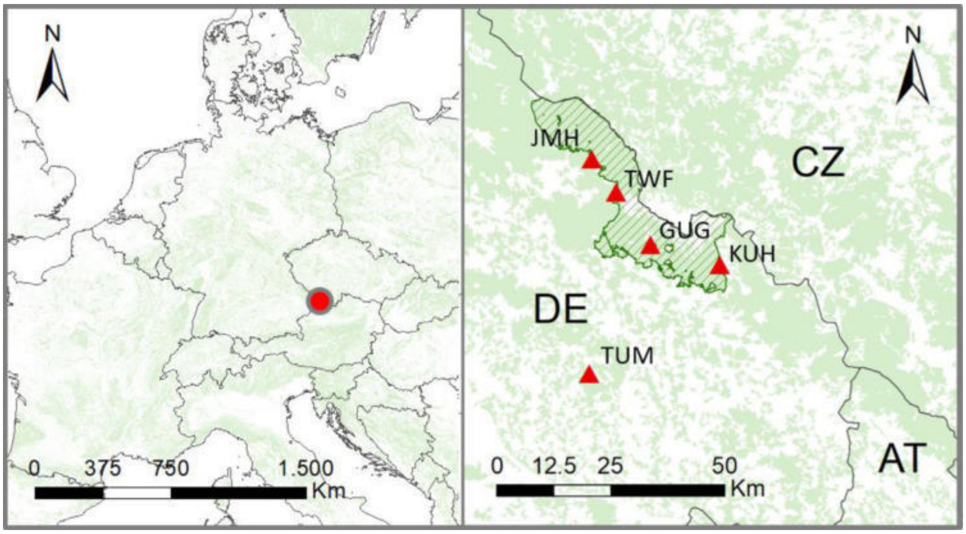


Figure 1. Study area. The red dot marks the study location in Central Europe. Red triangles represent the five experimental sites. Shaded areas delineate the Bavarian Forest National Park, and green areas denote forest cover.

provides shelter from the sun (Marcolin et al., 2019).

2. Material and Methods

2.1. Study area

Our experiment was conducted in southeastern Germany close to the boarder of Czechia and Austria (Fig. 1). In particular, four sites are located in the Bavarian Forest National Park (GUG, JMH, KUH, TWF), and one is in Thurmansbang (TUM) in the vicinity of the National Park. The sub-montane forests studied here are all dominated by European beech (Table 1), with minor shares of Norway spruce and other tree species. Forests originated from secondary succession, and are of low structural diversity, characterized by only one canopy layer and limited age variation. They are in a mature development stage with similar basal area, stand density and tree dimensions across study sites. Active forest management ceased several decades ago. While the national park has experienced the largest unimpeded bark beetle outbreak in European forests in recent decades, our sites have not been affected by these disturbances (Heurich and Englmaier, 2010).

2.2. Experimental design

We manipulated canopy cover and deadwood at five experimental sites. In a randomized factorial block design, we selected eight plots per site and assigned different treatments to them, with an additional plot serving as the untreated control (i.e., 5 sites × (8 treatments + 1 control) = 45 plots in total) (Fig. 2). Plots were randomly distributed within each site, and consisted of squares of 50 m × 50 m (i.e., 2,500 m^2). In October 2015, gaps were created to mimic disturbances of individual trees and groups (Figs. 2, 3). At all treated plots, disturbance severity was held constant at approximately 25 % of basal area removed. Trees were cut either in spatially aggregated groups of 25 m x 25 m (625 m^2) around the plot center or as individual trees distributed randomly across the plot (two different treatments regarding the spatial pattern of disturbance, cf. the rows in Fig. 2). In these gaps we retained downed, standing or both downed and standing deadwood, or removed deadwood altogether (four different deadwood treatments, cf. the columns in Fig. 2). To create standing deadwood trees were cut below the first strong branch of the crown, which was on average at a height of 8.3 m. Resulting from the factorial design of our manipulation experiment, the average amount of standing and downed deadwood was similar across sites (Table 1). Remaining differences can be partly attributed to differences in deadwood before treatments and local variation in stand structure.

2.3. Data collection

In May 2016, we installed an automatic data logger (model UT 330C) in the center of each plot on a pole ca. 1.2 m above the ground. Data loggers measured temperature and relative humidity every hour during the summer seasons (June, July, August) of the years 2016 –

Table 1

Site topography and forest attributes after treatment. Presented are means and standard deviations (in parentheses) across all plots and treatments per site. H' (Shannon) diversity is based on the basal area of live trees.

Site	GUG	JMH	KUH	TUM	TWF
Coordinates (UTM)	32 U 824074 5429269	32 U 815223 5440885	32 U 834390 5426884	32 U 816421 5410171	32 U 819000 5436191
Elevation (m)	837	857	852	483	1055
Slope (°)	7.1	13.0	18.1	10.9	11.0
Aspect	W	N	E	N	NE
Live basal area (m^2 ha^{-1})	32.4 (5.6)	30.9 (5.3)	34.3 (5.5)	31.6 (4.0)	41.4 (4.5)
Stand density (N ha^{-1})	540 (164)	418 (159)	388 (89)	443 (89)	864 (173)
Mean DBH (cm)	24.3 (5.2)	29.1 (4.9)	30.7 (2.5)	26.3 (3.6)	23.4 (2.3)
Mean Height (m)	26.1 (2.5)	29.4 (3.9)	28.3 (1.7)	25.9 (2.0)	21.9 (3.1)
Beech basal area share (%)	83.4 (14.0)	92.0 (3.1)	70.4 (18.1)	77.5 (16.7)	81.2 (8.2)
H' diversity	0.5 (0.3)	0.3 (0.1)	0.6 (0.2)	0.5 (0.3)	0.5 (0.1)
Standing deadwood basal area (m^2 ha^{-1})	3.3 (3.4)	3.4 (3.1)	2.9 (3.0)	3.1 (2.5)	4.0 (3.4)
Downed deadwood volume (m^3 ha^{-1})	21.8 (27.2)	30.1 (36.7)	27.0 (32.2)	19.8 (20.8)	23.6 (30.9)

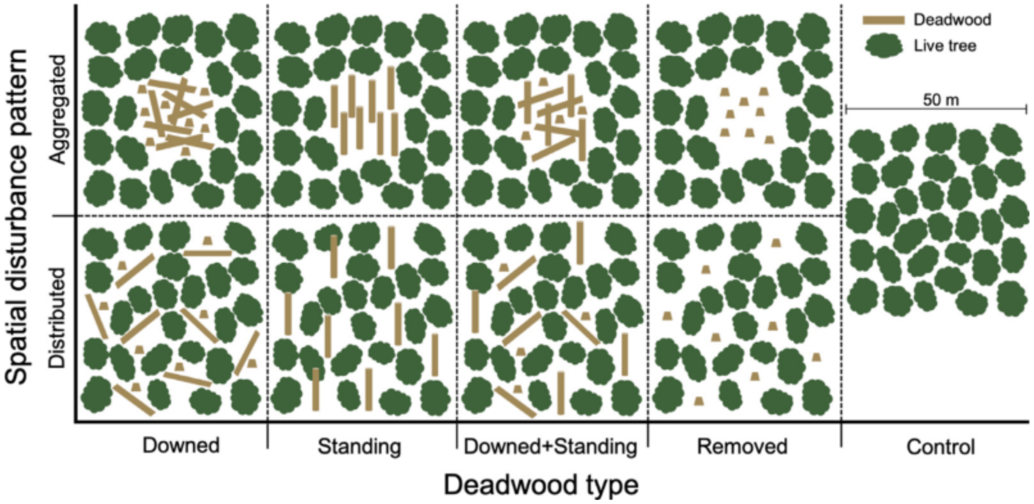


Figure 2. Experimental design. Two spatial disturbance patterns were created while keeping disturbance severity constant at ~25 % basal area removed. For each spatial disturbance pattern four different deadwood treatments were studied. Including the untreated control plot each of the five experimental sites comprised nine factorial combinations of spatial disturbance patterns and deadwood types.

2019 (four years). We focused on summer because forests have been shown to have a particularly strong effect on the microclimate during this particular season (Baker et al., 2014). The summer season is also of crucial importance for the growth and survival of tree recruits (Chen et al., 1999).

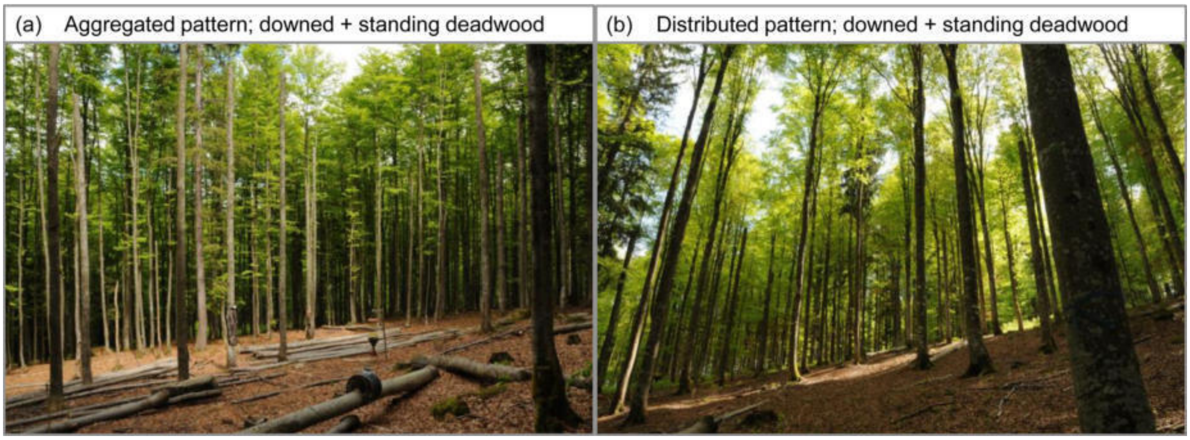
As we expected the modulation of the light regime to be the main process through which canopy openings influence forest microclimate, we collected information about the light regime throughout our experimental plots. We measured light as the total site factor (TSF) (i.e., the total solar radiation including direct and diffuse light, relative to open conditions) at the same height as data loggers at four locations using hemispherical photography (Solariscope SOL 300B) in the first summer after implementing the treatments. The instrument measures the shading of forest canopies relative to open field conditions. Accounting for the theoretical path of the sun (depending on geographical orientation and latitude) it obtains an accurate sub-canopy light estimate (Canham et al., 1990). Light measurements were taken at the four corners of a 10 m × 10 m square centered around the plot center (see Figure S1 in the Supplementary material). For further analysis we aggregated these measurements to plot averages.

2.4. Analysis

First, we harmonized and cleaned the collected data. To that end, the data logger records were inspected for unrealistic values and missing measurements. For instance, we omitted days in which hourly records were incomplete to avoid aggregation bias.

Subsequently, we used temperature and relative humidity to derive vapor pressure deficit (VPD). VPD is the difference between saturated and actual vapor pressure and quantifies the amount of water vapor in the air. VPD constitutes an important driver of plant hydraulic functioning (Ficklin and Novick, 2017). As VPD acts as mediator between atmospheric conditions and stomatal conductance, it also represents the drying capacity of the air. A higher VPD thus implies increasing water stress of plants (Williams et al., 2013).

Next, we aggregated hourly observations to daily values. In particular, we derived extreme values (maxima), and the variation (standard deviation, SD) of temperature and VPD within a day. These microclimatic parameters were selected as they provide important information for growth and survival of tree recruits. High maximum temperature (T_{max}) and VPD (VPD_{max}) induce stress during the warmest and driest time of the day, potentially limiting growth (e.g., due to stomata closing) and resulting in mortality (e.g., due to water stress). Besides weather extremes, high variation in temperature (T_{SD}) and VPD (VPD_{SD}) can cause stress for plants as microclimate variation influences ecosystem processes, including plant and soil respiration rates (Chen et al., 1999). For instance, a sudden rise in temperature close to lethal limits requires plants to keep pace in producing heat-shock proteins to protect their tissue (Lambers et al., 2008). The ability to produce such proteins differs among species. The effects of diurnal fluctuations in microclimatic conditions on ecosystem processes can thus, *inter alia*, alter forest regeneration dynamics (Brown, 1993). We assessed the dependencies among microclimate parameters using Pearson's correlation coefficients. In particular, we were interested in the association between extremes and variations in microclimate as they could cause compounding effects on plants (with higher maxima and


(a) Aggregated pattern; downed + standing deadwood

(b) Distributed pattern; downed + standing deadwood

Figure 3. An example of the aggregated and distributed disturbance treatment with both downed and standing deadwood.

higher variation indicating particularly challenging conditions for the growth and survival of seedlings and saplings).

We derived the difference between treated and untreated plots at each site to assess the overall treatment effects on microclimate. The difference between treated and untreated plots indicates the disturbance-induced change in the buffering capacity of intact forests with regard to temperature and VPD, respectively. We also compared the interannual variation in the buffering capacity to test for differences with climate variability (e.g., in warm and dry years). Based on the data of Germany's National Meteorological Service (Deutscher Wetterdienst), there was a trend towards warmer and drier conditions from 2016 to 2019, with 2019 being the warmest and driest year of the observation period (Figs. S2, S3). On average over the five experimental sites, T_{max} was 0.6°C, 1.4°C, and 2.7°C higher in the summer of 2019 compared to the summers of 2018, 2017, and 2016, respectively. Concurrently, summer precipitation was 11 mm, 29 mm, and 57 mm lower in 2019 compared to 2018, 2017, and 2016, respectively. We tested annual differences in the buffering capacity of microclimate parameters for statistical significance employing Tukey's Honest Significant Difference ($\alpha = 0.05$).

Using the full dataset including untreated plots (i.e., 45 observations), we investigated the effects of spatial disturbance patterns and deadwood type on light conditions using a Bayesian analysis framework. Bayesian models capture parameter uncertainty when estimating the probability distribution of treatment effects on the response variable and allow the integration of prior information (McElreath, 2016). In contrast to maximum likelihood approaches that provide point estimates of the highest likelihood of model parameters, Bayesian inference involves the full range of parameter values and their probabilities. Prior information is used to restrict parameters to plausible ranges (McElreath, 2016). Incorporating Markov Chain Monte Carlo (MCMC) sampling, Bayesian approaches achieve accurate results when assessing complex (e.g., multi-hierarchical) data and are not restricted by the model's degrees of freedom (Rossi and Allenby, 2003). We expected more light to penetrate the canopy in aggregated compared to distributed disturbance patterns, and hypothesized an interaction effect between aggregated disturbance patterns and standing deadwood on light conditions. However, as the model with spatial disturbance pattern as only fixed effect clearly outperformed models including deadwood type (see evaluation criteria below), we omitted the latter from the final model. In effect, we fitted a multi-hierarchical Bayesian model with site as random effect and spatial disturbance pattern as the only fixed effect. Surface light was log-transformed prior to the analysis to normalize the data distribution.

Subsequently, we used all daily records aggregated from data loggers (i.e., 7,487 observations) in multi-hierarchical Bayesian models to analyze the impacts of surface light (expecting a direct link between light conditions and microclimate) and deadwood type (expecting an additional evaporative cooling effect from deadwood evaporation) on each microclimate parameter. Consequently, each model included surface light and deadwood type as fixed effects. We specified a conservative prior to regulate the inference of surface light effects to a reasonable range (i.e., a weakly informative prior) (McElreath, 2016). Random effects for site and year allowed for variable intercepts and slopes of the response variables. Both VPD variables were square-root-transformed to normalize their data distributions. As microclimate models were based on time-series data, we modelled the first-order autoregressive effects of residuals.

All Bayesian models were evaluated with posterior predictive checks. The leave-one-out (LOO) adjusted R^2 was calculated to avoid an overestimation of the variance explained by adding explanatory variables to the model, and residuals were tested for normality. Additionally, residuals of the microclimate parameter models were tested for temporal autocorrelation using generalized Durbin-Watson statistics. All analyses were performed using the R language and environment for statistical computing (R Development Core Team, 2019). In particular, we employed the packages tidyverse (Wickham, 2017) and reshape2 (Wickham, 2017) for data organization; brms (Bürkner, 2018) and loo (Vehtari et al., 2019) for Bayesian models and their evaluation; car (Fox et al., 2019) to test temporal autocorrelation; and ggplot2 (Wickham, 2009) for visualizations.

3. Results

3.1. High correlation between variation and extremes in microclimatic

Variation and extreme values of microclimate parameters were highly positively correlated. In particular, we identified a strong association between VPD_{SD} and VPD_{max} ($r = 0.948$), indicating that days with a high fluctuation in aridity were also driest. Also T_{SD} and T_{max} were clearly positively correlated ($r = 0.777$), indicating that days with a high temperature variation were also hottest, but their association was weaker than the one between VPD_{SD} and VPD_{max}. As temperature is one of the two components defining VPD (see above), hot and dry conditions interact inherently. Consequently, days with a high T_{SD} and T_{max} generally also experienced a high VPD_{SD} and VPD_{max}.

3.2. Climate buffering capacity increases in warm and dry years

The importance of intact forest canopies for the microclimate increased under warm and dry conditions (Table 2). The buffering capacity of intact canopies (i.e., the difference between all treated and untreated plots) was higher in warm and dry years (2018 and 2019) compared to relatively cold and wet years (2016 and 2017). In 2019, T_{max} and VPD_{max} in undisturbed forests were 2.25°C and 0.53 kPa higher compared to 2016. At the same time, the buffering capacity of undisturbed forests increased statistically significantly by 0.45°C and 0.08 kPa on average between those two years. Consequently, intact forests compensated on average 20.0 % and 15.1 % of elevated summer T_{max} and VPD_{max}, respectively. Moreover, the buffering capacity of T_{SD}

Table 2

Microclimate buffering capacity of intact forest canopies. Presented are the average summer conditions across all data loggers in undisturbed and disturbed forests, as well as the average buffering capacity. Note that the buffering capacity is the average across diurnal differences between disturbed and undisturbed plots, in effect, subtracting one control plot from eight treatments per day and site. As missing observations alter the weight of control plots (e.g., if one control plot is compared against seven instead of eight treatments) subtracting microclimate parameters after aggregation to annual averages would result in slightly different buffering capacities than presented in the table. T_{SD} and VPD_{SD} represent the daily standard deviation of temperature and vapor pressure deficit, respectively. T_{max} and VPD_{max} denote maximum temperature and vapor pressure deficit, respectively. Letters indicate significant differences between years ($\alpha = 0.05$). All measurements were taken hourly by data loggers during the summers of 2016 – 2019, and were aggregated to daily values.

Average microclimate conditions in undisturbed forests					Average microclimate conditions in disturbed forests				Average buffering capacity			
Year	T_{SD}	T_{max}	VPD_{SD}	VPD_{max}	T_{SD}	T_{max}	VPD_{SD}	VPD_{max}	T_{SD}	T_{max}	VPD_{SD}	VPD_{max}
2016	2.81^{a}	21.69^{a}	0.25^{a}	0.82^{a}	3.00^{ab}	22.70^{a}	0.30^{a}	1.05^{a}	0.26^{a}	1.08^{a}	0.05^{ab}	0.22^{a}
2017	2.73^{a}	22.23^{ab}	0.30^{ab}	1.14^{b}	2.95^{a}	22.60^{a}	0.31^{a}	1.19^{b}	0.41^{b}	1.45^{b}	0.05^{ab}	0.23^{a}
2018	2.74^{a}	23.25^{bc}	0.32^{b}	1.23^{bc}	3.08^{b}	24.30^{b}	0.37^{b}	1.46^{c}	0.35^{b}	1.46^{b}	0.05^{a}	0.25^{a}
2019	2.98^{a}	23.94^{c}	0.36^{c}	1.35^{c}	3.31^{c}	25.00^{c}	0.41^{c}	1.56^{d}	0.41^{b}	1.53^{b}	0.06^{b}	0.30^{b}

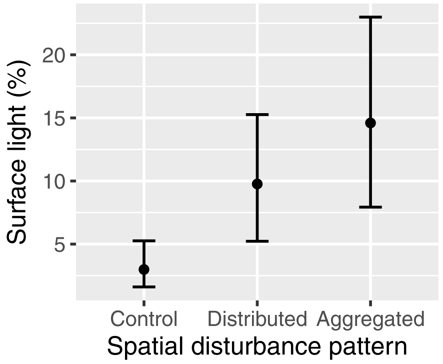


Figure 4. Disturbance effects on surface light conditions. Presented are means (dots) and 95% credibility intervals (whiskers).

increased significantly by 0.16°C from year 2016 to 2019, compensating 54.8 % of the higher diurnal variation in temperature in 2019. In contrast, changes in the buffering capacity of VPD_{SD} between those two years were not significant, and the buffering capacity of closed canopies reduced VPD_{SD} only marginally (9.1%).

3.3. Disturbance impacts on surface light

Disturbances increased light penetration through the canopy (Fig. 4). On average, only 3.0 % of the sunlight reached the ground in control plots. Where disturbances were distributed, on average 9.8 % of light reached the ground (i.e., an increase of 226.7 % relative to control plots). With on average 14.6 % (i.e., +386.7 % relative to control plots) the highest light levels were observed under the aggregated disturbance pattern. Although disturbance treatments were standardized, their effects on light conditions varied considerably within each disturbance pattern (due to the variable distribution of trees at each plot). Credibility intervals were especially wide for the effect of aggregated disturbances. Overall, spatial disturbance patterns explained 56.7 % of the variation in surface light in the multi-hierarchical Bayesian model as indicated by the LOO-adjusted R^2.

3.4. Light regime drives microclimate

An increase in light close to the forest floor was associated with a warmer and drier microclimate (Fig. 5). Surface light was positively correlated with all four microclimate variables. A 10 % increase in light on the ground increased the variation in microclimatic conditions throughout the day by 0.11°C (T_{SD}) and 0.02 kPa (VPD_{SD}). The same increase in light intensified daily extreme values by 0.42°C (T_{max}) and 0.04 kPa (VPD_{max}). The Bayesian multi-hierarchical models explained between 58.5 % (T_{SD}) and 68.1 % (VPD_{SD}) of the variance in microclimatic parameters. The generalized Durbin-Watson statistics were between 2.3 and 2.4, indicating low residual autocorrelation of the models.

3.5. Minor deadwood effects on microclimate

Deadwood effects on microclimate were small and ambiguous (Fig. 6). Across all microclimatic parameters, we found no significant effect of retaining deadwood on the variation and extremes of microclimatic parameters relative to the removal of all deadwood. Our data show only a weak indication that retaining both downed and standing deadwood after disturbance is more beneficial for the microclimate than only retaining one deadwood type or removing all deadwood.

4. Discussion

4.1. Forest microclimate can partially compensate climate change

Forest canopies alter microclimate, and their microclimatic buffering capacity increases in warmer and drier years (Table 2). Based on our findings, it is conceivable that the microclimatic buffering capacity of forest canopies could partly offset the impacts of global climate change on subcanopy processes. On average, intact forest canopies mitigated increases in temperature and VPD extremes by 20.0 % and 15.1 % compared to disturbed forests. It is important to note that the disturbances studied here opened the forest canopy only moderately, with maximum surface light levels remaining below 30 % of open conditions in all plots. We thus assume that the microclimate effect of intact canopies is considerably greater when compared against high severity disturbances or other land-use systems. For instance, the Atlantic tropical forest of Brazil mitigates up to 62 % of T_{max} increases using the air temperature outside of forests as reference (Ewers and Banks-Leite, 2013). Further, it is possible that our analysis underestimates the increase of the microclimate buffering effect of intact forest canopies in warmer and drier years. Light measurements were only available for the year 2016, and we assumed surface light not to change significantly in the following three years. However, European beech forest canopies can recover quickly after disturbance (Valverde and Silvertown, 1997). Thus, the difference in light regimes between disturbed and undisturbed forests have likely become smaller over time, and it can be expected that the buffering capacity of disturbed sites has already increased.

Microclimatic buffering of weather extremes might be of great importance to sustain forest ecosystems in the future (Davis et al., 2019; De Frenne et al., 2019, 2013). However, climate change could also result in tipping points, exceeding the microclimatic buffering capacity of forest ecosystems. If the water available for evaporative cooling is increasingly limited under climate change, for instance, microclimatic buffers might be lost. Also, additional evapotranspiration in a warmer and drier environment could lead to drought-induced mortality (Greenwood et al., 2017) or increase the predisposition towards other disturbance agents (Anderegg et al., 2015; Krams et al., 2012), which could result in canopy loss and reduce the microclimatic buffering effect of forests.

4.2. Increasing disturbance activity dampens microclimatic buffering

Disturbances increase surface light (Fig. 4) and alter the forest microclimate towards warmer and drier conditions (Fig. 5). Our findings highlight that even disturbances of small spatial extent (2,500 m^2) and relatively low severity (25 % of basal area disturbed) can change the microclimate considerably. This is important because the area disturbed has doubled since the mid-1980s in Central Europe, with low-severity disturbances increasing more strongly than stand-replacing disturbances (Senf et al., 2018). Nonetheless, high severity disturbances of larger size are likely to have a stronger impact on the microclimate (Schmidt et al., 2017). Disturbance activity is expected to increase in many parts of the world as a result of climate change (Seidl et al., 2017), which will expose the forest floor more frequently to the full force of weather extremes without the buffering effect of forest canopies.

On average, an additional 10 % of surface light increased T_{max} by 0.42°C and VPD_{max} by 0.04 kPa during summer. Similar results have also been reported from other parts of the world (Schmidt et al., 2017). For instance, a study conducted in tropical forests of Borneo found a positive correlation between surface light (using leaf area index as a substitute) and daily temperature and VPD extremes as well as the variability in microclimatic conditions (Hardwick et al., 2015). Another analysis assessing the effect of a small gap (mean diameter 24 m) on the microclimate of European beech dominated forests confirms the strong

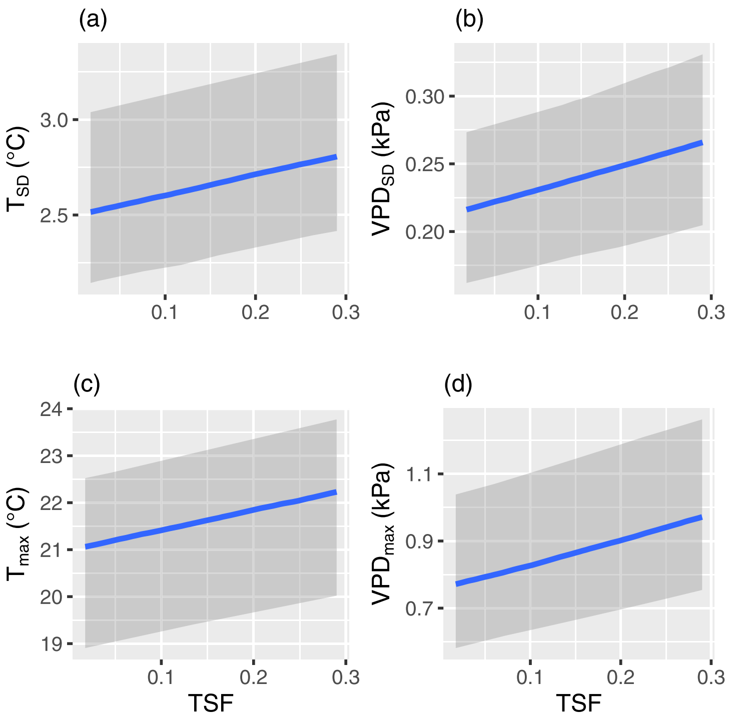


Figure 5. Effects of surface light conditions on microclimate. (a) T_{SD}: Standard deviation of daily temperature; (b) VPD_{SD}: Standard deviation of daily vapor pressure deficit; (c) T_{max}: maximum daily temperature; (d) VPD_{max}: maximum vapor pressure deficit. Shaded areas denote the 95 % credibility interval.

disturbance impact on local summer temperatures (Ritter et al., 2005). They found daily T_{max} to be increased in the gap center by up to 10°C compared to adjacent intact forests. Our study documented a linear trend between surface light and microclimatic parameters. This suggests a stand-replacing disturbance event could increase T_{max} by 4.2°C and VPD_{max} by 0.4 kPa. In addition, disturbances also affect the diurnal variation in microclimatic conditions. Microclimatic extremes and variations were positively correlated, and increased simultaneously with surface light. Interactions between microclimatic extremes and variations may amplify the effects of future disturbance regimes on forest floor vegetation, and could severely impede the recovery after disturbances (Johnstone et al., 2016).

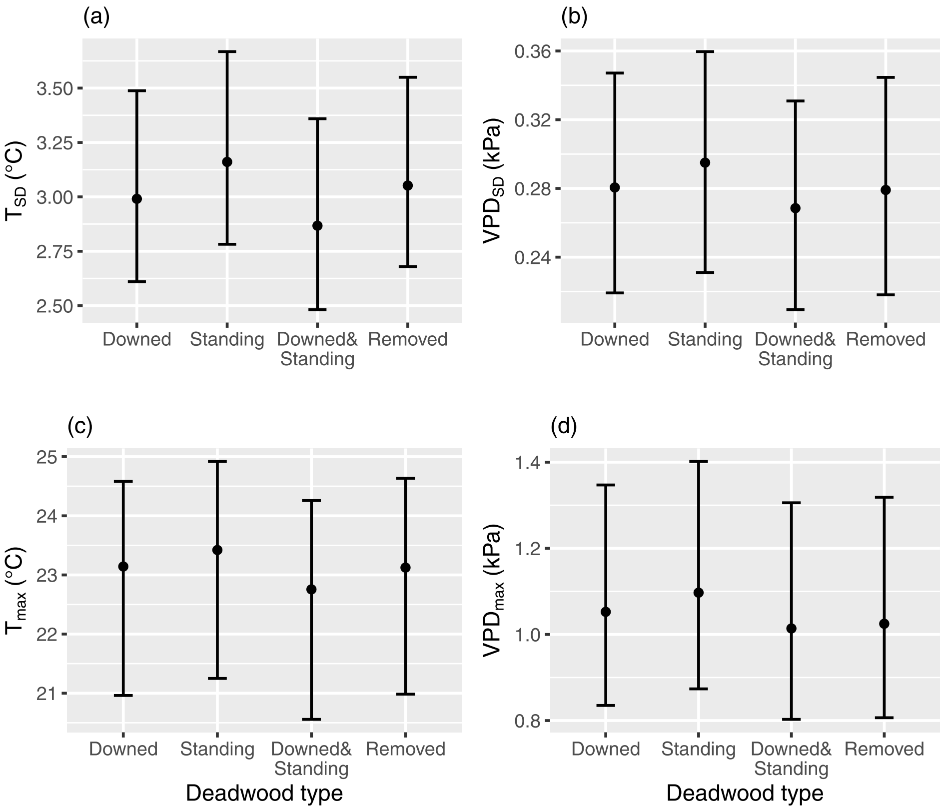


Figure 6. Deadwood effects on microclimate. (a) T_{SD}: Standard deviation of daily temperature; (b) VPD_{SD}: Standard deviation of daily vapor pressure deficit; (c) T_{max}: maximum daily temperature; (d) VPD_{max}: maximum vapor pressure deficit. Presented are the means (dots) and 95% credibility intervals (whiskers) of microclimate parameters for each deadwood type.

The spatial patterns of disturbance had a strong modulating effect on their microclimatic impacts. At similar severities (here: basal area removed), aggregated spatial disturbance patterns caused a stronger increase in surface light, and consequently resulted in warmer and drier conditions, than distributed disturbance patterns. Thus we conclude that the influence of disturbance on forest microclimate depends on the combination of different components of the disturbance regime, such as disturbance size, severity, and frequency (cf. Turner, 2010). High disturbance severity paired with a large disturbance extent will have particularly strong impacts on forest microclimate (Baker et al., 2014; Davis et al., 2019). The combined effects of disturbance severity and size on the microclimate could be multiplicative and non-linear. Also increases in disturbance frequency will play a critical role for future microclimate, as it may take decades to recover intact forest canopies (and thus to reinstate microclimatic buffers) after disturbance (Baker et al., 2014). A limitation of our analysis is that we here only studied the initial treatment effect, and did not consider the dynamic changes in the forest canopy after disturbance. Future work should thus analyze the change in microclimatic buffering with time since disturbance, particularly since European beech invests into additional branch growth after disturbance to fill available canopy space (Bayer and Pretzsch, 2017).

Downed and standing deadwood did not notably influence the microclimatic buffering effect in our study system. Specifically, we could not detect an interaction effect between deadwood type and spatial disturbance pattern on surface light conditions. Moreover, our results did not support the hypothesis of deadwood legacies partially mitigating disturbance effects on microclimate. We found a weak indication for a positive buffering effect on microclimate on plots where both downed and standing deadwood remained after disturbance. However, this effect was very uncertain. We note that we removed the crown in topping trees to create standing deadwood in our manipulation experiment. Disturbances that do not remove all branches could provide a higher level of shading, resulting in a stronger microclimatic buffering effect. We thus suggest that disturbance effects on microclimate depend on disturbance type and agent. For instance, many biotic disturbance agents (e.g., insects and fungi) cause a protracted loss of twigs and branches, whereas abiotic disturbances (e.g., fire, wind, snow) may remove the entire canopy, and thus are likely to have a stronger impact on the forest microclimate.

4.3. *Integrating considerations of microclimate into adaptive forest management*

Climate change and novel disturbance regimes will increasingly challenge the sustainable supply of ecosystem services to society (Albrich et al., 2018; Duveneck and Scheller, 2015; Schröter et al., 2005). Ensuring the functional and structural recovery of forests after disturbance could be increasingly challenging, as tree recruits are very susceptible to hot and dry conditions (Anderson-Teixeira et al., 2013; E Silva et al., 2012). A central aim of future forest management is thus to mitigate the coupled impacts of changing climate and disturbance regimes (Lindner et al., 2010; Millar et al., 2007; Seidl, 2014). Based on our findings, management should aim to reduce large-scale high-severity disturbances, as these have the strongest negative impacts on microclimatic buffering in forests. Homogeneous monocultures experience these disturbances more frequently than mixed forests of higher structural complexity (Felton et al., 2016). Thus, increasing tree species and structural diversity will likely reduce disturbance size and severity, and sustain a more suitable microclimate for many forest-dwelling species. Moreover, tree species and structural diversity are highly correlated with functional diversity (Cadotte et al., 2011). Increasing functional diversity will provide ecosystems with greater flexibility to react on future changes (Aubin et al., 2016; Silva Pedro et al., 2015). For instance, enriching ecosystems with drought-tolerant species will support forest regeneration after disturbance (O'Brien et al., 2017), and thus facilitates the establishment of a suitable microclimate for species with lower drought tolerance. Strategies to reduce disturbances and their effects on ecosystems should also account for landscape heterogeneity. A central European study has shown that disturbance risk and management effectiveness to reduce disturbances can differ considerably within a landscape (Seidl et al., 2018). Thus, strategies to avoid canopy disturbances should be adapted locally. For instance, managing for deep rooting tree species at wind exposed sites can lower disturbance predisposition considerably (Mitchell, 2013).

In addition to managing natural disturbances tree harvesting should not create large canopy openings in order to retain the microclimatic buffering effect for the regenerating tree cohort. Forest management practices that maintain a continuous canopy cover are likely better able to prevent regeneration from drought stress and heat than clear-cut systems (Hlásny et al., 2014). For instance, the ecosystem-based silvicultural systems that have been developed in recent years (Puettmann et al., 2015) are likely to sustain suitable microclimate conditions for regeneration. In particular, single-tree selection systems minimize harvesting effects on the forest microclimate. If gaps are cut into forests in drought-prone regions, their direction should be considered to reduce surface light. An east-west facing gap (e.g., in the form of an ellipse that is long from east to west, but narrow from north to south) is better sheltered from the sun by surrounding trees than a comparable gap in north-south direction. Accounting for gap direction is particularly important for south-exposed slopes in the northern hemisphere (north-exposed slopes in the southern hemisphere), where canopy openings alter surface light conditions, and thus the microclimate, most strongly.

Fostering specific forest types is another potential strategy to improve the microclimate. Broadleaf-dominated forests generally have a higher evaporative cooling effect than conifer-dominated forests of similar stand age in central Europe (Schume et al., 2004; Thom et al., 2017), which is, *inter alia*, related to differences in leaf area and hydraulic architecture between conifers and broadleaves (Oksanen et al., 2018). For instance, in single-canopy, mature forests in Austria, the evapotranspiration rate of European beech-dominated stands is up to 84 % higher than of Norway spruce-dominated stands (Schume et al., 2004). Depending on water availability, management should thus aim for a high share of broadleaved trees to buffer the effects of climatic extremes in summer. Further, microclimate varies with forest development stages. Norris et al. (2012) showed that biomass-rich, cool temperate old-growth forests in Germany, Ukraine, and the UK attenuate temperature more efficiently than young and mature plantation forests of similar species composition. Hence, managing forest structure for late-development conditions may provide another option to buffer future climate change. In recent decades, silvicultural methods have been developed to create old-growth forest structures early in stand development (Bauhus et al., 2009; Keeton, 2006). These approaches could be beneficial for the microclimate, while fostering biodiversity and ecosystem services at the same time (Ford and Keeton, 2017; Franklin et al., 2002). However, if climate conditions of European cool temperate forests become increasingly Mediterranean, evaporative cooling may even decrease with stand development. Delzon and Loustau, 2005 found a decrease in evapotranspiration in even-aged maritime pine (*Pinus pinaster* Ait.) stands, driven by drought-related decreases in leaf area and canopy conductance. In conclusion, managing microclimatic buffering has the potential to partially offset negative consequences of climate change, but strategies to improve the microclimate need to be adapted locally considering the specific stand and site conditions.

Declaration of Competing Interests

None.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.agrformet.2020.108066.

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Supplement

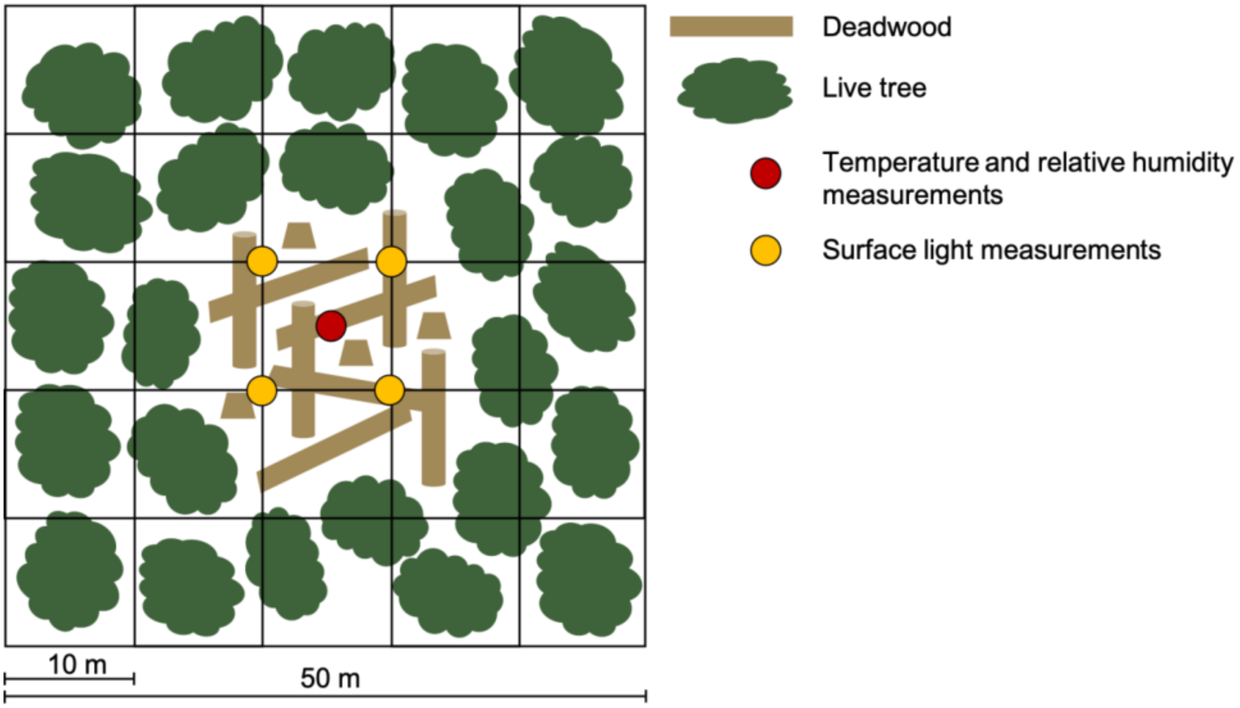

Figure S1: Position of the data logger and surface light measurements. The position was equal across treatments and control plots.

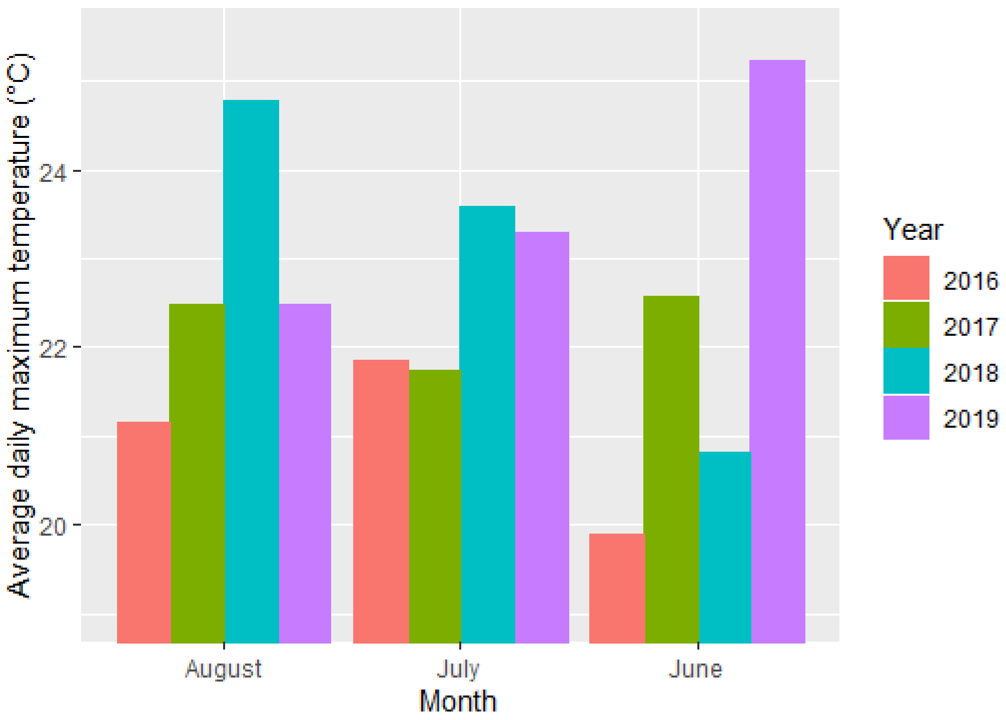

Figure S2: Average over the daily maximum temperature (T_{max}) at the experimental sites. Each bar represents the average temperature across the five sites. Values for each site were retrieved from 1.5 km grids of Germany's National Meteorological Service (Deutscher Wetterdienst), available at https://www.dwd.de/DE/klimaumwelt/cdc/cdc_node.html (accessed 02/17/2019).

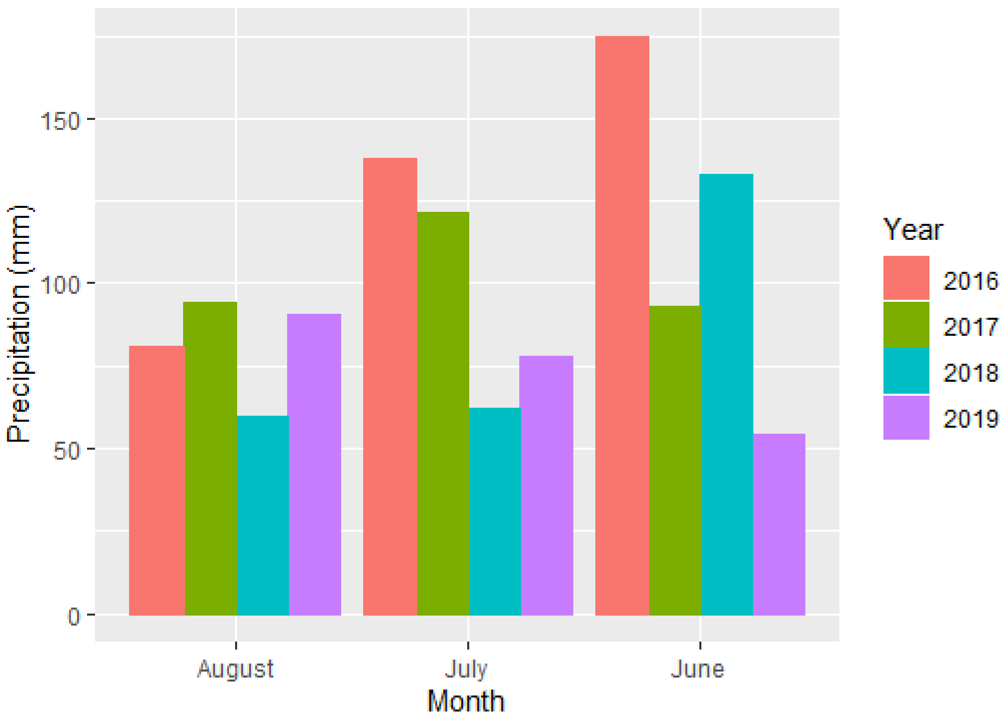

Figure S3: Monthly precipitation sum at the experimental sites. Each bar represents the average precipitation across the five sites. Values for each site were retrieved from 1.5 km grids of Germany's National Meteorological Service (Deutscher Wetterdienst), available at https://www.dwd.de/DE/klimaumwelt/cdc/cdc_node.html (accessed 02/17/2019).