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DISTURBANCE IMPACTS ON FOREST SUCCESSION, BIODIVERSITY, AND ECOSYSTEM SERVICES IN A CHANGING WORLD

Dissertation

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“A society grows great when old men plant trees whose shade they know they shall never sit in.”

Greek Proverb

Preface

The main body of this thesis comprises three peer-reviewed scientific papers which can be found in the Appendix of this work (sections 9.1 to 9.3). Please note that the format of each article follows the requirements of the respective journal. Whereas detailed descriptions of the experimental design and results of my work can be found in each paper, the synthesis of sections 1-8 aims to frame and interlink the findings of my dissertation in order to highlight the contribution of my thesis to filling existing knowledge gaps on disturbance dynamics in a changing world. In this way, my synthesis provides a common structure for the individual articles, and stimulates a discussion of the results beyond the scope of each paper. Moreover, I here present new hypotheses based on the advances made in my thesis, which I consider worth investigating in the future.

I hope the reader of my thesis feels excited by the research provided here and gains inspiration for his or her own investigations. I also like to mention that although I am certain about the validity of the methods used in this study, as in all fields of natural sciences no results should be considered without uncertainty. If there is one thing I learned during my PhD, it is that nothing we do and conclude from our findings is just black and white, but everything is shaded in grey. Hence, I believe that there is no perfect solution to a problem or only one outcome, but one can strive to find a good compromise and reduce the uncertainty among possible outcomes.

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Abstract

Forest ecosystems are dominated by long-living organisms with limited ability to migrate in space and time. Rapid changes in the climate system cause an increasing maladaptation of forests to their environment. Besides the direct impacts of climate change on forest ecosystems, climate change also modifies natural disturbance regimes. During the last decades, disturbance activity has significantly increased in many parts of the world, and a further increase as a result of climate change is very likely. Yet there is high uncertainty about the impacts of climate change and disturbance on the conservation of biodiversity and the provisioning of ecosystem services to society.

This thesis aimed to reduce this uncertainty by (i) synthesizing the effects of natural disturbances on biodiversity and ecosystem services in a global literature review, (ii) assessing the long-term development of tree species under varying climate and disturbance regimes by means of process-based landscape modelling, and (iii) investigating the role of climate change and disturbances on a wide range of forest biodiversity indicators in space and time.

I screened in total 1958 peer-reviewed papers for disturbance impact on biodiversity and ecosystem services, and reviewed 478 in detail. Subsequently, I simulated the autonomous adaptation of forests and their associated biodiversity under different climate and disturbance scenarios at Kalkalpen National Park (KANP). To account for the complexity of changes in ecosystems I employed the individual-based forest landscape and disturbance model (iLand).

I found strongly diverging disturbance impacts on forests: while disturbances increased biodiversity, they decreased ecosystem services provisioning. My results indicated that tree vegetation and associated biodiversity take centuries to adapt to changed climatic conditions, but also revealed a catalyzing effect of disturbances accelerating adaptation to a changing environment.

I conclude that disturbances create opportunities for ecosystems to reorganize themselves with potentially positive implications for the biodiversity and resilience of future forest ecosystems. Management should focus on the diversification of forests to provide ecosystems with the flexibility to react on changes of the environment and safeguard biodiversity and ecosystem services provisioning in a changing world.

Keywords: autonomous adaptation, biodiversity, climate change, disturbance, ecosystem services, forest ecosystem management, forest ecosystem dynamics, iLand, modelling, succession

Kurzfassung

Waldökosysteme werden von langlebigen Organismen dominiert, die nur bedingt ihren Standort verändern können. Der schnell voranschreitende Klimawandel kann somit zu einer Fehlanpassung von Ökosystemen an ihre Umweltbedingungen führen. Das Klima verändert Ökosysteme jedoch nicht nur direkt, sondern auch über Änderungen im Störungsregime. In den letzten Jahrzehnten wurde bereits ein Anstieg von Störungen in vielen Teilen der Welt beobachtet und eine weitere Zunahme gilt als sehr wahrscheinlich. Bislang herrscht große Unsicherheit über die Wirkung von Klimawandel und Störungen auf Biodiversität und Ökosystemleistungen.

Mit meiner Dissertation habe ich daher (i) die Effekte natürlicher Störungen auf Biodiversität und Ökosystemleistungen mithilfe einer globalen Übersichtsarbeit untersucht, (ii) die langfristige Entwicklung der Baumartenvegetation unter Annahme verschiedener Klima- und Störungsszenarien mit einem prozessbasierten Landschaftsmodel simuliert und (iii) die Rolle von Klimawandel und Störungen auf eine Reihe von unterschiedlichen Biodiversitätsindikatoren räumlich und zeitlich abgeschätzt.

Insgesamt habe ich 1958 wissenschaftliche Artikel auf ihren Inhalt überprüft und 478 für die Analyse von Störungseffekten auf Biodiversität und Ökosystemleistungen einbezogen. Anschließend habe ich die autonome Anpassung von Wäldern und ihrer Biodiversität im Nationalpark Kalkalpen unter verschiedenen Klima- und Störungsszenarien simuliert. Um der Komplexität von Ökosystemen gerecht zu werden, habe ich das individuenbasierte Waldlandschafts- und Störungsmodell (iLand) benutzt.

In meiner Studie konnte ich stark unterschiedliche Störungseffekte identifizieren und zeigen, dass Störungen Biodiversität erhöhen, aber gleichzeitig Ökosystemleistungen reduzieren. Simulationen zeigten einen Anpassungszeitraum der Baumvegetation und assoziierter Biodiversität auf veränderte Klimabedingungen von mehreren Jahrhunderten, aber auch eine Beschleunigung des Anpassungsprozesses durch Störungen.

Meine Schlussfolgerung ist, dass Störungen eine Chance für die Reorganisation von Ökosystemen bedeuten und positive Folgen für die Biodiversität und Resilienz von zukünftigen Waldökosystemen haben können. Managementstrategien sollten sich auf die Förderung von Biodiversität konzentrieren, damit Waldökosysteme den drastischen

Umweltänderungen gewappnet sind und auch in Zukunft Biodiversität erhalten sowie Ökosystemleistungen bereitstellen können.

Stichwörter: autonome Anpassung, Biodiversität, iLand, Klimawandel, Modellierung, Ökosystemleistungen, Störungen, Sukzession, Waldökosystemdynamik, Waldökosystemmanagement

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1 Introduction

Ongoing climatic changes may constitute the biggest challenge to mankind in the future. In particular, forest ecosystems may be strongly affected by climate change, as they are strongly restricted in their capability to react to rapid environmental changes. Trees are long-lived organisms and unable to change their spatial position. Migration of tree species is restricted to seed dispersal of mature tree individuals. Hence, it is unlikely that tree species can track the expected rapid climatic changes (Corlett and Westcott 2013). As a result forests will be increasingly maladapted to their environments, which may have severe consequences for ecosystem functioning (Maciver and Wheaton, 2005). Mountain forest ecosystems are expected to be particularly vulnerable to climate change as they are characterized by steep environmental gradients and upwards migration is limited by topography (Dirnböck et al., 2011; Engler et al., 2011).

Climate change does not only affect forests directly (i.e., via unmediated impacts of climate variables such as temperature and precipitation), but also indirectly (i.e., via impacts of climate change on mediators that subsequently have an impact on forests). Natural disturbance is likely the most prominent indirect driver of ecosystem change, as disturbance regimes are strongly coupled to the climatic system, abruptly modify the resource availability of forests, and consequently initiate the reorganization of ecosystems (Holling, 2001). Climate change has been identified as key driver of increases in natural disturbances in forest ecosystems worldwide (Dale et al., 2001). Most notably, an intensification of disturbance activity has been suggested for fire in tropical (Hoffmann et al., 2003), subtropical (Pitman et al., 2007), Mediterranean (Moriondo et al., 2006), and boreal (Balshi et al., 2009) ecosystems, as well as for insects, particularly bark beetles, in temperate ecosystems (Seidl et al., 2014).

While climate change is commonly hypothesized to negatively affect biodiversity (Butchart et al., 2010; Sala, 2000), disturbances are expected to have a positive effect on biodiversity (Müller et al., 2008; Roxburgh et al., 2004). A general proposition is thus to emulate the natural disturbance regime in forest management to sustain adequate levels of biodiversity in production forests (O'Hara and Ramage, 2013). However, future disturbance activity might be outside of the range of natural variability (Millar and Stephenson, 2015), and ultimately have negative consequences for biodiversity. In this regard it is important to note that changes in the various dimensions of a disturbance regime (i.e., disturbance frequency, return interval, rotation period, size, intensity, severity, and residuals (Turner, 2010)) may have divergent impacts on biodiversity. For instance, frequent small-scale (e.g., gap or patch size) disturbance events continuously provide small amounts of deadwood and lead to a heterogeneous horizontal and vertical forest structure, ultimately resulting in highly diverse forest ecosystems (Franklin and van Pelt, 2004). Large infrequent disturbance events, on the other hand, provide large amounts of deadwood within a short period of time, which is essential for the survival of very specialized species such as saproxylic beetles (Müller et al., 2008). However, large disturbance events potentially lead to more homogenous ecosystems compared to frequently disturbed systems in the long-run (Kuuluvainen, 2009). How divergent disturbance regimes contribute to biodiversity over varying temporal and spatial scales remains largely unclear to date.

In contrast to disturbance impacts on biodiversity, disturbance-induced alterations of ecosystem services are generally regarded as negative by forest managers. Disturbances *inter alia* reduce the size of merchantable timber stocks (Hanewinkel et al., 2011) and release carbon from ecosystems (Weng et al., 2012). Therefore, foresters generally aim to minimize disturbance. They, for instance, reduce the susceptibility of forests to wind disturbance by shortening rotation periods (Zell and Hanewinkel, 2015), or perform salvage logging and sanitation fellings to prevent bark beetle outbreaks after windthrow (Wermelinger, 2004). In ecosystems where fire is the dominant disturbance agent, and specifically in low severity fire regimes, it is common practice to reduce the amount of fuel by means of prescribed burning to prevent crown fires of larger trees (Ryu et al., 2006).

Yet, forest ecosystem managers are facing large uncertainties with regard to the spatio-temporal trajectories of forest ecosystems under changing climate and disturbance regimes, and their impacts on biodiversity and ecosystem services. Moreover, if forests are managed to fulfil a multitude of functions and services simultaneously (for instance, in most parts of Central Europe,), drivers of ecosystem change may simultaneously have positive and negative impacts on these goals (see e.g., Huston & Marland, 2003). As a result of these uncertainties and ambiguities, there is hesitation in implementing adaptation measures to climate change. Detailed scientific analyses are required to reduce this uncertainty, and to provide recommendations on how to make forests more resilient to possible future changes (Seidl et al., 2016).

Broad-scale investigations of tree species change and associated changes in biodiversity and ecosystem services provisioning have been conducted using species-distribution models (Hanewinkel et al., 2012; Thomas et al., 2004). These models describe the fundamental niche of species, however, they do not account for demographic processes (e.g., regeneration, competition, and disturbances) influencing the realized niche of species. Studying the spatio-temporal responses of tree species to climate change and changing disturbance regimes is the domain of process-based simulation models, which account for both environmental drivers and demographic processes. Another advantage of these models is their potential to explicitly address forest management under varying environmental and socio-economical conditions (Rammer and Seidl, 2015). Hence, dynamic process-based models are needed to investigate biodiversity and the provisioning of ecosystem services in a changing world.

2 Objectives

The overall aim of this thesis was to investigate potential impacts of natural disturbances and climate change on the conservation of biodiversity and the provisioning of ecosystem services, i.e. the primary goals of forest ecosystem management. In particular my objectives were to (i) synthesize the global understanding on disturbance impacts on biodiversity and ecosystem services, (ii) assess the response of tree species composition and associations to climate change and disturbances, and (iii) investigate the role of climate change and disturbance on a wide range of forest biodiversity indicators in space and time.

Disturbances *inter alia* generate deadwood, an important component of biodiversity as many species are dependent on deadwood as habitat (Thorn et al., 2016), promote species-rich early-successional ecosystems (Swanson et al., 2011), and provide a suitable micro-climate for a range of species (Fischer et al., 2013). The emulation of natural disturbance regimes is thus commonly promoted to foster biodiversity in managed forests (Franklin et al., 2002; Kuuluvainen and Grenfell, 2012). For these reasons, I hypothesized positive disturbance impacts on biodiversity. In contrast, disturbances reduce the amount of merchantable timber (Seidl et al., 2008), and carbon stored in forest ecosystems (Law et al., 2001), they affect net primary productivity (Hicke et al., 2003), and can even lower the aesthetic value of forests for recreationists (Hunt and Haider, 2004). Thus I assumed a negative impact of disturbances on all functional groups of ecosystem services (i.e., provisioning, regulating, supporting, and cultural services). As trees are long-living organisms and are limited to seed dispersal in their ability to migrate, I expected considerable time lags in the autonomous adaptation of forests to climate change. However, I also hypothesized that intensifying disturbance activity catalyzes the adaptation of forest ecosystems through an increased portion of forests being in the phase of reorganization (see also Holling, 2001). Finally I assumed negative consequences of climate change for biodiversity, but at the same time a mitigation of climate change impacts on biodiversity through increasing disturbance activity. The time lags in the final response of forest-dwelling species were hypothesized to coincide with the response of tree species to climate change, as forest-dwelling species are often associated to specific tree species (Kirk and Hobson, 2001; Tikkanen et al., 2006).

3 Materials and Methods

3.1 Workflow

In order to provide an overview of the methods used in this thesis, I summarize the main steps to address my questions and hypotheses in Figure 1. All papers (Appendix 9.1 – 9.3) are thematically connected, i.e., Paper I provided an overview of disturbance impacts on ecosystem services and biodiversity, Paper II simulated climate and disturbance impacts on the forest development in a mountainous landscape, and Paper III used the same simulation approach to quantify climate and disturbance impacts on spatio-temporal trajectories of biodiversity in detail. While the methods applied in Paper I were decoupled from the other papers, Papers II and III utilized a similar methodological approach.

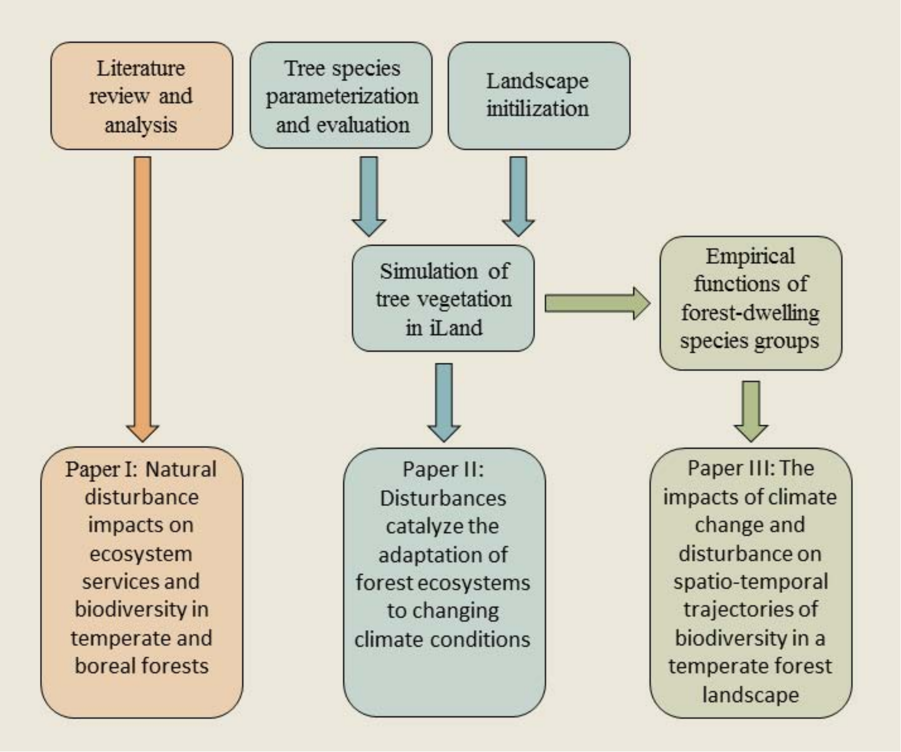


Figure 1: Short summary of the methods used to derive the papers of this thesis (see Appendix 9.1 – 9.3).

3.2 Literature review and meta-analysis

I performed a literature search using the Scopus database (https://www.scopus.com) to identify peer-reviewed studies on the impacts of fire, wind, and bark beetles on ecosystem services and biodiversity in temperate and boreal biomes (see also Appendix 9.1). I initially screened a total number of 1958 papers. Of those I selected 478 studies for further analysis. I allowed multiple entries per study into my analysis table if, for instance, a study reported on several disturbance agents, ecosystem services, and biodiversity indicators. Furthermore, I recorded the time since disturbance (in order to address changing disturbance effects over time) as well as disturbance severity (as, for instance, stand-replacing disturbances may alter ecosystems more strongly than low-severity disturbances). The final database derived from the literature contained 887 entries of disturbance effects on ecosystem services (n=348) and biodiversity (n=539).

From this body of literature, I first derived the overall impact of disturbances on ecosystem services and biodiversity by categorizing disturbance impacts into positive, negative, neutral and mixed effects. To test the hypothesis of diverging disturbance impacts on ecosystem services and biodiversity I compared disturbance effects by means of independence tests. As this test is useful to analyze the significance of differences between two samples, but does not provide insights into the size of the difference, I took a subset of entries and conducted a quantitative meta-analysis. Specifically, I investigated variables related to either biodiversity, i.e., species richness (S') and Shannon-Index (H') or carbon storage, i.e., total ecosystem carbon (TEC), aboveground living carbon (ALC), dead aboveground carbon (DAC) and soil organic carbon (SOC), and derived the relative change of a variable after disturbance to an undisturbed control. For this quantitative subset of the data, I analyzed the disturbance effect size by means of multiple linear regression using time since disturbance and 1-disturbance severity (i.e. with the intercept a standardized disturbance effect for a severity of 100%) as covariates. Moreover, I used independence tests to analyze the effect of salvage logging and prescribed burning on biodiversity and ecosystem services in order to assess how these two widely-used approaches in disturbance management alter disturbance impacts.

3.3 Case study area

The review of Paper I (Appendix 9.1) provides an overview of disturbance impacts on a broad range of ecosystem services and biodiversity indicators, but the global scale of the analysis distorts disturbance impacts on local to regional scale which is the spatial extent of forest management planning. Furthermore, owing to its broad scope the review was neither able to analyze biodiversity at the level of relevant species groups for nature conservation (e.g., taxonomic groups and red-list species), nor did it provide projections of disturbance impacts under changing environmental conditions. Therefore, I performed an in-depth analysis of the trajectories of forest development and associated biodiversity indicators at Kalkalpen National Park (KANP), the largest contiguous protected forest area in Austria (Fig. 1 in Appendix 9.2 and Fig. 1 in Appendix 9.3).

The national park is located at the northern front range of the Alps and has a total area of 20,850 ha. The complex terrain encompasses altitudes from 385 to 1963 m a.s.l., therefore temperature and precipitation vary considerably within the landscape (the mean annual temperature ranges from 3.6 – 9.0°C and the annual precipitation sum from 1205 – 1741mm). The dominant soil types are shallow Lithic and Rendzic Leptosols as well as Chromic Cambisols over calcareous bedrock. Since 1997 KANP is accredited by the IUCN under category II (National Park), and management has been ceased completely in the core zone of the park. Some of the most important forest types of Central Europe can be found at KANP, including European beech (*Fagus sylvatica* [L.]) dominated forests at low altitudes, mixed forests of Norway spruce (*Picea abies* [K.]), silver fir (*Abies alba* [Mill.]) and European beech in mid-elevations, and subalpine spruce forests in the highest reaches of the landscape.

3.4 Simulation model

I employed iLand (the individual-based forest landscape and disturbance model) to simulate forest development at KANP. iLand was developed to simulate forest landscapes at high resolution (Seidl et al., 2012a; 2012b), and accounts for the dynamic feedbacks between tree vegetation, climate (change), and disturbance regimes. To this end, the model incorporates processes in a hierarchical multiscale approach, i.e., iLand considers processes at the single tree level (e.g., resource competition, growth, mortality), stand level (e.g., light, water, and nitrogen availability), and landscape level (e.g., seed dispersal and disturbances). I parameterized in total 29 Central European tree species for simulation with iLand. I tested and evaluated the tree species parameters against independent inventory data on 34 forest stands distributed over Austria, two landscapes in the Austrian Alps, and one landscape in the Swiss Alps. The parameter tests included analyses of the growth performance of tree species, their mortality rates, as well as their dominance under varying environmental conditions (see also Supporting Information in Appendix 9.2 for the parameter tests at KANP). A more detailed description of iLand can be found in Appendices 9.2 and 9.3 of this thesis, in Seidl et al. (2012a) and Seidl et al. (2012b), as well as on the iLand homepage (http://iLand.boku.ac.at).

3.5 Initial conditions and drivers

Simulations with iLand require inputs of climate, soil, and current tree vegetation (i.e., initial conditions). Climate and soil conditions were considered at a spatial grid of 100 × 100 m (1 ha) in iLand, covering a total of 19,200 ha at KANP. Initial tree vegetation (i.e., the vegetation condition at the start of the simulation) on a net stockable forest area 13,865 ha was implemented at 10 × 10 m cells.

The simulation of future trajectories of forest development at KANP considered four different climate scenarios. For the baseline climate I randomly sampled years within the period 1950 – 2010. In addition, three different combinations of global and regional circulation models under A1B forcing (Jacob, 2001; Pal et al., 2007; Radu et al., 2008) were derived to simulate transiently changing climatic conditions until the end of the 21st century. Beyond the year 2099, a stabilization of the climate at the level of the last 20 years of the 21st century was assumed. Relative to baseline climate conditions, this period represented a temperature change between +3.1°C and +3.3°C, and a precipitation change between –89 mm and +141 mm.

I characterized soil conditions at KANP using inventory data on soil depth, type, texture, and plant available nitrogen. Soil depth and type (Kobler, 2004) as well as soil texture were derived from a regular 300 × 300 m inventory grid over KANP (n=622). Plant available nitrogen was derived by means of stratified sampling over ecoregion, elevation, soil depth, aspect, and slope, using a dataset developed for the grid of the Austrian National Forest Inventory (n=557) (Seidl et al., 2009).

A number of different data source were synthesized to initialize the current tree vegetation of KANP at the level of stand polygons (10 × 10 m resolution), and to estimate the stockable area within each stand polygon. These sources included terrestrial inventory plots (n=1122) as well as forest planning data, aerial photography analysis, and airborne LiDAR products (Light Detection And Ranging) of the landscape. Based on these data I derived tree species composition, diameter at breast height (dbh), tree age and height as well as the position of trees within the landscape. In total, I initialized more than $2\ 10^6$ trees from 17 different species. As these empirically derived data sources roughly characterize the state of tree vegetation at KANP in the year 1999, and as the KANP has been affected by severe disturbance events since then, I simulated the forest landscape from 1999 until 2013 incorporating the spatial explicit disturbance records of KANP (see also Seidl and Rammer, 2016). Ultimately, 2013 was the initial year for all scenario analyses. More information on initial conditions of the landscape and drivers of forest dynamics can be found in Appendix 9.2 and 9.3.

3.6 Simulation design

Starting from the current state of vegetation, I simulated forest development over 1000 years under the four climate scenarios described in the previous section (see also Appendix 9.2 and 9.3). Additionally, I simulated different generic disturbance scenarios in which disturbance frequency, severity, and size were altered independent of each other for each climate scenario. Parameters of disturbance frequency, severity, and size were selected to represent the current disturbance regime in the low-intensity variant, while the high-intensity variant assumed an intensification of disturbance activity in line with future projections of disturbance changes (Seidl et al., 2014). In total, I simulated 36 unique combinations of climate and disturbance scenarios (four climate scenarios × two disturbance frequencies × two disturbance severities × two disturbance sizes to investigate the development of tree vegetation and biodiversity under changing climate and disturbance regimes. To account for stochasticity of the simulation, each scenario combination was simulated 10 times (i.e., in total 360 runs were performed). The analyses of Paper II and III (Appendices 9.2 and 9.3) were based on the same set of simulation runs.

3.7 Analysis of autonomous adaptation of tree vegetation

First, I investigated the autonomous adaptation of tree vegetation at KANP, and the role of disturbance therein by analyzing the time required until the vegetation composition was in dynamic equilibrium with climate conditions. Second, I analyzed species change by calculating the spatial pattern of tree species turnover on the landscape (see also Appendix 9.2). I considered the vegetation as being in equilibrium with climate when the temporal variation in basal area of each individual tree species on the landscape was within ± 2 m^2 ha^{-1} of their respective simulation endpoint (defined as the average basal area per tree species in the last 200 years of the simulation). Moreover, I estimated migration speed over elevation based on the mean annual change rates of a species' leading edge, defined as the 90th percentile of the elevation distribution of a species on the landscape. Spearman's rank correlation was used to test whether species changed individually or in associations. To test for disturbance effects on forest adaptation, I unraveled the differential effects of disturbance extent (i.e., percent of the landscape area disturbed) and disturbance impact (i.e., percent of basal area disturbed) on the time until a dynamic equilibrium of the species composition emerged on the landscape. Finally, I quantified the species turnover triggered by climate change at the level of 100 m grid cells.

3.8 Analysis of trajectories of biodiversity

I performed an in-depth analysis on the trajectories of biodiversity change resulting from the simulated climate change and disturbance scenarios at KANP (see also Appendix 9.3). To that end I selected eleven indicators of biodiversity and analyzed their individual responses to the investigated scenarios in time and space. The effective number of tree species (the exponent of the Shannon index), and the structural heterogeneity of the tree canopy were directly derived from iLand simulation outputs. Diversity of ground vegetation was determined using selected releves of the AlpFlor database (n=852) (Dullinger et al., 2012). Eight indicators of animal diversity were deduced from 52 inventory plots distributed over neighboring Bavaria. For each of the nine indicators that were not directly derived from iLand simulation outputs, I developed negative binomial generalized linear models (glms) with a logarithmic link function where the response variable (number of species) was related to mean annual precipitation sum (P_{sum}) and mean annual temperature (T_{mean}) (indicators of the climate regime), canopy cover (an indicator for light availability and the local thermal regime), as well as to the identity and relative share of individual canopy tree species (indicators of species association). These empirically derived models were then used to predict the species number for each group using climate data and iLand simulation outputs as covariates. For the analyses of climate change effects over time I aggregated all 100-m grid cells to landscape-level mean responses and compared each simulation under climate change with the mean over the baseline period under the same disturbance scenario. Likewise, the disturbance effect was calculated by relating scenarios of different disturbance frequencies, severities and sizes to the respective undisturbed scenario for any given climate regime. Spatial changes in biodiversity were addressed by an analysis of biodiversity hotspots. As the loss of functionally unique species is more important for ecosystem functionality than the number of species (O'Gorman et al., 2011), I defined a biodiversity hotspot as area where every indicator exceeded its 25th percentile value.

4 Results

4.1 Disturbance impacts on biodiversity and ecosystem services

I found strong support for diverging disturbance effects on biodiversity and ecosystem services provisioning, which was independent of time since disturbance (Fig. 2 in Appendix 9.1). While biodiversity was positively related to disturbance ($p<0.001$), the ecosystem services provisioning in all categories (i.e., supporting, provisioning, regulating and cultural services) decreased markedly with disturbance ($p<0.001$). Albedo, a service important for the regulation of the climate through the reflection of radiation, was the only ecosystem service showing a positive disturbance response (Fig. 3 in Appendix 9.1). A large majority of studies reported timber, primary production, fresh water provisioning, protection against natural hazards, and carbon storage as being negatively affected by disturbance. All indicators of biodiversity (diversity indices, species richness, and habitat quality) were overall positively affected by disturbance. However, a number of studies also reported negative impacts of disturbance on these variables, indicating a higher uncertainty in the generalization of disturbance effects on biodiversity compared to ecosystem services.

The mean standardized effect of a stand-replacing disturbance revealed significant impacts on all carbon compartments (Fig. 4 in Appendix 9.1). In particular ALC (-91.3 ± 9.1%) and DAC (+155.5± 71.5%) were strongly affected by disturbance. For all investigated compartments time since disturbance significantly explained disturbance effects on carbon storage (Table 3 in Appendix 9.1). With every passing year after a stand-replacing disturbance event the disturbance impact on ALC and DAC decreased by +0.6% and -1.4%, respectively. In contrast, the assessed biodiversity indicators (S' and H') did not change significantly with time since disturbance. The analysis of the mean standardized disturbance effect provided insights into the diverging disturbance effects on biodiversity and carbon storage: While a disturbance event with 100% severity had a positive impact on species richness (+35.6 ± 32.3%), it had a comparable negative impact on total ecosystem carbon (-38.5 ± 8.3%). The analysis on the effects of disturbance management on ecosystems services and biodiversity revealed only one significant effect, and that was an increased negative consequence of prescribed burning on ecosystem services compared to wildfire ($p<0.001$). However, this result should be interpreted with caution as it is based on only 13 observations for the effects of prescribed burning.

4.2 Forest development at KANP under changing climate and disturbance regimes

The analysis on future forest development at KANP revealed that if the effect of disturbances was neglected the tree vegetation took 558 years to reach a dynamic equilibrium even under baseline climate, as a result of past management legacies (Fig. 2 and Table 3 in Appendix 9.2). Climate change prolonged the time to reach a dynamic equilibrium by 148 years. In contrast, disturbances reduced the time to reach a dynamic equilibrium on average over all scenarios by 119 years under baseline climate conditions (-21.3%), and by 72 years under changed climatic conditions (-10.2%).

European beech benefited most from climate change compared to baseline climate conditions at the end of the simulation period, as indicated by an absolute increase of +28.5 and + 32.2 percentage points in simulations with and without disturbances, respectively (p<0.001). Also oak species (*Quercus petraea* [Matt.] and *Quercus robur* [L.]) increased notably by +20.0 and +22.9 percentage points (p<0.001). On the contrary, Norway spruce and silver fir which are main tree species under baseline climate declined substantially in a changing climate (-19.4 and -16.7 percentage points and -13.5 and -8.1 percentage points, respectively, p<0.001). Disturbance effects on late serial species were all negative while disturbance strongly favored early seral species, most notably silver birch (*Betula pendula* [Roth]), European larch (*Larix decidua* [Mill.]), and aspen (*Populus tremula* [L.]). A subsequent analysis at the level of the individual dimensions of the simulated disturbance regime revealed a synergistic effect between disturbed basal area and disturbed landscape extent on the adaptation speed of the landscape, i.e., if the disturbance impact on basal area was low, the extent of disturbance had only a weak influence on the adaptation speed (Fig. 3 in Appendix 9.2). While an increasing share of area disturbed at KANP was beneficial for the adaptation of the tree vegetation, an increase in the mean size of disturbance events had the opposite effect, i.e., the scenarios with increased disturbance size needed on average 24.8 years longer to reach dynamic equilibrium compared to scenarios assuming historical disturbance sizes. In contrast, an increase in disturbance frequency and severity accelerated forest adaptation (-64.3 and -54.5 years, respectively).

The adaptation of forests to changing climatic conditions at KANP also involved an upwards shift in elevation of several hundreds of meters for many tree species. The maximum average change rate was +0.37 m asl yr^{-1} (silver fir). Another concomitant effect of forest adaptation to a changing climate was a change in species associations. For instance, European beech and oak species were clearly positively related under baseline climate conditions, but moderately negatively associated under climate change. Altered species ranges and associations also resulted in the emergence of local novelty in tree species composition. For instance, a comparison between baseline climate under the historic disturbance regime with climate change under the most extreme disturbance regime revealed a species turnover (i.e., a change in locally present tree species) of 51.8%, with most pronounced changes being simulated at the lowest and highest elevations of the national park (Fig. 5 in Appendix 9.2).

4.3 Spatio-temporal trajectories of biodiversity change at KANP

The empirically derived models of diversity revealed various direct and indirect responses of species groups to climate change. At the end of the 1000-year simulation period, six indicators showed positive direct responses, while five indicators were negatively affected by climate change. Direct climate change impacts were overall beneficial for the diversity of ground vegetation, Hemiptera, Hymenoptera, Mollusca, Symphyta and Syrphidae, but reduced the diversity of Araneae, Carabidae and saproxylic beetles as well as the canopy complexity of forests (Fig. 2 and Table 3 in Appendix 9.3).

While climate change impacts on the studied diversity indicators were strong but ambiguous, disturbance effects were generally positive, but less distinctive (Fig. 3 and Table 3 in Appendix 9.3). The slow response of indicators after an initial, direct response to climate change highlights their tracking of the delayed tree vegetation adaptation. Consistent with the results on the divergent effects of disturbance regime dimensions on the adaptation of tree vegetation, I found that an increase in disturbance frequency and severity are beneficial for biodiversity, while an increase in mean disturbance size decreases biodiversity.

The analysis of biodiversity hotspots underlined the effects of a changing environment on biodiversity. After 1000 simulated years the hotspot area decreased significantly under climate change compared to baseline climate simulations ($p<0.001$), and shifted from low-moderate elevations to higher elevation zones (Fig. 4 in Appendix 9.3). In contrast, disturbances increased the extent of hotspots ($p<0.001$), for instance, by 146.1% under baseline climate.

5 Discussion

5.1 Biodiversity and ecosystem services provisioning in a changing world

Here I presented the impacts of disturbances on biodiversity and ecosystem services assessed by a large body of peer-reviewed scientific articles. I showed that, on the one hand, disturbances have a strong negative impact on ecosystem services while, on the other hand, they have a distinct positive impact on biodiversity, confirming the hypothesis of diverging disturbance impacts on management goals (Fig. 2, 3, and 4 in Appendix 9.1). An in-depth analysis of disturbance impacts on biodiversity at KANP supported the results obtained from the global review of the literature (Fig. 3 in Appendix 9.3). The simulations were also in line with the expectation of disturbance being a facilitator of long-lasting forest (Fig. 2 in Appendix 9.2) and associated biodiversity (Fig. 2 in Appendix 9.3) adaptation under changed environmental conditions (Fig. 3 in Appendix 9.3). However, the direct effects of climate change on biodiversity at KANP were rather ambiguous compared to the findings of disturbance effects (cf. Fig. 2 in Appendix 9.3 with Fig. 2 in Appendix 9.1).

Broad-scale investigations have suggested a strong climate change-induced decline of biodiversity (Sala, 2000; Thuiller et al., 2005) and ecosystem services (Hanewinkel et al., 2012; Schröter et al., 2005) in many parts of the world during the 21st century. In contrast to the assessment of the spatio-temporal dynamics of forest biodiversity at fine spatial grain such as presented in Appendix 9.3, those studies have largely focused on direct impacts of climate change on biodiversity and ecosystem service provisioning (e.g., temperature and precipitation), largely disregarding indirect impacts (e.g., modification of habitat of forest-dwelling species from increasing disturbance activity). However, as demonstrated here, indirect effects can be crucial determinants for the magnitude of change in biodiversity under climate change, and this indirect effect is likely similar for ecosystem service supply as indicated by the pronounced disturbance effects on ecosystem services in Paper I. For instance, intensifying disturbance activity (Seidl et al., 2014) may amplify positive disturbance impacts on biodiversity, and this may in turn mitigate negative impacts of climate change on biodiversity. My thesis finds support for such a compensatory effect of disturbances, as increasing disturbance levels partly offset negative impacts of climate change on some of the investigated indicators. However, climate change also potentially promotes the occurrence of “mega-disturbance” events in the future (Millar and Stephenson, 2015). This increase in disturbance activity may push systems across a tipping point beyond which disturbances neither foster the adaptation of forest ecosystems to changing environments (as ecosystems become unstable), nor support biodiversity (due to a homogenization of ecosystems). Disturbance regimes that are currently characterized by small but frequent disturbance events may change to disturbance regimes that are dominated by large scale disturbance events, which could ultimately also lead to a lower disturbance frequency (as ecosystems need a long time to recover from mega-disturbances). Consequently these new regimes could endanger both the sustainable provisioning of ecosystem services and biodiversity, and thus challenge forest ecosystem management. Future investigations are needed to identify such tipping points in forest ecosystems.

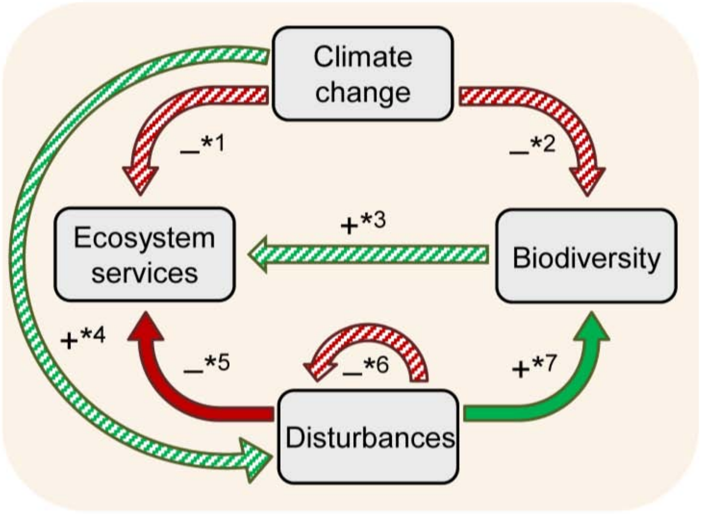
5.2 Management implications

Driven by the simplicity of even-aged forest management and the goal to achieve the highest possible revenues from timber production, forest management activities have strongly altered ecosystems and created widespread plantations of monocultures in many parts of the world with negative consequences for biodiversity and several ecosystem functions and services (Felton et al., 2016). Recent investigations have shown that – against initial intentions – such monocultures often do not produce larger amounts of timber compared to mixed forests (Pretzsch et al., 2010), and that the expected revenues from such management systems are strongly dependent on economic assumptions (Hanewinkel et al., 2014; Pukkala, 2016). Furthermore, simplified calculations on timber and economic outputs of forests usually disregard the potentially strong effects of natural disturbances (Knoke et al., 2008). Previous assessments of disturbance drivers provided evidence that monocultures are highly susceptible to disturbance (Thom et al., 2013), and it is likely that the dimension of disturbance events is already beyond the natural range of variability in some regions as a result of altered forest structure and composition. Examples for regions where forest management has strongly increased the intensity of disturbance regimes can be found in different parts of the world, for instance in Central Europe (Seidl et al., 2011) or North America (Westerling, 2006). Increases in disturbance activity will likely counteract this trend as disturbance will foster biodiversity in forests (Fig. 2 , 3 and 4 in Appendix 9.1 and Fig. 3 in Appendix 9.3) which may support their resilience towards environmental changes. Therefore, forest managers should not regard disturbance impacts as entirely negative, but they should take disturbances as opportunity to adapt forests to changing environments (Appendix 9.2, Fig. 2). However, if the size of disturbance events becomes much larger in comparison to the historic disturbance regime, the benefits for biodiversity will be reduced or even reversed. Such an effect is suggested by the intermediate disturbance hypothesis (due to niche partitioning of species within the segments of canopy gap (Roxburgh et al., 2004)), and was supported by the results of this study (Appendix 9.3, Fig. 3). Where disturbance size potentially leads to a homogenization of ecosystems, forest management should consider to actively plant different tree species to foster resilience.

My global review on common disturbance management methods indicates that salvage logging and prescribed burning have only a limited potential to facilitate management objectives (Appendix 9.1). The only statistically significant impact of these management measures was a positive effect of prescribed burning on biodiversity, while at the same time ecosystem services were negatively affected. Over all analyzed papers in the global review the analysis of salvage logging did not substantiate a strong advantage of this management practice for the analyzed indicators, i.e., it neither had a significant positive effect on ecosystem services provisioning nor on biodiversity. In the context of future mega-disturbances alternative (long-term) management strategies are thus required. Concepts that aim to emulate the natural historic disturbance regime are often promoted as a solution to deal with future uncertainties (Drever et al., 2006; Kuuluvainen and Grenfell, 2012). However, natural forest ecosystem dynamics and disturbance regimes may differ considerably in the future (see also O'Hara 2016). Hence I suggest that adaptive forest management goes beyond concepts that aim to mimic the past. Moving from highly susceptible monocultures towards forest ecosystems of high biodiversity and including tree species that can be expected to tolerate projected climate conditions is required to limit impacts of potential changes in climate and disturbance regimes. My thesis indicated an increasing maladaptation of forest ecosystems under climate change (Appendix 9.2, Fig. 2). As the response of tree species to changing environments lags considerably behind climatic changes, ecosystem management must take long lead times into account in adapting forests to changing environmental conditions, and hence to promote ecosystem services provisioning and biodiversity in the future.

5.3 *Implications for future research*

In addition to the effects of increasing disturbance regimes studied here also other possible secondary effects of climate change need further attention to comprehensively estimate climate change impacts on biodiversity and ecosystem services (Fig. 2). For example, it is widely recognized that biodiversity promotes ecosystem service supply (Isbell et al., 2011; Pasari et al., 2013), i.e., if biodiversity is increased as a result of higher disturbance activity under climate change this increase likely mitigates some of the negative effects of elevated disturbance levels and climate change on ecosystem service provisioning. Furthermore, it is likely that changes in disturbance regimes will be buffered by negative feedbacks, i.e., an increase in disturbance activity in the near future could lead to a reduction of disturbances in the long-run (negative interaction effect). This dampening feedback can be driven by tree species change towards species with lower susceptibility to the emerging disturbance regime (e.g., in most parts of KANP Norway spruce, a species highly susceptible to wind and bark beetle disturbance, was replaced by the more disturbance resistant European beech in the simulations with changed climatic forcing). Future studies should thus further investigate the complexity of climate change impacts on biodiversity and ecosystem service provisioning by addressing not only direct impacts of climate change, but also indirect and interaction effects.



[*1] Schröter et al. (2005)
[*2] Sala et al. (2000)
[*3] Isbell et al. (2011)
[*4] Seidl et al. (2014)
[*5] Thom and Seidl (2016)
[*6] Temperli et al. (2013)
[*7] Thom et al. (2016)

Figure 2: Expected long-term impacts of climate change on disturbances, biodiversity and ecosystem services. The figure illustrates direct (arrows from climate change to ecosystem services, biodiversity, and disturbances), indirect (arrow from disturbances to biodiversity and ecosystem services as well as arrow from biodiversity to ecosystem services), and interaction

(arrow from disturbance back to disturbance) effects driven by climate change. Solid arrows indicate effects investigated in this study while lined arrows show effects based on other studies. Green: positive impact, red: negative impact. Asterisks and numbers provide examples for studies which support the hypothesized effects.

To understand the response of ecosystems, and their associated biodiversity and ecosystem services, it is also important to investigate impacts of environmental change over different temporal (Fig. 2 in Appendix 9.2 and 9.3) and spatial scales (Fig. 4 in Appendix 9.3) . For instance, the assumption that highly diverse ecosystems also provide a broader range of ecosystem services (Isbell et al., 2011; Silva Pedro et al., 2016) introduces a paradox, if disturbances have positive impacts on biodiversity and at the same time negative impacts on ecosystem services as presented in my thesis (Appendix 9.1, Fig. 2, 3, and 4). This raises the question whether ecosystem service provisioning is lower in frequently disturbed but diverse forest ecosystems compared to infrequently disturbed but less diverse ecosystems. Even though I found evidence for a reduction of ecosystem services provisioning after disturbance, it is possible that frequently disturbed forests are highly diverse and provide high amounts of ecosystem services simultaneously without violating the general findings of this study, if disturbance responses are considered in the long run and for multiple disturbance events (Fig. 3). This should be tested in future investigations by comparing the temporal variation and average levels of ecosystem service supply and biodiversity of frequently disturbed ecosystems with ecosystems that are characterized by low disturbance frequency over a long time period. In this context, important ecosystem processes for such an investigation such as tree species migration require simulations of larger spatial entities, while processes such as tree growth require a much finer spatial resolution (e.g., individual trees), hence study designs are needed that include hierarchical process structures. Moreover, resistance and resilience are likely higher in heterogeneous ecosystems with high biodiversity than in homogeneous ecosystems with low biodiversity (see e.g., Silva Pedro et al., 2015). Hence it can be expected that disturbance severity and size are lower for disturbance events in highly diverse ecosystems, and that those ecosystems have an accelerated rate of recovery to the level of ecosystem service provisioning prior to disturbance (see also Turner *et al.*, 2013). To better understand the complexity of dynamic ecosystem responses to climate change, also these interrelations need further attention in future investigations.

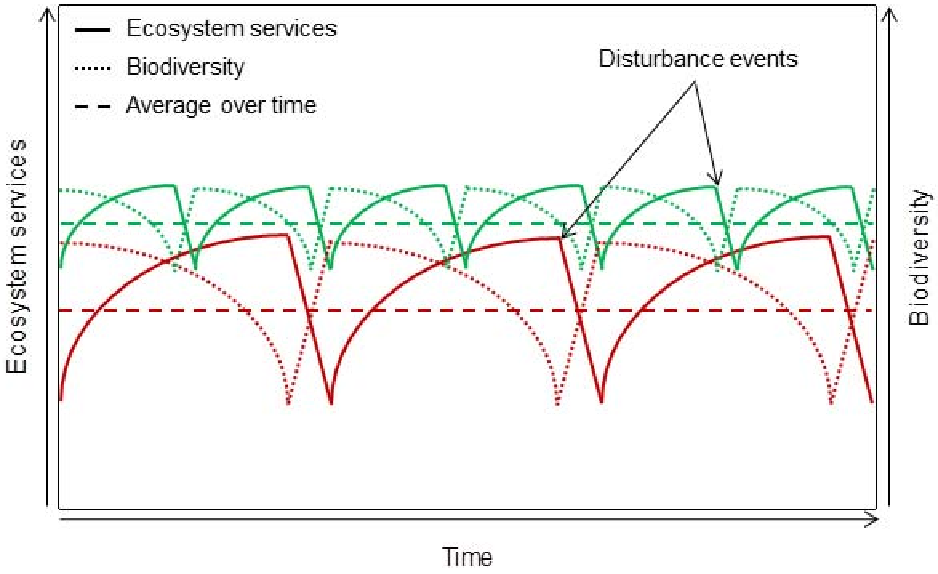


Figure 3: Hypothesized relation between disturbance regimes, ecosystem services and biodiversity over time. Green lines represent an ecosystem with high disturbance frequency, while red lines indicate an ecosystem with low disturbance frequency. Broken lines indicate the average of biodiversity and ecosystem service supply over time. The green scenario demonstrates that frequently disturbed ecosystems can promote higher biodiversity and at the same time provide increased amounts of ecosystem services in comparison to the red scenario with lower disturbance frequency. The figure demonstrates that the findings of this thesis regarding diverging disturbance impacts on forest management goals are not in contradiction with the general opinion that ecosystems with high biodiversity also provide high amounts of ecosystem services.

6 Conclusions

My thesis demonstrated the diverging effects of disturbances on ecosystem services and biodiversity (Appendix 9.1, Fig. 2, 3, and 4). Moreover, I found an increasing maladaptation of forest ecosystems under climate change, but also that disturbances create opportunities for ecosystems to reorganize themselves (Appendix 9.2, Fig. 2). As a result it is likely that the resilience of disturbed ecosystems will be higher in the future, and that their maladaptation towards novel climatic condition will be decreased compared to undisturbed forest ecosystems. Depending on management goals the positive response of biodiversity after disturbance (Appendix 9.3, Fig. 3) may even serve to better fulfil objectives of forest ecosystem managers (e.g., in national parks or where forests are managed for multiple purposes). I thus propose that disturbances should not *a priori* be regarded as negative in forest ecosystem management, but instead as an integrated and important part of ecosystem dynamics. However, forest managers must be aware that with climate change disturbance activity can exceed a tipping point, beyond which disturbance threatens biodiversity and the sustainable supply of ecosystem services. As indicated by my work (Appendix 9.2, Fig. 2), adaptation of forest ecosystems has to take long lead-times into consideration. Yet, there is considerable uncertainty how different ecosystems will respond to climate change and disturbance regimes that transgress the historical range of variability as historical reference conditions are of limited value to predict a changing world. Future studies should investigate the complexity of forest ecosystem responses in paired long-term studies, i.e., they should simultaneously compare ecosystem service supply and biodiversity in ecosystems with varying climate and disturbance regimes while covering a large spectrum of possible environmental changes. To deal with the uncertainty of future environments, I propose a diversification of management regimes away from simplified forest plantations such as monocultures towards mixed forests. Only a management that diversifies forests will provide ecosystems with the flexibility to react on drastic changes of the environment and safeguard biodiversity and ecosystem services provisioning in a changing world.

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9 Appendix

9.1 Paper I: Natural disturbance impacts on ecosystem services and biodiversity in temperate and boreal forests

Thom, D., Seidl, R., 2016. Natural disturbance impacts on ecosystem services and biodiversity in temperate and boreal forests. Biol. Rev. 91, 760–781.

Natural disturbance impacts on ecosystem services and biodiversity in temperate and boreal forests

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ABSTRACT

In many parts of the world forest disturbance regimes have intensified recently, and future climatic changes are expected to amplify this development further in the coming decades. These changes are increasingly challenging the main objectives of forest ecosystem management, which are to provide ecosystem services sustainably to society and maintain the biological diversity of forests. Yet a comprehensive understanding of how disturbances affect these primary goals of ecosystem management is still lacking. We conducted a global literature review on the impact of three of the most important disturbance agents (fire, wind, and bark beetles) on 13 different ecosystem services and three indicators of biodiversity in forests of the boreal, cool- and warm-temperate biomes. Our objectives were to (*i*) synthesize the effect of natural disturbances on a wide range of possible objectives of forest management, and (*ii*) investigate standardized effect sizes of disturbance for selected indicators *via* a quantitative meta-analysis.

We screened a total of 1958 disturbance studies published between 1981 and 2013, and reviewed 478 in detail. We first investigated the overall effect of disturbances on individual ecosystem services and indicators of biodiversity by means of independence tests, and subsequently examined the effect size of disturbances on indicators of carbon storage and biodiversity by means of regression analysis. Additionally, we investigated the effect of commonly used approaches of disturbance management, i.e. salvage logging and prescribed burning.

We found that disturbance impacts on ecosystem services are generally negative, an effect that was supported for all categories of ecosystem services, i.e. supporting, provisioning, regulating, and cultural services ($P<0.001$). Indicators of biodiversity, i.e. species richness, habitat quality and diversity indices, on the other hand were found to be influenced positively by disturbance ($P<0.001$). Our analyses thus reveal a “disturbance paradox”, documenting that disturbances can put ecosystem services at risk while simultaneously facilitating biodiversity. A detailed investigation of disturbance effect sizes on carbon storage and biodiversity further underlined these divergent effects of disturbance. While a disturbance event on average causes a decrease in total ecosystem carbon by 38.5% (standardized coefficient for stand-replacing disturbance), it on average increases overall species richness by 35.6%. Disturbance-management approaches such as salvage logging and prescribed burning were neither found significantly to mitigate negative effects on ecosystem services nor to enhance positive effects on biodiversity, and thus were not found to alleviate the disturbance paradox. Considering that climate change is expected to intensify natural disturbance regimes, our results indicate that biodiversity will generally benefit from such changes while a sustainable provisioning of ecosystem services might come increasingly under pressure. This underlines that disturbance risk and resilience require increased attention in ecosystem management in the future, and that new approaches to addressing the disturbance paradox in management are needed.

Key words: fire, wind, bark beetles, disturbance effect, biodiversity, ecosystem services, forest management, salvage logging, prescribed burning, disturbance paradox.

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INTRODUCTION

In recent decades, forest disturbance regimes have intensified in many parts of the world (Chapin *et al.*, 2000; Schelhaas, Nabuurs & Schuck, 2003; Balshi *et al.*, 2007; Gardiner *et al.*, 2010). The frequency of large wildfires in western North America has, for instance, increased by nearly four times in the period 1987–2003 compared to the average for 1970–1986 (Westerling *et al.*, 2006), while at the same time bark beetle damage has reached unprecedented levels (Meddens, Hicke & Ferguson, 2012). A similar trend is evident for wildfire, windthrow, and bark beetles in Europe (Schelhaas *et al.*, 2003; Seidl *et al.*, 2014). This trend is likely to continue in the future as a result of the climatic changes expected for the coming decades (Seidl, Schelhaas & Lexer, 2011*b*; Temperli, Bugmann & Elkin, 2013; Li *et al.*, 2013; Reichstein *et al.*, 2013; Seidl *et al.*, 2014). In many areas, changes in the disturbance regime (i.e. in the distinctive type, size, severity, and frequency of disturbance over extended spatio-temporal scales) are expected to be among the most severe climate change impacts on forest ecosystems (Lindner *et al.*, 2010; Turner, 2010). Disturbances are important natural drivers of forest ecosystem dynamics (Franklin *et al.*, 2002; Kuuluvainen & Aakala, 2011), and strongly modulate the structure and functioning of forest ecosystems (Weber & Flannigan, 1997; Turner, 2010). Changing disturbance regimes might thus considerably alter forest ecosystems, with potentially far-reaching impacts on their biological diversity and capacity to provide ecosystem services to society.

With the aim to provide ecosystem services to society while fostering biodiversity, ecosystem management requires a comprehensive understanding of the impacts of natural disturbances. Notwithstanding this high relevance, natural disturbances have hitherto been discussed inconclusively in the context of ecosystem management, with views and recommendations ranging from strict avoidance of disturbance (due to negative effects on selected ecosystem services) to emulating disturbance in management (to utilize their beneficial effects on biodiversity). On the one hand, substantial efforts are undertaken in research and management to quantify disturbance risk, with the aim to minimize their negative impacts through increasing the resistance of forests to disturbances (e.g. Jactel *et al.*, 2009; Overbeck & Schmidt, 2012). Measures such as fostering individual-tree stability through thinning (Schelhaas, 2008), adapting landscape-scale harvesting patterns to disturbance risk [e.g. stand edges *versus* the main wind direction (Byrne & Mitchell, 2013)], and choosing a rotation period that balances disturbance risk with economic considerations (Loisel, 2014) have long been practiced in forestry in order to avoid disturbance-related losses particularly with regard to timber production. On the other hand, with the advent of science-based ecosystem management and a growing understanding of the integral role of disturbances in natural forest ecosystem dynamics, mimicking natural disturbance regimes to foster elemental processes of ecosystem dynamics is increasingly advocated (e.g. Toivanen & Kotiaho, 2007; Newton *et al.*, 2011). Hypothesizing a positive effect of disturbances on biodiversity and acknowledging their role in creating keystone habitats within forested landscapes, these ideas view disturbances as inherently positive. In human-altered boreal forest ecosystems, for instance, where fire is the major natural disturbance agent, there are suggestions for the application of prescribed burning as a measure to restore natural forest conditions (Bergeron *et al.*, 2002; Toivanen & Kotiaho, 2007; Olsson & Jonsson, 2010). In wind- and bark beetle-dominated disturbance regimes the creation of gaps of various sizes and shapes is recommended to mimic natural disturbance regimes and stimulate biodiversity (Franklin *et al.*, 2002; Seymour, White & DeMaynadier, 2002; Kern *et al.*, 2014).

The valuation of disturbances and their role in management thus seems to vary strongly with the particular objective considered (e.g. biodiversity conservation *versus* timber production). However, only a small proportion of forests serve a sole objective: only about 5% of the world's forests are strict reserves for the conservation of biodiversity (Hoekstra *et al.*, 2005), while a similar fraction are designated plantations for the production of wood and biomass (Carnus *et al.*, 2006). The large majority of forest landscapes need to fulfill a multitude of functions and services simultaneously, including but not limited to serving as habitat, protecting the soil from erosion, producing timber and biomass, storing carbon, etc. In such situations where multiple objectives need to be met within a forest landscape, disturbances can be expected to have both positive and negative impacts on possible objectives of ecosystem management (see e.g. Huston & Marland, 2003), a hypothesis that we here refer to as the "disturbance paradox". Considering that not only disturbances have increased recently but also the range and demand for societally relevant ecosystem services has been growing steadily in recent decades, we estimate that addressing this paradox will be a key challenge for future forest ecosystem management.

Here we attempt to describe and quantify the various effects of natural disturbances in a literature review and meta-analysis of disturbance impacts at the global scale. In particular, we examine the effects of three of the most detrimental disturbance agents globally [i.e. fire, wind, and bark beetles (FAO, 2010)], focusing on forest ecosystems of the boreal and temperate biomes, a forest area of approximately 13.5 million km² (Hansen, Stehman & Potapov, 2010). Acknowledging the growing societal importance of a variety of different ecosystem services we not only survey disturbance impacts on traditionally important forest goods (such as timber production) but also include a total of 13 different ecosystem services from all four categories distinguished by the Millennium Ecosystem Assessment in our analysis: provisioning, supporting, regulating, and cultural services (MEA, 2005). Furthermore, we also investigated disturbance impact on three important indicators of biodiversity. Our overall objectives were (*i*) to synthesize the effect of natural disturbances on a wide range of possible objectives of forest ecosystem management, and (*ii*) to investigate standardized effect sizes of disturbance impacts for selected indicators *via* a quantitative meta-analysis. Based on these analyses we discuss pathways to addressing disturbances in ecosystem management in the particular context of changing disturbance regimes.

MATERIALS AND METHODS

(1) Literature review

We searched the literature for studies on disturbance by fire, wind and bark beetles, and their impacts on ecosystem services as defined by the Millennium Ecosystem Assessment (MEA, 2005), as well as their effects on biodiversity, focusing on species richness and habitat quality as well as on indices of diversity (e.g. Shannon-Index, Simpson-Index, etc.). We restricted our literature review to boreal and temperate forest ecosystems as subtropical and tropical forests differ considerably in ecological processes and anthropogenic impacts. In particular, extratropical forests are generally less diverse than tropical forests, and share a common set of genera as well as drivers of forest dynamics (e.g. temperature) (Thomas & MacLellan, 2002). Furthermore, land-use history and recent management differ strongly between tropical and extratropical regions, with a long history of intensive human use and several decades of sustainable management in the temperate and boreal zone (Siry, Cubbage & Ahmed, 2005; Canadell & Raupach, 2008). Focusing solely on the boreal and temperate subset of the literature controlled for these broad differences in our analysis, and thus increased the inferential potential with regard to disturbance effects. The literature search was performed using the *Scopus* database (SciVerse Scopus, 2013), and the cutoff date for the inclusion of publications was June 6th, 2013. The search terms and synonyms used are listed as supporting online information in Appendix S1. In total, 1958 papers were identified for screening. From this overall body of literature, reviews and syntheses were excluded in order to avoid double counting and the potential transfer of artifacts or errors from one review to the next (Whittaker, 2010). Furthermore, we excluded articles which did not compare disturbed forests with long-lasting undisturbed "control" sites. Depending on the study scale and context, either the state before a disturbance, an undisturbed reference, or an assumption about an equilibrium condition was assumed as a reference to determine the disturbance effect. From the 1958 papers screened initially 478 were selected for further analysis. For each of these studies we collected information on geographical location, spatial and temporal scales, assessment methodologies and management treatments (Tables 1 and 2, Appendix S2). We furthermore recorded whether the reported disturbance effect is related to single or multiple disturbance events (i.e. disturbance regime). If studies included expert opinions on certain disturbance effects they were initially included in our database, but were subsequently omitted from quantitative analyses. We allowed multiple entries per study, for instance if a study examined more than one disturbance agent, ecosystem service or biodiversity indicator. Furthermore, considering that ecological effects can change over time, we also recorded the temporal time frame for every study. In order to alleviate potential autocorrelation issues, effects were grouped into four different time horizons (i.e. short term: 1–5 years, mid term: 6–25 years, long term: 26–100 years, very long term: >100 years). The final database for analysis contained 887 entries of disturbance effects on ecosystem services and biodiversity.

Table 1. Geographic distribution of observations (*N*=887) of disturbance impacts on ecosystem services and biodiversity reported in 478 peer-reviewed publications included in the analysis. Note that two observations addressing fire and wind impact, respectively, at the global scale, are not included.

		Disturbance agent		
Biome	Continent	Fire	Wind	Bark beetles
Boreal	Africa	-	-	-
	Asia	11	1	0
	Europe	28	23	3
	North America	221	24	30
	South America	0	0	0
	Australasia	0	0	0
Cool temperate	Africa	0	0	0
	Asia	2	10	0
	Europe	54	38	11
	North America	198	25	18
	South America	9	0	0
	Australasia	28	6	0
Warm temperate	Africa	2	0	0
	Asia	10	0	0
	Europe	33	0	0
	North America	55	18	0
	South America	2	0	0
	Australasia	24	1	0
Total		677	146	62

Table 2. Assessment methodology and focal scale of observations (*N*=887) regarding disturbance impacts on ecosystem services and biodiversity reported in 478 peer-reviewed publications included in the analysis. Stand: 1–10 ha, Patch: 11–100 ha, Landscape: 101–100,000 ha, Region: >100,000 ha. NA: undefined temporal of spatial scale.

Temporal scale	Spatial scale	Assessment methodology					
		Empirical	Remote sensing	Simulation	Questionnaire	Expert opinion	Mixed
Short term (1–5 years)	Stand	237	1	12	0	14	1
	Patch	23	0	2	0	0	0
	Landscape	28	0	5	2	14	3
	Region	6	2	24	0	4	2
	Global	0	0	0	0	0	0
Mid term (6–25 years)	Stand	117	0	16	0	7	0
	Patch	16	0	2	0	3	0
	Landscape	12	0	9	0	8	2
	Region	5	10	23	1	3	1
	Global	0	0	0	0	0	0
Long term (26–100 years)	Stand	50	0	12	0	6	0
	Patch	5	0	2	0	3	0
	Landscape	4	0	11	0	4	0
	Region	1	1	24	1	10	0
	Global	0	0	2	0	0	0
Very long term (>100 years)	Stand	22	0	6	0	8	0
	Patch	1	0	2	0	2	0
	Landscape	4	0	11	0	16	0
	Region	4	0	14	0	17	0
	Global	0	0	0	0	0	0
NA	Stand	0	0	0	0	2	0
	Patch	0	0	0	0	1	0
	Landscape	3	0	0	0	10	0
	Region	0	0	3	4	5	0
	Global	0	0	0	0	0	0
	NA	0	0	0	0	1	0
Total		538	14	180	8	138	9

(2) Analysis

We analyzed our literature-derived database of disturbance effects in two steps. First, we assessed the disturbance effect on indicators of ecosystem services and biodiversity. To that end, a descriptive classification of the disturbance impact was made based on the findings reported in the literature (i.e. negative, neutral, mixed, or positive impact of disturbance on the respective indicator). This classification allowed us to synthesize results consistently from different methodological approaches. It furthermore enabled a comparison of disturbance impacts between ecosystem services measured on different scales (e.g. recreational value *versus* carbon storage in a forest landscape), as well as between the impacts on ecosystem services and biodiversity. Initially, we tested whether the observed distribution of studies over response categories differed significantly from a random distribution, i.e. we assessed whether a significant disturbance effect can be established from the literature. Subsequently, we tested for differences in disturbance impact among agents, biomes, and study approaches, evaluating the variation of disturbance impacts with these categories. In an attempt to confirm or reject the hypothesized diverging impacts of disturbance on criteria of relevance for ecosystem management (disturbance paradox hypothesis) we also tested whether disturbance impacts differ between indicators of ecosystem services and biodiversity. Another controversial issue in the context of disturbance management is the effect of salvage harvesting after disturbance, i.e. partial or complete removal of disturbance-killed trees from a site (Donato *et al.*, 2006; Lindenmayer, Burton & Franklin, 2008*a*; Thorn *et al.*, 2014). We thus also tested the hypothesis that disturbance effects after salvage differ significantly from unsalvaged conditions. Finally, we also compared impacts of prescribed burning to those of wildfires, in order to test for differences in disturbance impacts from intended and unintended fires. All these tests were conducted using independence tests, a powerful, permutation-based approach to test the null hypothesis that two variables (measured on arbitrary scales) are independent of each other (Hothorn *et al.*, 2008), using the package coin (Hothorn *et al.*, 2013) within the R language and environment for statistical computing (R Development Core Team, 2014).

In a second step, in order to determine effect size, we conducted a meta-analysis based on quantitative information on disturbance impact for two particularly well-researched criteria: biodiversity and carbon storage. For biodiversity, we analyzed disturbance-induced changes in species richness (S', N=57) and species entropy (H', N=28), the latter represented by the

Shannon-Index of diversity. Due to the limited sample size further subdivision into the effects of disturbance on specific taxonomic groups was not possible. With regard to carbon storage, we distinguished between disturbance effects on total ecosystem carbon (TEC, *N*=27), aboveground live carbon (ALC, *N*=38), dead aboveground carbon (DAC, *N*=25), and soil organic carbon (SOC, *N*=39) in our meta-analysis. For all variables the effect size was calculated as the per cent change induced by disturbance relative to the reference condition (control). Only entries from single disturbance events without subsequent salvage logging were considered in this second analysis step. We used multiple linear regression analysis to examine the size and statistical significance of disturbance effects on indicators of carbon storage and biodiversity. To generalize the disturbance regime and allow a comparison across studies we used time since disturbance (in years) and disturbance severity (i.e. proportion of timber volume, basal area, or forest area affected by disturbance, using a scale of 0–1) as covariates in the analysis. These parameters were recently used by Miller, Roxburgh & Shea (2011) in an attempt to generalize disturbance effects on diversity. We analyzed the residuals of our regression models for trends as well as for temporal autocorrelation (using a Durbin–Watson test), and found support for the assumptions of homoscedasticity and independence. From these regression models we analyzed both the intercepts (i.e. the standardized effect at fixed severity and time since disturbance) and slopes (i.e. how the disturbance effect changes with time and severity). To aid the interpretation of the former we transformed severity to 1–severity in our analysis, making the intercept a standardized effect of 100% severity. Additionally, we fitted multiple linear regression models with disturbance agents and biomes as covariates in order to test for the generality of our findings across agents and geographical locations.

RESULTS

(1) Disturbance effects on ecosystem services and biodiversity

Overall, 478 studies from the boreal (34.9%), cool (47.1%) and warm temperate (18.0%) biomes addressing effects of disturbances on forest ecosystems were reviewed. The overwhelming majority of articles originated from North America (63.8%), followed by Europe (21.3%) and Australasia (8.8%) (Fig. 1, Table 1). With regard to disturbance agents the effects of forest fires were addressed most frequently (78.0%), while only 15.4% of studies investigated impacts of wind and 6.6% of bark beetles. 60.9% of the research results compiled in our database were empirical, while 19.3% were based on expert opinion, 16.0% derived from simulation studies, and the remaining 3.8% either investigations based on remote sensing, public questionnaires or a combination of different approaches (Table 2). Studies from recent years were overrepresented in our database, with publications on disturbance impact increasing at a rate of approximately 3.1 papers per year between 1996 and 2012 (before 1996 the number of studies was sparse and irregular). This rate of increase of 11.9% year^{-1} is considerably higher than that of the general literature on, e.g. ecosystem management, which was +7.0% over the same period (Seidl, 2014).

Overall, there is strong evidence for a distinct impact of disturbances on criteria relevant to ecosystem management, with only 19.3% of entries in our database showing no or mixed effects of disturbance. The fact that in our sample of the literature negative impacts (45.1%) and positive effects (35.6%) were nearly equally distributed confirms the hypothesized disturbance paradox in ecosystem management. These divergent impacts are primarily driven by the disparity of disturbance effects on biodiversity and ecosystem services (Fig. 2). We found that all ecosystem service categories [i.e. supporting, provisioning, regulating and cultural services (Appendix S3)] were affected predominately negatively by disturbance ($P<0.001$). At the level of individual ecosystem service indicators, the only investigated aspect that was positively influenced was albedo (Fig. 3), as related to the climate change mitigation function of forest ecosystems (Jin *et al.*, 2012). Timber and primary production, fresh-water provisioning as well as protection against gravitational natural hazards were found to be predominately negatively affected by disturbances. Moreover, the large majority of studies reported a negative disturbance impact on carbon storage, mainly due to a reduction of live biomass in the ecosystem. However, there were also some examples of a positive disturbance effect on carbon storage: in a boreal forest ecosystem in Ontario, ALC peaked 92 years after disturbance then declined to a significantly lower level during the following decades, stabilizing 140 years after disturbance (Seedre & Chen, 2010). For the same forest, SOC peaked between 29 and 140 years after disturbance, before decreasing by approximately one-third over the next 63 years (Chen & Shrestha, 2012). This suggests that not only direct disturbance-related C losses in ALC but also the enhanced growth of a regenerating forest as well as the rate of decomposition of dead organic matter need to be considered for a comprehensive assessment of disturbance effects on forest C budgets. Overall, however, 96.3% of 27 observations on C cycle impacts indicated a negative effect of disturbances on TEC.

By contrast, we found an overall positive effect of disturbances on biodiversity (*P*<0.001). Species richness, habitat quality, and diversity indices were equally positively affected by disturbance. However, the disturbance effect is less consistent for biodiversity than for many ecosystem service indicators, and a number of studies also report negative impacts of disturbances on the indicators of biodiversity investigated here. Hingston & Grove (2010), for example, reported reduced bird species richness in Tasmanian lowland wet eucalypt forests during the first 50 years after wildfire. By contrast, Klaus *et al.* (2010) found a positive effect of fire on the number of bird species in southern Appalachian upland forests. This illustrates that some species groups might react differently to disturbances depending on the context and specific ecosystem investigated. Also belowground diversity is affected by disturbances, yet dedicated studies are still rare to date. Negative impacts on earthworm biomass and diversity at sites with uprooted trees were reported from areas as different as Belgium and northern Iran (Nachtergale *et al.*, 2002; Kooch & Hosseini, 2010). Another belowground species group that was reported to be negatively affected by windthrow (salvaged) and fire disturbance was Oribatida in the Slovakian High Tatra Mountains (Lóšková *et al.*, 2013). However, a positive impact of fire was reported on soil collembolan diversity in a northern hardwood forest (Huebner, Lindo & Lechowicz, 2012) as well as on soil microbial communities in Spain (Fontúrbel *et al.*, 2012), indicating that disturbances can have both positive and negative impacts on soil diversity. Overall, however, 73.1%, 69.8% and 65.3% of studies reported either a positive or neutral response of diversity, species richness and habitat quality, respectively, to disturbance.

At the level of different disturbance agents we found no support for significant differences between the effects of fire, wind, and bark beetles on indicators of biodiversity. With regard to ecosystem services, however, the impacts of fire differed significantly from those of wind and bark beetles (*P*<0.001 and *P*=0.006, respectively), with the latter agents being more frequently reported to have no influence on ecosystem services. This indicates that bottom-up disturbances such as fire (i.e. susceptibility decreasing with tree size and/or age) might have different impacts than top-down disturbances such as wind and bark beetles (where susceptibility increases with tree size and/or age). Differences in disturbance impacts between biomes were evident in our data: the effect of disturbances on ecosystem services differed among the boreal and temperate biomes ($P<0.001$ and $P=0.005$ for cool- and warm-temperate biomes, respectively), while boreal and cool-temperate biomes differed with regard to disturbance impacts on biodiversity ($P=0.022$). Generally, disturbance effects were least distinctive in the boreal biome, with negative disturbance impacts on ecosystem services more pronounced in the temperate biomes compared to boreal ecosystems. However, disturbances also had a stronger positive effect on biodiversity in the cool-temperate biome than in the boreal biome.

By comparing results across different types of methodologies, e.g. simulation studies *versus* empirical approaches, we found some noteworthy deviations from the null hypothesis of consistent disturbance impacts across study methods. Concerning the impacts of disturbances on ecosystem services we found a significant difference between empirical studies and simulation studies ($P=0.030$) as well as an indication for differences between empirical studies and expert opinions ($P=0.057$), with simulation studies and experts reporting a stronger negative effect than empirical analyses. With regard to the effects of biodiversity, we found that both simulation studies ($P=0.007$) and expert opinions ($P<0.001$) differed significantly from empirical studies. Here, our data indicate that simulation studies underestimate the positive effects of disturbance on biodiversity compared to empirical analyses, while experts overestimate this positive effect. It is also interesting to note that neutral effects (i.e. no disturbance impact on biodiversity) were more commonly reported in empirical studies than in any other methodological approach.

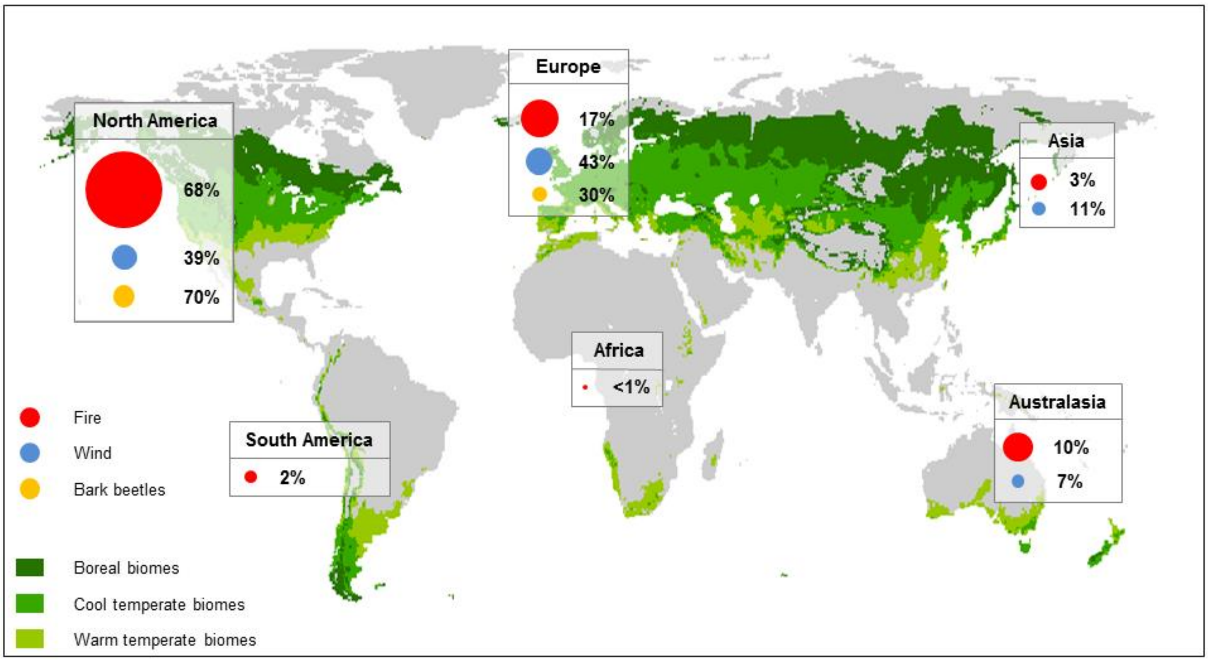

Fig. 1. Geographical distribution of papers addressing the impacts of fire (red, comprising wildfire and prescribed burning), wind (blue) and bark beetles (orange) on ecosystem services and biodiversity. The size of the circles represents the number of peer-reviewed papers per agent and region, while percentages indicate the relative share of disturbance agents per continent. The focal areas of our analysis were the boreal, cool- and warm-temperate biomes as defined by Holdridge (1947, modified using World Clim data), illustrated here in different shades of green.

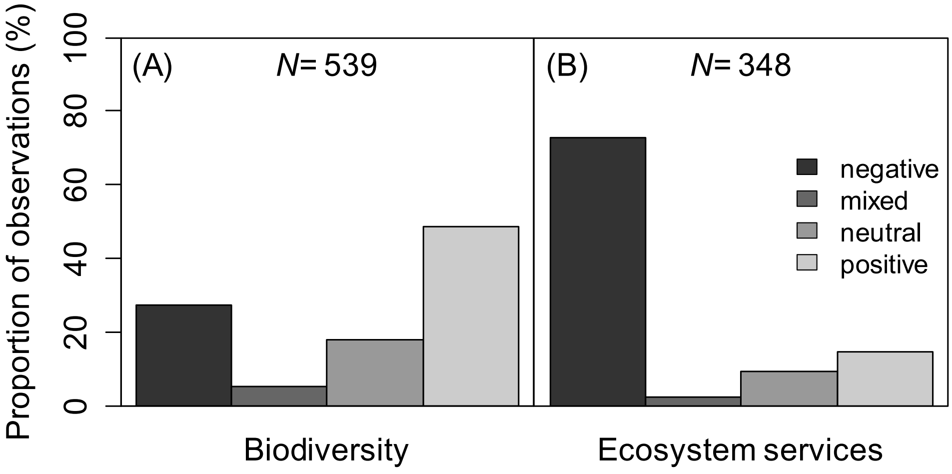

Fig. 2. Disturbance effects on (A) biodiversity and (B) ecosystem services. *N* indicates the number of observations in our database of disturbance effects synthesized from 478 peer-reviewed articles.

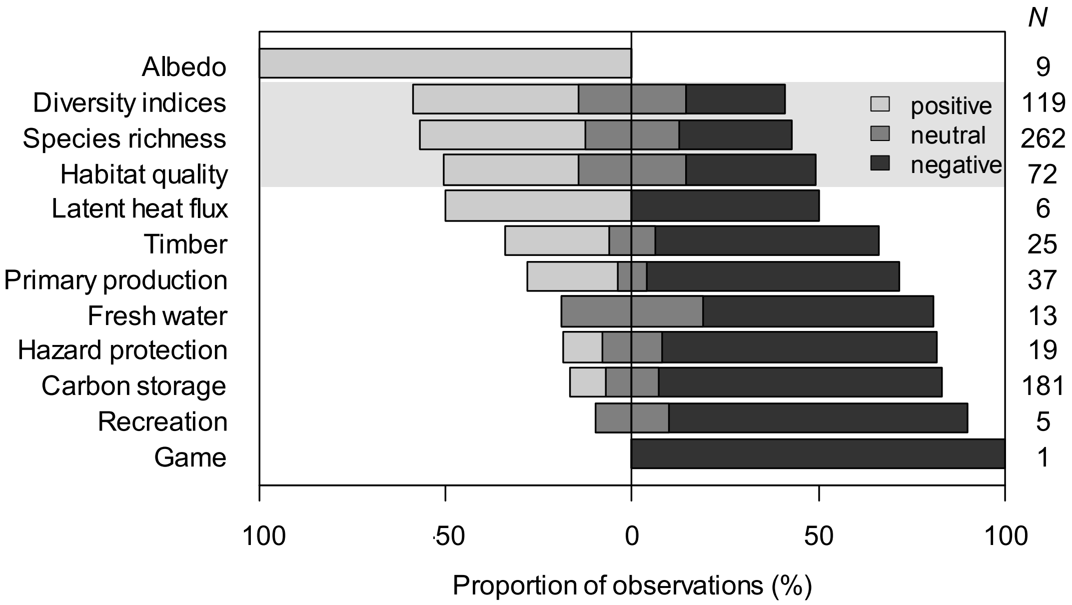

Fig. 3. Disturbance effects on indicators of ecosystem services and biodiversity (shaded). Bars show the distribution of positive, neutral and negative disturbance effects per indicator; *N* denotes the total number of observations. Note that neutral and mixed effects were subsumed under the neutral category here, and that findings based on expert opinions were excluded.

(2) The effect of salvage logging and prescribed burning

We tested whether the reported disturbance impacts of prescribed burning differed relative to those of wildfires, hypothesizing that controlled burns will have fewer negative effects on ecosystem service provisioning. We found no support for this hypothesis: prescribed burns were more frequently reported to have a negative impact on ecosystem services than wildfires ($P<0.001$). Yet, this result must be interpreted with caution as it is based only on a small sample of studies for the effect of prescribed burning ($N=13$). With regard to the predominately positive effects of fire on indicators of biodiversity, prescribed burns did not differ significantly from wildfires ($P=0.413$).

Another frequently discussed management intervention in the context of disturbance management is salvage logging. Based on previous findings, we hypothesized a negative impact of salvage logging on biodiversity (Lindenmayer *et al*., 2008*a*). Although a slight trend was evident in our data (i.e. the positive disturbance effect on biodiversity indicators was more pronounced for non-salvaged forests), it was not significant in our comparison of 38 observations on salvage logging with 145 observations of unsalvaged disturbance effects ($P=0.205$). Moreover, with regard to the impact on ecosystem services no significant differences between salvaged and unsalvaged studies were found ($P=0.168$), however the data reveal a negative trend for salvaged forests.

(3) The size of disturbance effects on biodiversity and forest carbon storage

Disturbance effects on forest ecosystems differ greatly with disturbance severity and time since disturbance, which is why we studied effect sizes using these two variables as covariates. Time since disturbance significantly explained disturbance effects for all investigated carbon compartments (Table 3). Effects on ALC and DAC were particularly strongly related to this variable, and differences to undisturbed conditions (–91.3% and +155.5% in the first year after disturbance for ALC and DAC, respectively) decreased by +0.6% (ALC) and –1.4% (DAC) on average with every passing year following disturbance. Disturbance severity was not significant in any model, but was retained in the analysis due to its ecological relevance (see also Miller *et al*., 2011). While the analysis of disturbance impacts on indicators of C storage yielded acceptable coefficients of determination (R^2 from 0.736 to 0.124), the explanatory value of disturbance regime covariates was poor with regard to species richness and entropy. Neither species richness nor entropy was found to differ significantly with time since disturbance and disturbance severity. Tests for differences between agents and biomes overall supported a common global meta-analysis under consideration of disturbance regime covariates for both response variables (data not shown).

The analysis of the standardized disturbance effect (i.e. the calculated impact for a year of an event with 100% severity) showed that indicators of biodiversity as well as deadwood C stocks increased with disturbance, while aboveground and soil carbon stocks decreased (Fig. 4). The mean ± 95% C.I. standardized effect of disturbance on total ecosystem carbon was –38.5 ± 8.3% ($P<0.001$), while species richness was significantly increased by +35.6 ± 32.3% ($P=0.035$).

Table 3. Meta-analysis (multiple linear regression) of disturbance effects on indicators of carbon and biodiversity (response variables) and their relation to covariates describing the disturbance regime. ALC, aboveground live carbon; TEC, total ecosystem carbon; DAC, dead aboveground carbon; SOC, soil organic carbon; *S*', species richness; *H*', species entropy (Shannon-Index).

	Time since disturbance		1–severity		
	Coefficient	*P*-value	Coefficient	*P*-value	R^2
ALC	0.606	<0.001	33.461	0.064	0.736
TEC	0.192	0.006	12.860	0.361	0.280
DAC	–1.435	0.014	–477.129	0.200	0.258
SOC	0.260	0.042	–9.075	0.792	0.124
S'	–0.307	0.291	–19.400	0.576	0.022
H'	–2.608	0.589	–175.386	0.555	0.020

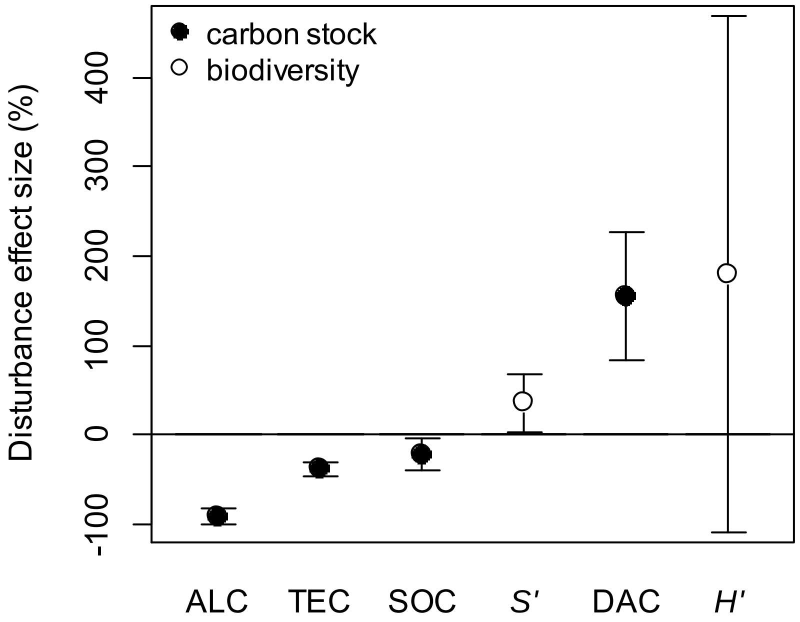

Fig. 4. Standardized disturbance effect size (i.e. per cent disturbance-induced change relative to reference condition) for indicators of carbon stock (filled symbols) and biodiversity (open symbols). Values are standardized coefficients for a disturbance severity level of 100%, and whiskers denote the 95% confidence interval. ALC, aboveground live carbon; TEC, total ecosystem carbon; SOC, soil organic carbon; DAC, dead aboveground carbon; *S*': species richness; *H*', species entropy (Shannon-Index).

DISCUSSION

(1) What we know about disturbance impacts on forest ecosystems

We investigated disturbance effects of fire, wind, and bark beetles in a search for general differences in disturbance impacts on ecosystem services and biodiversity. The large number of studies available for analysis not only indicates the importance of disturbance impacts to forest ecosystems, but also provides a suitable basis for a global synthesis on disturbance effects. The increasing number of publications over time may represent a response of the scientific community to the increase in disturbance frequency observed in recent decades (Westerling *et al.,* 2006; Seidl *et al.,* 2014), and should imply a growing understanding of disturbance processes. However, while disturbance impacts on biodiversity are increasingly well researched, we found more variability in information on different ecosystem services. While the main focus of the reviewed papers was on regulating services (predominately on C storage as an important mechanism of climate regulation), supporting and provisioning services are less well studied. The disturbance impact on cultural services has barely been assessed to date (Appendix S3).

In addition, the information available on disturbance impacts also differs with disturbance agent and region. The impact of fire on biodiversity and ecosystem services is the most intensively studied disturbance agent, reflecting the dominant role of wildfire in disturbance regimes around the globe (e.g. Conard *et al.*, 2002; Schelhaas *et al*., 2003; Littell *et al.*, 2009; Newton *et al.,* 2011; Knox & Clarke, 2012). Regional differences were apparent in our database of published studies on disturbance impacts: Asia, for instance, is underrepresented in our analysis; we found only 10 unique studies on disturbance impacts on biodiversity and 11 on ecosystem services for that continent. However, it has to be noted that not the entire geographic imbalance in disturbance studies is likely to be related to regional differences in scientific understanding of disturbance processes. The main cause of such variation in peer-reviewed information available from different regions is likely to be the language barrier (Powell, 2012). Differences in local research agendas are also likely to play a role (see e.g. Kajala & Watson, 1997). Nonetheless, we advocate research programs that facilitate a broader study of disturbance effects (geographically as well as in terms of the indicators studied), in order to close some of the remaining gaps in our understanding of the role of disturbances in forest ecosystems.

(2) Challenges for synthesizing disturbance impacts

One challenge for a global synthesis lies in a comparison of the different methodological approaches used to study disturbance impacts. Simulation approaches appear to underestimate the effect of disturbances on biodiversity perhaps because current disturbance models are rarely able to assess effects on diversity over a broad variety of guilds. Future improvements in simulation modelling should thus aim to capture the multiple impacts of disturbances better on ecosystems and their diversity (see also Seidl *et al.*, 2011*a*). Another interesting finding was that expert knowledge differed significantly from the results of empirical studies. Part of this difference could be explained by expert knowledge being reported for different systems and contexts, i.e. systems and indicators that are less well represented by empirical studies. However, the finding that disturbance impacts estimated by experts are more negative on ecosystem services and more positive on biodiversity than those estimated empirically strongly suggests that expert opinions should be omitted from further quantitative analysis (Whittaker, 2010). It should also be noted that our data – like most published literature reviews – are likely to incorporate a degree of publication bias (Møller & Jennions, 2001), i.e. neutral or mixed effects are likely to be underrepresented.

A second challenge relates to the general ability to synthesize the published literature. Although we found a large number of papers dealing with disturbance impacts on biodiversity and carbon storage, only a limited number (18.4% and 22.4%, respectively) could be used in a quantitative meta-analysis. In most instances we had to exclude studies due to inconclusive reporting of disturbance severity, or the absence of a proper control, consequently making it impossible to quantify the disturbance effect. We thus call for better reporting, especially the inclusion of summary statistics in publications, and advocate a BACI (before – after, control – impact) design (Stewart-Oaten, Murdoch & Parker, 1986) to facilitate future syntheses on this topic. The increasing requirement to make the results of studies available upon publication, either as an electronic supplement or in archiving services such as Dryad (http://datadryad.org/) should benefit such syntheses in the future. However, some variation in the choice of an appropriate control to disturbed systems is likely to persist, as, for example, the definition of “old-growth” conditions often differs regionally. Note also that historic land-use and management practices may influence reference conditions as well as disturbance drivers and impact (e.g. Carcaillet *et al.*, 2009), an aspect that cannot be rectified in a global review and meta-analysis such as that presented here.

Another difficulty for synthesis and generalization arises from the inherent complexity of disturbance regimes in temperate and boreal forests (see also White & Jentsch, 2001). While we studied three of the most influential disturbance agents globally, other agents of high regional significance were not considered. For example, ash dieback, a disease affecting common ash (*Fraxinus excelsior* L.) trees of all age-classes, is currently strongly impacting forest ecosystems in many European countries (Halmschlager & Kirisits, 2008; Ogris, Hauptman & Jurc, 2009), but was not included in this analysis. Our first analysis step revealed significant differences in impact among disturbance agents, documenting that the unique ecology of every agent is important for understanding its effects (e.g. which trees are affected and how). In the second step of our analysis we included severity and time since disturbance as covariates in order to generalize across agents in our meta-analysis. Tests of this generalization assumption show that differences among agents could be explained satisfactorily with these two covariates (data not shown), enabling a statistical analysis across agents and scales. This underlines the potential for a process-based analysis of disturbance regimes in synthesizing knowledge from individual observations to reach general patterns and principles (Turner *et al.*, 1993; White & Jentsch, 2001; Seidl *et al.*, 2011*a*; Miller *et al.*, 2011).

However, this ability to generalize might to some degree be attributed to the inclusion of only temperate and boreal forest ecosystems in our data set. Whether the general patterns deduced for these biomes also hold for tropical forests remains to be tested. Martin, Newton & Bullock (2013), conducted a review on the effects of anthropogenic disturbance on carbon stocks and plant diversity for more than 600 secondary forest sites in the tropics. They show that both biodiversity and carbon storage were negatively affected by clearing (a high-severity disturbance), and took several decades to recover. Assuming that salvage logging after natural disturbance results in an impact comparable to anthropogenic clearing we here find contrasting results for biodiversity effects in temperate and boreal forests: our data suggest a weak positive effect of disturbance on biodiversity (not significantly affected by salvage logging, *P*=0.205). This indicates that further studies are needed to establish whether the disturbance paradox described here also applies to tropical forests.

The existence and strength of simultaneous positive and negative impacts of disturbances on objectives of ecosystem management, described here as the disturbance paradox, might not only vary geographically but is likely also strongly dependent on the indicators selected for analysis, and hence the local relevance of specific ecosystem services and aspects of biodiversity. Generalist species might, for instance, benefit strongly from disturbance events while specialists and late-seral species – which are often a priority for conservation – could be negatively affected (Devictor & Robert, 2009). Moreover, disturbances might benefit invasive alien species (see e.g. Crawford *et al.*, 2001), widely regarded as negative for biodiversity. Owing to the broad scope of this study such aspects were not explicitly considered in our analysis. They might, however, be of high relevance in local assessments and management decisions, and could thus strongly modify the disturbance paradox, described here based on a global synthesis for boreal and temperate forests. A context-specific assessment of biodiversity effects at the level of guilds, red-listed species, and alien/native/endemic species in future studies is thus suggested in order to scrutinize further the generality of the disturbance paradox presented here.

(3) The disturbance paradox and how to address it in ecosystem management

We found strong evidence for the existence of the disturbance paradox in our global analysis of disturbance impact. Disturbance effects on ecosystem services and biodiversity clearly differ in the published literature, with ecosystem services being overall negatively affected while biodiversity is predominately positively influenced by natural disturbances. Our meta-analysis of the disturbance effect on species richness and total ecosystem carbon storage aptly illustrates this paradox: while species richness increases by 35.6% on average for a high-severity disturbance event, a simultaneous loss of 38.5% of total ecosystem carbon storage is to be expected. When management goals are to increase carbon storage while at the same time fostering biological diversity, managers are faced with ambiguity with regard to assessing the impact of a disturbance event, and gauging the implications of future disturbance regimes. Are disturbances to be prevented (as far as possible) to reduce negative impacts on ecosystem services, or are they to be welcomed and incorporated into management due to their positive effects on biodiversity?

While our global study cannot resolve this paradox of ecosystem management – which needs to be addressed in the local context of stakeholder preferences, habitat quality, and other constraints – several interesting insights for disturbance management can be deduced from our analysis. Since negative disturbance impacts on carbon storage are strongly reduced with time since disturbance, but positive effects on biodiversity do not vary significantly over time, our global meta-analysis suggests that managing for a low- to medium-frequency disturbance regime would result in limited impacts on provisioning services while still benefiting biodiversity. In other words, our data indicate that the disturbance event itself matters for biodiversity, while having enough time between these events ensures recovery of ecosystem services. Albeit not significant in our analysis, the same is true with regard to severity, i.e. moderate- or mixed-severity disturbances (see e.g. Perry *et al.*, 2011) are likely to be the best balance between negative effects on ecosystem services and positive effects on biodiversity. Traditional disturbance management approaches such as salvage harvesting and prescribed burning, for instance, are not able to moderate between negative ecosystem service impacts and positive diversity effects according to our analysis. We even found a higher proportion of papers reporting negative effects from prescribed burning on ecosystem services provisioning compared to wildfire. However, due to sample-size limitations we were not able to analyze these data for differences in effect size, although differences in severity (i.e. mean severity over all studies for prescribed burning=26.2%, wildfire=88.1%) suggest a positive effect of prescribed burning (Hurteau & North, 2009; Meigs *et al.*, 2009).

Ongoing climatic changes will likely increase disturbance frequency and severity in many parts of the world (Temperli *et al.*, 2013; Li *et al.*, 2013; Seidl *et al.*, 2014) which – according to our findings – may have negative implications for ecosystem service provisioning. Hence, adaptation of forest ecosystems to such changes in disturbance regime is of great importance in current forest ecosystem management, in order to sustain future ecosystem services provisioning to society. However, as many important drivers of the disturbance regime such as species composition respond to management changes only on time scales of decades to centuries (e.g. Hicke & Jenkins, 2008; Thom *et al.*, 2013), such management considerations need to take long lead-times into account. On the other hand, our analysis indicates that intensifying disturbance regimes may also represent an opportunity to foster biodiversity in forest ecosystems, and might thus to some degree alleviate the ongoing biodiversity crisis (Thomas *et al.*, 2004; Stuart *et al.*, 2004). In this context it is interesting to note that more diverse ecosystems are often more resistant and resilient to disturbance impacts (Bengtsson *et* *al.*, 2000), so that in the long term disturbance effects on ecosystem services might be buffered by increasing structural and compositional diversity.

CONCLUSIONS

(1) Over the last decades, the number of peer-reviewed publications on forest disturbances and their effects has increased, mirroring the increasing relevance of disturbance regimes and the changes therein. However, the available literature is heterogeneously distributed over agents and regions, with most studies addressing forests in North America and Europe, and mainly focusing on fire impacts.

(2) Disturbances in forest ecosystems can have both positive and negative impacts on objectives relevant to ecosystem management. We here find that ecosystem services of all four categories defined by the MEA (2005) (provisioning, supporting, regulating, and cultural) are predominately negatively impacted by natural disturbances. Biological diversity, as represented by species richness, habitat quality, and diversity indices is, on the other hand, predominately positively affected by natural disturbances.

(3) In a meta-analysis we determined that on average a disturbance event decreases total ecosystem carbon by 38.5% (standardized coefficient for a stand-replacing disturbance event in the year of the disturbance), while species richness increases by on average 35.6%.

(4) For ecosystem management, which aims to provide ecosystem services sustainably to society while preserving and fostering biodiversity, these divergent disturbance impacts present a paradox – they are at the same time risk factors and facilitators of management objectives. Our analysis suggests that measures of disturbance management such as salvage logging and prescribed burning do not significantly moderate these diverging impacts. However, a meta-analysis of carbon storage (an important regulating service in the context of climate change mitigation) and biodiversity suggests that managing for a disturbance regime of low to medium frequency and severity could limit impacts on ecosystem services while still being beneficial for biodiversity.

(5) Our review suggests that intensifying disturbance regimes under climate change will largely benefit biological diversity of forest ecosystems. Ecosystem services provisioning on the other hand will mostly be negatively impacted by such changes in the disturbance

regime. This might require a timely adaptation to changing disturbance regimes in order to provide important ecosystem services sustainably in the future.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article.

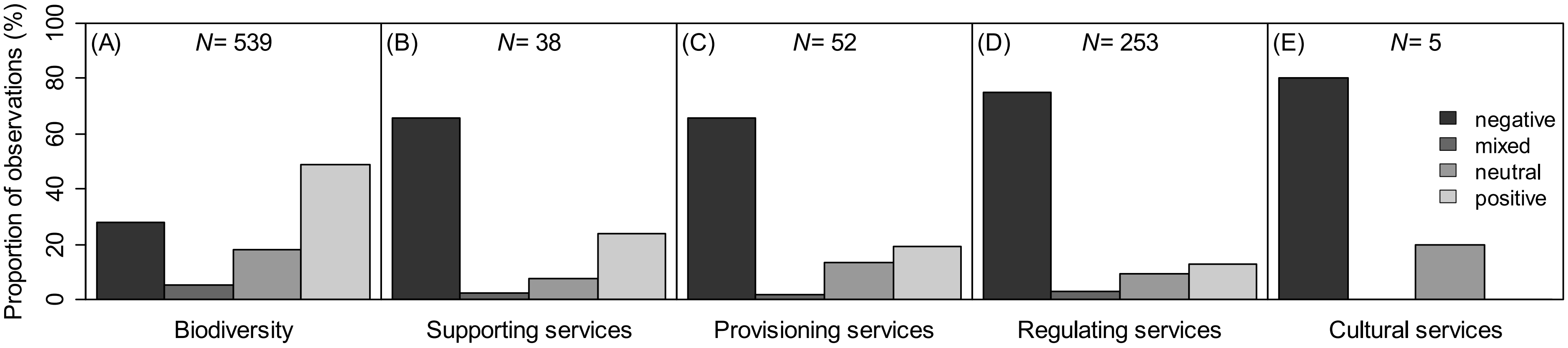
Appendix S1. Indicators of biodiversity and ecosystem services and their respective synonyms used in the literature search.

Appendix S2. Database of disturbance impacts on ecosystem services and biodiversity derived from the literature.

Appendix S3. Reported disturbance effects on biodiversity and ecosystem service categories (following the definition of the Millenium Ecosystem Assessment, 2005).

Appendix S1. Indicators of biodiversity and ecosystem services and their respective synonyms used in the literature search. The search text combined the indicators and synonyms indicated here with each of the focal disturbance agents (i.e. fire, wind and bark beetles).

Criterion	Indicator	Synonyms
Biodiversity		
Biodiversity	Species richness	
	Habitat	Living space; biotope; structural diversity; species abundance
	Diversity indices	Species diversity; biodiversity; genetic diversity
Supporting services		
Primary production	Primary production	Primary productivity; NPP; GPP
Oxygen production	Air quality	Oxygen
Provisioning services		
Timber	Timber	Biomass production; biomass productivity; timber production; timber productivity; fuelwood
Fresh water	Fresh water	Drinking water; water supply; water provisioning; water purification
Food (plants)	Vegetables	Berries; mushrooms; nuts; herbs
Food (game)	Meat	Animal food; carnal food; fleshy food; hunting; game; venison; deer; elk
Regulating services		
Protection against gravitational natural hazards	Protection against gravitational natural hazards	Rockfall protection; rockslide; avalanche protection; flooding protection; floodwater; flood; mudflow protection; mudslide; landslide; protection against soil erosion; soil loss; erosion
Climate regulation	Carbon storage	Carbon sequestration; net ecosystem productivity; net ecosystem exchange; net ecosystem carbon balance; NEP; NEE; NECB
	Albedo	
	Latent heat flux	
Cultural services		
Recreation	Recreation	Tourism; mountainbiking; hiking; camping; scenic beauty; scenic value
Inspiration	Inspiration	Art; folklore; writing; essay; painting; drawing; sculpture
Intellectual development	Intellectual development	Science; education; cognitive development



Appendix S3: Disturbance effects on biodiversity and ecosystem service categories (following the definition of the Millennium Ecosystem Assessment, 2005): (a) biodiversity, (b) supporting services, (c) provisioning services, (d) regulation services and (e) cultural services. *N* indicates the number of observations.

9.2 Paper II: Disturbances catalyze the adaptation of forest ecosystems to changing climate conditions

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Disturbances catalyze the adaptation of forest ecosystems to changing climate conditions

Running head: “Disturbances catalyze forest adaptation”

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Keywords: climate change adaptation, forest ecosystem management, forest dynamics, Kalkalpen National Park, natural disturbance, novel ecosystems, species turnover, succession

Original research article

Abstract

The rates of anthropogenic climate change substantially exceed those at which forest ecosystems – dominated by immobile, long-lived organisms – are able to adapt. The resulting maladaptation of forests has potentially detrimental effects on ecosystem functioning. Furthermore, as many forest-dwelling species are highly dependent on the prevailing tree species, a delayed response of the latter to a changing climate can contribute to an extinction debt, and mask climate-induced biodiversity loss. However, climate change will likely also intensify forest disturbances. Here, we tested the hypothesis that disturbances foster the reorganization of ecosystems and catalyze the adaptation of forest composition to climate change. Our specific objectives were (i) to quantify the rate of autonomous forest adaptation to climate change, (ii) examine the role of disturbance in the adaptation process, and (iii) investigate spatial differences in climate-induced species turnover in an unmanaged mountain forest landscape (Kalkalpen National Park, Austria). Simulations with a process-based forest landscape model were performed for 36 unique combinations of climate and disturbance scenarios over 1,000 years. We found that climate change strongly favored European beech and oak species (currently prevailing in mid- to low elevation areas), with novel species associations emerging on the landscape. Yet, it took between 357 and 706 years before the landscape attained a dynamic equilibrium with the climate system. Disturbances generally catalyzed adaptation and decreased the time needed to attain equilibrium by up to 211 years. However, while increasing disturbance frequency and severity accelerated adaptation, increasing disturbance size had the opposite effect. Spatial analyses suggest that particularly the lowest and highest elevation areas will be hotspots of future species change. We conclude that the growing maladaptation of forests to climate and the long lead times of autonomous adaptation need to be considered more explicitly in the ongoing efforts to safeguard biodiversity and ecosystem services provisioning.

Introduction

For long-lived organisms such as trees, the rapid progress of anthropogenic climate change (Collins *et al.*, 2013) means that they will experience a distinctly different environment towards the end of their life compared to the conditions under which they have established, resulting in disequilibrium between the vegetation composition and the environment. Such a growing maladaptation of the prevailing vegetation to climate is likely to negatively affect the provisioning of a wide range of ecosystem services to society (Temperli *et al.*, 2012; Lavorel *et al.*, 2015). Furthermore, the occurrence of forest-dwelling species is strongly linked to the prevalence of specific tree species (Bergman *et al.*, 2012; Thom *et al.*, 2016). Increasingly maladapted forests may thus commit ecosystems to an extinction debt (i.e., a delayed extinction of species due to a protracted response of the ecosystem) (Kitzes & Harte, 2015), and mask the rate and severity of the ongoing biodiversity loss (Thuiller *et al.*, 2005) due to a delayed response of tree species to a changing climate. Consequently, rapid climate change induces high uncertainty into the management of forest ecosystems for the provisioning of ecosystem service and the conservation of biodiversity (Millar *et al.*, 2007; Seidl & Lexer, 2013), as experiences made under relatively constant climatic conditions (with climate and vegetation in equilibrium) are increasingly rendered inapplicable.

Theory suggests that disturbance catalyzes change in ecosystems (Gunderson & Holling, 2001), and can thus reduce the disequilibrium between the prevailing species composition and changing environmental conditions. This notion applies to both natural disturbances in unmanaged systems and silvicultural interventions in managed systems, given that management allows adaptation processes such as natural regeneration to ensue after a disturbance. We here refer to a reduction of the disequilibrium between vegetation composition and climate through natural processes as “autonomous adaptation” (in short referred to as adaptation in the remainder of the text). Processes through which disturbance fosters adaptation include the modification of competition among species, increased resource availability, and a reset of system-level connectedness after disturbance (i.e., a shift from primarily system-internal control mechanisms such as the competition for light to mainly external controls from, for instance, climate and the availability of seeds) (see e.g., Pickett *et al.*, 1989; Pulsford *et al.*, 2016). As a result of these processes, disturbances can initiate ecosystem reorganization by providing opportunities for new species to invade a site, or giving already present but suppressed species the chance to attain dominance.

Studies that have investigated disturbance-climate relationships generally suggest an intensification of natural disturbance activity in the future as a result of climate change (Dale *et al.*, 2001; Seidl *et al.*, 2014a). Hitherto, these disturbance changes have been mainly discussed as a potential threat to ecological resilience (Johnstone *et al.*, 2016, Seidl *et al.*, 2016). However, based on theoretical understanding of ecosystem dynamics (Gunderson & Holling, 2001) such changes can also be hypothesized to facilitate the adaptation of forests to climatic changes, as more disturbance results in a larger share of landscapes being in the state of reorganization that follows after disturbance (see also Serra-Diaz *et al.*, 2015). The increasing level of natural disturbance observed in many ecosystems around the globe currently could thus also be interpreted as a mechanism through which ecosystems reduce a growing maladaptation to a rapidly changing climate. The role of disturbance in shaping future ecosystem composition and reducing the climate-vegetation disequilibrium has as of yet been widely overlooked in the discussion of changing disturbance regimes under climate change.

Yet, changes in key ecosystem processes such as disturbances can also lead to profoundly altered ecosystem dynamics in both natural and managed forests. This has the potential to result in ecological novelty (i.e., dissimilarity of a system relative to a reference baseline (Radeloff *et al.*, 2015)) and the emergence of no-analog combinations of species (i.e., species communities that did not exist under past climatic conditions (Williams & Jackson, 2007)). Whether such novel trajectories of ecosystems are compatible with goals of conservation and ecosystem services provisioning remains unclear to date.

Understanding the potential trajectories of forest ecosystems under climate change is thus of paramount importance for ecosystem management. A general proposition frequently found in the ecosystem management literature is that species will shift to higher latitudes and elevations due to global warming (Lenoir *et al.*, 2008; Chen *et al.*, 2011). Such trajectories are confirmed by many studies using empirically calibrated species distribution models (e.g., Hanewinkel *et al.*, 2013; Zimmermann *et al.*, 2013). Species distribution models are powerful tools representing the fundamental niche of a species, and allowing the potential future distribution of a species' niche to be mapped in relation to projected climatic changes. However, they do assume climate-vegetation equilibrium of the current vegetation, and do not consider relevant processes such as migration and competition among species (Elith & Leathwick, 2009). As a result, important aspects of adaptation such as time lags in the turnover of the current species composition to a changing future climate are disregarded (see e.g., Bertrand *et al.*, 2011; Meier *et al.*, 2012). Furthermore, since the effects of changes in species interactions in response to a changing climate are not considered, shifts in the realized niche of species and the potential rise of novel species communities remain scarcely investigated (but see e.g., Thuiller *et al.*, 2015).

Here, we studied the interactions between vegetation, disturbance and climate in a complex, unmanaged mountain forest landscape. Our objectives were to (i) assess the time lags in the response of tree species composition and association to changing climatic conditions, (ii) examine the role of disturbance as possible facilitator of this adaptation process, and (iii) study how species turnover in response to different climate and disturbance regimes differs in space. We hypothesized long time lags in the autonomous adaption of the tree species composition (i.e., a trajectory towards the species that are most competitive under the given environmental conditions, without a consideration of management interventions) to climate change (Aitken *et al.*, 2008; Meier *et al.*, 2012). Furthermore, we expected the adaptation processes to be catalyzed by intensifying disturbance activity (e.g., through opening niches for the establishment of locally novel species, eventually resulting in a change in the tree species competition), consequently reducing vegetation-climate disequilibrium. Specifically we hypothesized a stronger influence of disturbance frequency and size (i.e., creating more and bigger opportunities for reorganization) than disturbance severity (see also Gunderson & Holling, 2001; Turner, 2010). Finally, we hypothesized that changing climate and disturbance regimes create local novelty in forest ecosystems, i.e., future tree species compositions and associations that are currently not present at a site, as both processes alter local environmental conditions, the availability of resources, and the competitive relations between species (see also Seastedt *et al.*, 2008). In particular, we expected novelty to be most distinctive at low elevations where no-analog environmental conditions will emerge under climate change (see also Williams & Jackson, 2007).

Materials and Methods

Study area

We investigated Kalkalpen National Park (KANP), a forest landscape located at N47.47°, E14.22° in the northern front range of the Austrian Alps. We chose the landscape scale as the focal scale for our analyses, as it allows both large scale processes such as species migration and fine scale processes such as competition between individual trees to be addressed in an integrative manner. In addition to climate and natural disturbance – the processes of interest in this study – forest management is a prominent driver of tree species change (Naudts *et al.*, 2016). We here controlled for the influence of forest management by focusing our analysis on a national park landscape. KANP is the largest forest wilderness in Austria (total area of 20,856 ha), and covers an elevation range from 385 m to 1,963 m asl. Under current climatic conditions, the landscape encompasses three of the most important forest types of Central Europe, i.e., European beech (*Fagus sylvatica* [L.]) forests, Norway spruce (*Picea abies* [L.] Karst.) forests, and mixed forests of Norway spruce, silver fir (*Abies alba* [Mill.]) and European beech (Fig. 1). Since its establishment in 1997 active forest management has ceased in the core zone of KANP.

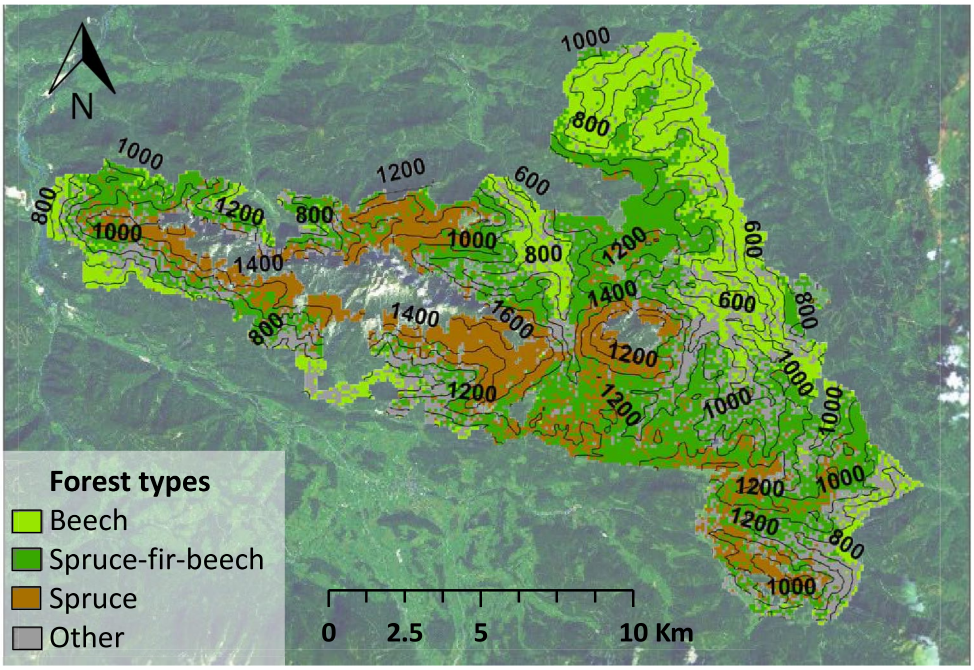

Figure 1: Simulated potential natural vegetation under historical climate at Kalkalpen National Park, showing the three most important forest types. Contour lines indicate elevation above sea level in meters.

Simulation model

We used the individual-based forest landscape and disturbance model iLand to simulate trajectories of tree species change under a range of different climate and disturbance scenarios at KANP. iLand is a high-resolution, process-based model operating on the grain of individual trees, simulating spatially explicit forest landscape dynamics (Seidl *et al.*, 2012a). Processes in iLand are embedded in a hierarchical framework, accounting for interactions between tree (e.g., growth, mortality, competition for resources), stand (availability of water, nutrients), and landscape levels (disturbance, seed dispersal). The resource availability of each individual tree is derived based on a light use efficiency approach combined with ecological field theory. Resource utilization explicitly considers the effects of temperature, radiation, soil water and nutrient availability as well as vapor pressure deficit at daily time steps, and atmospheric carbon dioxide (CO_2) concentration on an annual basis (Seidl *et al.*, 2012a). Individual tree mortality is determined by carbon starvation. Regeneration depends on the local availability of seeds (determined by species-specific seed dispersal kernels around mature trees) as well as on favorable environmental conditions (e.g., light availability, temperature) (Seidl *et al.*, 2012a, 2012b). iLand simulates ecosystem carbon stocks and fluxes and incorporates an agent-based forest management module (Rammer & Seidl, 2015). A wide range of disturbance regimes can be simulated by employing process-based disturbance modules. Currently, iLand includes modules for wildfire (Seidl *et al.*, 2014b), wind (Seidl *et al.*, 2014c) and bark beetle disturbance (Seidl & Rammer, 2016). To study disturbance impacts in detail users can also specify alternative disturbance regimes by specifying distributions for disturbance frequency, size, and severity. The model was successfully parameterized, tested, and applied in ecosystems in Central (Seidl *et al.*, 2012a; Silva Pedro *et al.*, 2015; Silva Pedro *et al.*, 2016; Thom *et al.*, 2016) and Northern Europe (Seidl *et al.*, 2014c) as well as in the northwestern US (Seidl *et al.*, 2012a, 2012b; Seidl *et al.*, 2014b). For the current study system, simulated productivity, climate sensitivity and potential natural vegetation composition were previously evaluated successfully against independent data (Thom *et al.*, 2016).

Initialization and drivers of landscape development

We compiled data for climate, soil and current vegetation at KANP to initialize and simulate future trajectories of landscape development. Simulations under baseline climate were conducted via resampling years from the period 1950 – 2010. We used three different combinations of global and regional circulation models under A1B forcing as our main projections of transiently changing climatic conditions until the end of the 21th century: CNRM-RM4.5 (Radu *et al.*, 2008) driven by the global climate models (GCM) ARPEGE, and MPI-REMO (Jacob, 2001) as well as ICTP-RegCM3 (Pal *et al.*, 2007) driven by the GCM ECHAM5. To evaluate the sensitivities of our findings to climatic change scenarios we furthermore studied the least and most severe representative concentration pathway (RCP) scenarios (RCP2.6 and RCP8.5, respectively) and tested whether they significantly altered our main findings regarding the time required to reach dynamic equilibrium (see Fig. S1 and Table S4 in the Supporting Information for details).

From 2100 onwards, we assumed a stabilization of the climate at the level of 2080 – 2099, with years being resampled randomly with replacement. This arbitrary cessation of climate change was assumed here to gauge the time required for the ecosystem to catch up with climate, and marks a clear starting point for assessing time lags of vegetation response to a changed climate (see also Solomon *et al*., 2009). The average climate assumed for the years beyond 2100 in the three A1B projections represents a temperature change of between +3.1°C and +3.3°C, and a precipitation change of between –89 mm and +141 mm relative to the baseline period. All climate data were bias-corrected by means of quantile mapping (Déqué 2007) against gridded weather station data at 1 × 1 km resolution (Haiden *et al*., 2011), and statistically downscaled to a 100 m × 100 m grid using daily weather gradients within the study area.

We employed the same 100 m × 100 m grid to initialize soil conditions in the simulations. Based on measurements of soil depth and soil type on a regular inventory grid across the KANP (N=710), Kobler (2004) developed statistical models of soil properties using environmental drivers as predictors. We utilized these models to derive wall-to-wall estimates of soil conditions across the landscape. Additional soil information required for simulation (i.e., soil texture and plant-available nitrogen) was imputed based on a stratified sampling from data derived from the Austrian National Forest Inventory (N=557) (Seidl *et al*., 2009).

Information on current tree vegetation was derived from a combination of different data sources. We used aerial photo analysis and terrestrial inventory plot data (N=1,122) to derive tree species composition, diameter at breast height (dbh) distributions, and stem density at the level of stand polygons (median stand size: 1.4 ha). Stand age was determined from forest inventory and planning data, and airborne LiDAR (Light Detection And Ranging) was used to estimate canopy height as well as the stockable area within a stand. LiDAR data were further utilized to determine the initial tree locations in iLand. Altogether, we initialized more than 2 10^6 trees of 17 different species in stand polygons representing 15,540 ha, characterizing the state of tree vegetation in the year 1999. To accommodate recent disturbance events at KANP, we subsequently simulated tree growth from 1999 to 2013, and imposed the recent disturbance history as recorded in the disturbance monitoring system of KANP (see also Thom *et al.*, 2016 for further details on landscape initialization). The year 2013 was subsequently used as the initial year for all scenario analyses. We assumed a small background probability of seeds from tree species in neighboring forests to enter the KANP landscape (see Table S2 for full list of tree species). The relative abundance of seeds from different tree species was determined from neighboring forest type, and dispersal into the study landscape was tree species specific following the same dispersal kernels as used in the dynamic simulation.

Simulation design

In order to capture the potentially extensive lead times of tree species adaptation, we simulated forest development at KANP over a period of 1,000 years. For each of the four main climate projections described in the previous section we investigated nine different disturbance scenarios, with one representing a no-disturbance control and the remaining eight imposing combinations of two levels of disturbance frequency, severity, and size (Table 1). Instead of dynamically simulating specific disturbance agents and their interaction with climate change (cf. Seidl & Rammer, 2016) we chose to employ generic disturbance scenarios and implement an orthogonal design in which disturbance frequency, severity, and size are independent of each other, and of the imposed climate projections. Studying all factorial combinations of independently varying frequencies, severities, and sizes under all different climate projections allowed us to robustly address our third hypothesis, namely that disturbance frequency and size affect adaptation more strongly than disturbance severity.

Our low-intensity disturbance variant (disturbance scenario 2, Table 1) assumed a disturbance rotation period of 250 years (see Thom *et al.*, 2013), a mean disturbance size of 5.3 ha (corresponding to the current mean disturbance size as determined from the disturbance inventory at KANP), and a disturbance severity of 50% (i.e., 50% of trees with dbh > 10 cm are killed within the disturbed perimeter; cf. Janda *et al*. (2016), who report average severities ranging from 29.0% to 74.9% of canopy removed in Central European mountain forests). This disturbance scenario thus roughly corresponds to the current disturbance regime at KANP, which is mainly dominated by wind and bark beetles (cf. Seidl & Rammer, 2016). In the disturbance scenario with the highest intensity (disturbance scenario 9) disturbance rotation period was halved to 125 years, severity doubled to 100%, and disturbance size increased 10-fold to a mean size of 53.4 ha. This extreme scenario thus represents the possibility of drastically changed disturbance regimes under future climate conditions (see Seidl & Rammer (2016) for an analysis of the climate sensitivity of wind and bark beetle disturbances at KANP). The location of disturbances was implemented stochastically in each simulation run, with disturbance size determined by drawing from a negative exponential distribution with the respective mean size. Whether one or more disturbance events occurred in a simulated year was determined by a probability function based on disturbance rotation period and disturbance size. To account for stochasticity in our analyses, we conducted 10 replicated simulations per scenario. To scrutinize the robustness of our results in the face of stochasticity we investigated the between-replicate coefficient of variation at the level of individual tree species (see Table S1 for details). In summary, our simulation design consisted of 4 climate projections × 9 disturbance scenarios × 10 replicates = 360 simulations of the 15,540 ha landscape over 1,000 years (i.e., 5.59 billion hectare-years simulated). The factorial design allowed us to separate the effects of different climate forcings from the different constituents of the disturbance regime (rotation period, severity, size) with regard to their influence on forest composition.

Table 1: Factorial design of disturbance scenarios, representing all possible combinations of two levels of disturbance frequency (here expressed as disturbance rotation period), severity, and mean disturbance size. Severity is characterized as trees with dbh >10 cm killed within the disturbed perimeter.

Disturbance scenario	R/S/M	Rotation period (years)	Severity (%)	Mean size (ha)
1	∞/0/0	-	-	-
2	250/50/5.3	250	50	5.3
3	125/50/5.3	125	50	5.3
4	250/100/5.3	250	100	5.3
5	125/100/5.3	125	100	5.3
6	250/50/53.4	250	50	53.4
7	125/50/53.4	125	50	53.4
8	250/100/53.4	250	100	53.4
9	125/100/53.4	125	100	53.4

Analyses

We tested for differences in the share of individual tree species among climate and disturbance scenarios at the end of the simulation period at a spatial grain of 100 m cells, using Wilcoxon rank sum test. As an indicator for the speed of adaptation to changing climatic conditions we used the elapsed time until the simulated landscape reached a dynamic equilibrium in species composition, i.e., the point in time after which fluctuations in tree species composition were negligible (White & Jentsch, 2001). We expected all simulations to eventually reach a dynamic equilibrium, as our landscape was large relative to disturbance frequency and size (on average none of the disturbance scenarios affected more than 1% of landscape area per year) (Turner *et al.*, 1993), and we assumed a stabilization of climate change beyond year 2100. We considered a simulation as being in dynamic equilibrium when the temporal variation in basal area of all species present on the landscape was within a range of ± 2 $m^2 ha^{-1}$ of their respective simulation endpoint (defined as the average basal area per tree species in the last 200 years of the simulation). To assess the influence of this *a priori* set equilibrium definition on our findings we conducted a sensitivity analysis, investigating the effect of different threshold values (± 1.5 $m^2 ha^{-1}$ and ± 2.5 $m^2 ha^{-1}$, respectively) on the estimated time until a dynamic equilibrium was reached.

Furthermore, we estimated migration speed in elevation as the mean annual change rate of a species' leading edge, defined as the 90th percentile of the elevation distribution of a species on the landscape. To test changes in the elevation distribution of species we derived species shares for each 100 m cell, and approximated the altitudinal distribution of each species using either a Gaussian (if a clear optimum was present) or a 2nd order polynomial function. Moreover, we asked whether species do change individually or in associations, using Spearman's rank correlation analysis to quantify the strength of association between species (and changes therein) at the same 100 m spatial grain.

To obtain a more mechanistic insight into the effect of disturbance on tree species adaptation, we utilized our set of orthogonal disturbance scenarios to test for differences between disturbance extent (i.e., percent area disturbed) and disturbance impact (i.e., percent basal area disturbed) on the emergence of a dynamic landscape equilibrium.

Finally, we analyzed the emerging tree species compositions under different climate and disturbance regimes with regard to their local novelty compared to baseline conditions. Specifically, we quantified species turnover triggered by climate change, i.e., the deviation of tree species shares under climate change from baseline values at the end of the simulation period, and its distribution across the landscape. To that end we summed the differences in tree species shares between scenarios across all species, and divided by two to account for the fact that a 10% increase in one species *ipso facto* has to lead to a 10% decrease in another species. The theoretical maximum species turnover was thus 100% for each cell, where 100% indicated that the tree species composition under climate change contains no species of the composition simulated under baseline conditions (see also Radeloff *et al.*, 2015).

Results

Adaptation of forests to changing environmental conditions

Temporal trajectories of forest succession

Forest management activities prior to 1997 and recent severe disturbances (most notably the storm Kyrill in 2007) have significantly affected KANP. Consequently, all scenarios resulted in a considerable increase in mean basal area during the first 50 – 100 years relative to the current forest conditions (Fig. 2). Although the most drastic tree species changes occurred during the first centuries of the simulation, we found that particularly European beech and oak species (*Q. petraea* [Matt.] and *Q. robur* [L.]) were slow to stabilize on the landscape. Our simulations indicated a distinct impact of climate change on forest succession (Fig. 2, Table S2). While the average time to reach dynamic equilibrium under baseline climate conditions was 558 years (Fig. 2a), a changing climate prolonged the time needed for the landscape to be in dynamic equilibrium with its environment by 148 years on average if disturbance was neglected (Fig. 2b). At the landscape scale, European beech benefited most strongly from changing climate conditions ($p<0.001$), and increased its tree species share by +28.5 and +32.2 percentage points compared to baseline climate for scenarios with and without disturbances, respectively. Although negligible under baseline climate, the abundance of oaks strongly increased with warming (+20.0 and +22.9 percentage points for *Q. petraea* and *Q. robur* combined; $p<0.001$). Norway spruce, one of the main tree species at KANP under baseline climate, strongly decreased within the first 300 – 400 years under climate change, and only held a minor share of the tree species composition at the end of the simulation period (-19.4 and -16.7 percentage points, respectively, $p<0.001$). Conversely, silver fir was suppressed by past forest management, and recovered during the first centuries of the simulation under baseline climate. However, similarly to Norway spruce, it declined substantially under climate change conditions (-13.5 and -8.1 percentage points, respectively, $p<0.001$).

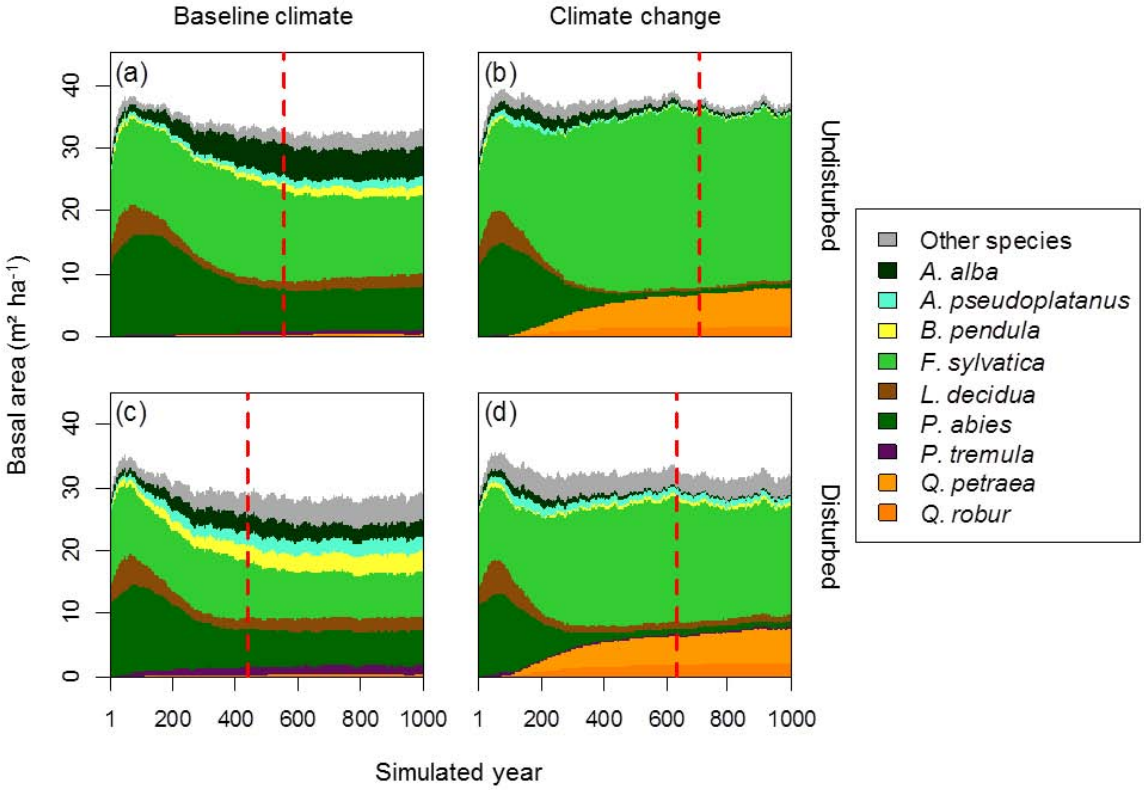

Figure 2: Trajectories of forest succession at KANP, summarized for four scenarios: (a) baseline climate without disturbance, (b) climate change without disturbance, (c) baseline climate with disturbance, and (d) climate change with disturbance. Values are averages over all scenarios and replicates in the respective categories. Tree species with ≥5% basal area in at least one of the four scenarios are shown explicitly (see Table S2 for more information). The red dashed line indicates the point in time when a dynamic equilibrium was reached on average.

The role of disturbance in forest adaptation to changing environmental conditions

In addition to climate, also disturbance strongly influenced the trajectories of forest succession at the landscape scale. Overall, disturbance strongly favored early seral species (most notably silver birch (*Betula pendula* [Roth]), European larch (*Larix decidua* [Mill.]), sycamore maple (*Acer pseudoplatanus* [L.]) and aspen (*Populus tremula* [L.])) at the expense of late successional species (Fig. 2c, 2d, Table S2). While European beech was most positively affected by climate change among all tree species, it was also the species affected most severely by disturbances under both baseline and climate change conditions (a reduction of -13.4 and -17.1 percentage points under baseline and climate change conditions, respectively, $p<0.001$). Also silver fir declined substantially by -5.8% under baseline climate conditions as a result of disturbance ($p<0.001$). Disturbances reduced the time to reach dynamic equilibrium by on average 119 years (21.3 %) under baseline climate conditions (Fig. 2c) and by 72 years (10.2 %) under changed climatic conditions (Fig. 2d).

A subsequent in depth analysis at the level of the individual constituents of the disturbance regime revealed that both disturbance extent and impact had an important influence on the adaptation of tree species to changing environmental conditions (Fig. 3). For instance, the adaptation speed was accelerated by more than 100 years compared to undisturbed conditions when disturbance affected 0.8% of basal area and 0.8% of landscape extent per year. Specifically, we found synergistic effects between disturbance extent and impact – if the disturbance impact on basal area was low, the spatial extent of disturbance had only a weak influence on the speed of adaptation. With increasing disturbance impact, however, also the effect of an increasing spatial extent of disturbance increased. Likewise, an increase in disturbance extent also amplified the effect of disturbance impact on the adaptation speed of the system.

While an increasing area affected by disturbance promoted forest succession, mean disturbance size was found to be negatively related to the speed of adaptation in most scenarios (Table 2). Overall, scenarios with a 10-fold increase in mean disturbance size (to 53.4 ha) prolonged the time it took for the landscape to reach dynamic equilibrium by +24.8 years compared to scenarios that assumed the historically observed mean disturbance size of 5.3 ha. In contrast, both increased severity (-64.3 years compared to current severity) and increased frequency (-54.5 years compared to current frequency) generally accelerated forest adaptation. Tree species composition at KANP adapted most quickly to the new climatic conditions in disturbance scenario 5 (disturbance rotation period 125 years, severity 100% and mean size 5.3 ha). In this scenario, species adaptation was 201 years (baseline) and 211 years (climate change) faster than in scenarios excluding disturbances.

A sensitivity analysis of the equilibrium definition used here showed that our results were generally robust to different threshold levels for defining stabilization in the species composition, but also revealed considerable sensitivity of the time needed for adaptation (Tables S3.1, S3.2). Furthermore, assuming more extreme climatic change (scenario RCP8.5) prolonged the times needed to adaptation by 68 years, while more moderate future climate conditions accelerated it by 19 years on average across all disturbance scenarios (Table S4). These more extreme scenarios did, however, not differ significantly from the ensemble of climate change projections studied here in 17 out of the 18 scenarios, and did not alter the overall results regarding the disturbance effect on tree species adaptation.

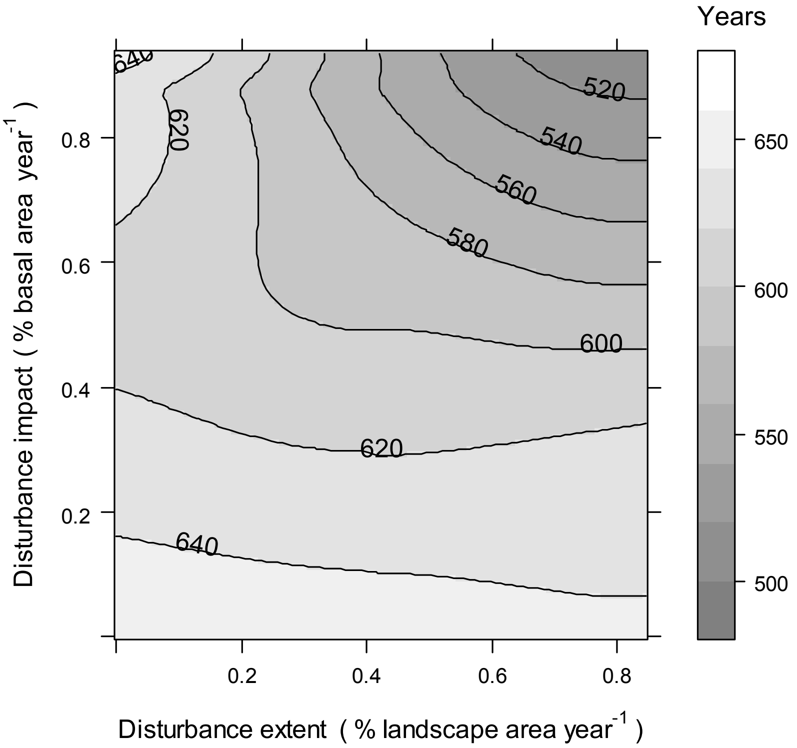

Fig. 3: Simulated time until the tree species composition at KANP is fully adapted to climate, as influenced by disturbance impact (in % of basal area removed per year) and disturbance extent (in % of the total area of KANP disturbed per year). Isolines indicate the time needed (in years) to reach a dynamic equilibrium in the tree species composition, and were derived via a loess regression. For the current analysis climate was assumed to change until the end of the 21st century and kept stable afterwards, allowing vegetation to catch up.

Table 2: The time the tree species composition needs to adapt to changing environmental conditions. Shown are the average years as well as standard deviations (SD) per disturbance scenario that are required until a dynamic equilibrium in the vegetation composition was reached on the landscape. Climate was assumed to change until the end of the 21st century and kept stable afterwards, allowing vegetation to catch up.

Disturbance scenario		Baseline climate		Climate change	
	R/S/Ms	Mean	SD	Mean	SD
1	∞/0/0	558	0	706	111
2	250/50/5.3	497	15	659	50
3	125/50/5.3	450	10	655	51
4	250/100/5.3	434	8	647	43
5	125/100/5.3	357	12	495	166
6	250/50/53.4	495	20	670	78
7	125/50/53.4	465	22	659	78
8	250/100/53.4	434	33	675	90
9	125/100/53.4	384	27	610	110

Species shifts and novel species compositions

Not all tree species shifted upwards in elevation in response to warming temperatures. While, most species, such as European beech (+0.26 m asl yr^{-1}), oak species (+0.24 m and +0.27 m asl yr^{-1} for *Q. petraea* and *Q. robur*, respectively), and silver fir (+0.37 m asl yr^{-1}), migrated upwards with climate change, the leading edges of the distribution of Norway spruce (-0.02 m asl yr^{-1}) and European larch (+0.00 m asl yr^{-1}) remained virtually constant compared to baseline climate. To further elucidate changes in species over elevation we examined their distributions over elevation at the end of the simulation (Fig. 4). This analysis showed that oak species (mainly *Q. petraea*) invaded the elevation band that was formerly beech dominated (cf. also Fig. S2.4 with Fig. S2.8 and Fig. S2.9). Norway spruce and European larch, on the other hand, which were prominent tree species at higher elevations under baseline climate, became scarce under changed climatic conditions even at their past elevation optima (Fig. S2.5, S2.6).

Our analyses also indicated that climate change modified species associations as a result of changing competitive relationships among species (Tables 3 and 4). For instance, we found a substantial change in the association between European beech and oak species: While they were clearly positively related under baseline climate conditions (indicating co-occurrence in the warmer, low-elevation areas of the landscape), they were moderately negatively associated under changed climatic conditions (indicating growing niche separation, with oaks outcompeting beech in the exceedingly warm low-elevation parts of the landscape, and beech moving into higher elevation portions of the landscape). The relation between European beech and Norway spruce, on the other hand, became less negative under climate change, and the association of silver fir with European beech and Norway spruce remained positive. Correlations among early successional species such as silver birch, European larch and European aspen were positive under both baseline climate and climate change scenarios.

These changes in individual species ranges and species associations resulted in the emergence of local novelty in tree species composition. Comparing baseline climate under the current disturbance regime (scenario 2, Table 1) with climate change under intensified disturbance (scenario 9) revealed a species turnover of 51.8% (CI ± 16.5%), indicating that more than half of the basal area of every stand will on average be replaced by novel tree species under changing climate and disturbance regimes (Fig. 5). In all scenarios, species turnover "hotspots" showed a distinct bimodal distribution over elevation, with most pronounced changes being simulated at the lowest and highest elevations. However, disturbances dampened this spatial pattern of novel tree species compositions on the landscape and resulted in species turnover being more evenly distributed across the landscape cf. (Fig. S3).

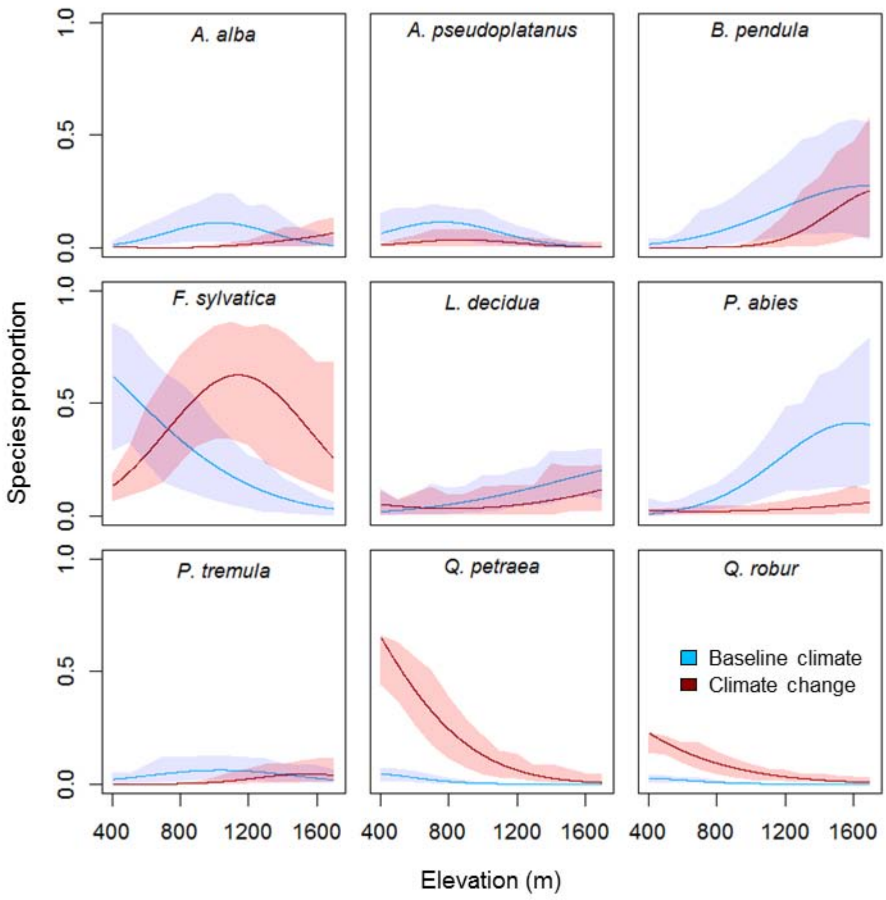

Fig. 4: Distribution of the nine most common tree species over elevation at Kalkalpen National Park at the end of the 1000 year simulation period (a species proportion of 1 indicates a basal area share of 100%). Lines represent fitted distributions over simulated species occurrence. Shaded areas indicate the 5th to 95th percentile range across all replicates and disturbance scenarios.

Table 3: Association between tree species under baseline climate conditions. Shown is Spearman's rank correlation coefficient, derived from all scenario combinations simulated.

Species	*A. alba*	*A. pseudo-platanus*	*B. pendula*	*F. sylvatica*	*L. decidua*	*P. abies*	*P. tremula*	*Q. petraea*	*Q. robur*
A. alba	1								
A. pseudoplatanus	0.17	1							
B. pendula	-0.385	-0.495	1						
F. sylvatica	0.446	0.477	-0.865	1					
L. decidua	-0.417	-0.658	0.754	-0.781	1				
P. abies	0.112	-0.578	0.449	-0.634	0.623	1			
P. tremula	-0.355	0.212	0.637	-0.468	0.269	-0.121	1		
Q. petraea	-0.063	0.44	-0.524	0.656	-0.456	-0.687	-0.097	1	
Q. robur	-0.063	0.448	-0.519	0.663	-0.467	-0.7	-0.082	0.925	1

Table 4: Association between tree species under changed climatic conditions. Shown is Spearman's rank correlation coefficient, derived from all scenario combinations simulated.

Species	*A. alba*	*A. pseudo-platanus*	*B. pendula*	*F. sylvatica*	*L. decidua*	*P. abies*	*P. tremula*	*Q. petraea*	*Q. robur*
A. alba	1								
A. pseudoplatanus	-0.313	1							
B. pendula	0.809	-0.175	1						
F. sylvatica	0.454	-0.305	0.154	1					
L. decidua	0.055	0.086	0.402	-0.625	1				
P. abies	0.182	0.107	0.324	-0.348	0.69	1			
P. tremula	0.772	-0.045	0.969	0.134	0.378	0.287	1		
Q. petraea	-0.856	0.178	-0.876	-0.358	-0.2	-0.219	-0.854	1	
Q. robur	-0.843	0.297	-0.78	-0.508	-0.013	-0.097	-0.746	0.952	1

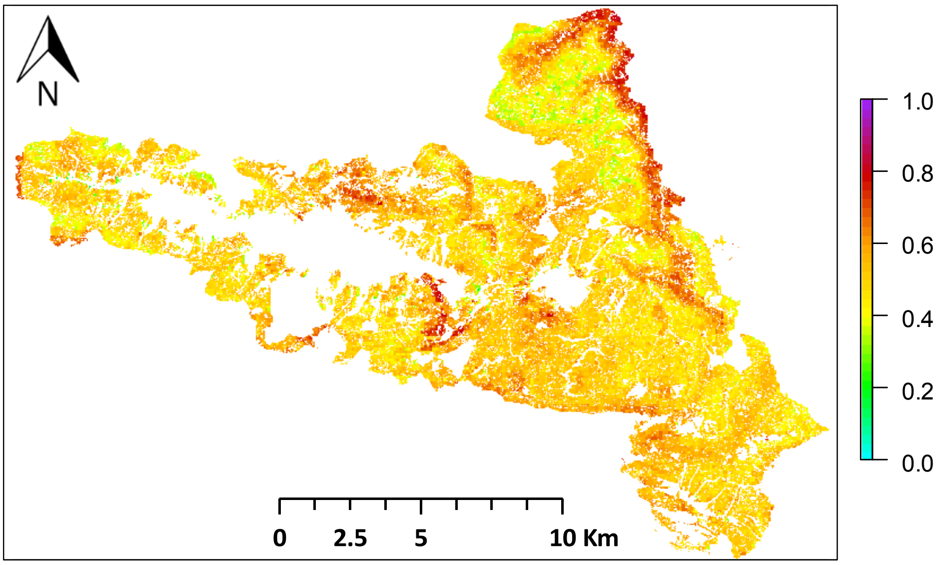

Fig. 5: Species turnover as a result of changing climate and disturbance regimes. The map shows local species change (100 × 100 m grid) as a result of climate change and intensified disturbances (disturbance scenario 9) compared to baseline climate under historic disturbance (disturbance scenario 2). A value of 1 indicates a replacement of 100% of the trees relative to baseline climate.

Discussion

Drivers of forest adaptation

Climate change will strongly modify environmental conditions within the lifetime of a single generation of trees, and thus results in high uncertainty with regard to the spatio-temporal trajectories of forest ecosystems. Here we showed that the adaptation of forests to these changing conditions can lag several centuries behind climatic trajectories, but also that disturbances significantly decrease the temporal mismatch between the vegetation composition and the climate system. To our knowledge, we here presented the first comprehensive analysis on how changes in disturbance frequency, severity, and size could influence the growing disequilibrium between forest vegetation and the climate system. Our study highlights the importance of landscape-scale processes such as seed dispersal and disturbance to understand how forest ecosystems will change with progressing climate change. The process-based modeling approach employed here did not only track the fundamental niche of species, but also simulated species movement and establishment, as well as changing relative resource use efficiency between species. Consequently, we were able to not only account for direct (e.g., temperature), but also indirect (e.g., changing competition) impacts of climate change.

As expected, we found the current vegetation composition at NPKA to differ considerably from the potential natural vegetation derived under current climate conditions. As in many parts of Central Europe (e.g., Emmer *et al.*, 1998; Knoke *et al.*, 2005), historic management has strongly favored Norway spruce at the expense of European beech in our study area. Although active management has ceased at NPKA almost 20 years ago, the current tree species composition is still to a large degree the legacy of past land-use. Hence forests at KANP are currently in disequilibrium with the prevailing climate conditions. Our simulations suggest that it takes several centuries before the vegetation composition is in a dynamic equilibrium with climate conditions at NPKA even in the absence of a changing climate. This comparably slow return to a natural tree species composition suggests that compositional changes in recently installed protected areas that have previously been altered by humans are currently more strongly driven by recovery from past land use than by climate change. It also underlines that in some areas targeted ecosystem restoration measures could be of value to accelerate the trajectory towards natural system states after intensive human alteration (e.g., Covington *et al.*, 1997; Zerbe, 2002).

The expected climate change will have a strong impact on the natural vegetation composition in Central European forest landscapes, and prolongs the time it takes for the current vegetation to adapt to its environment. Under past climate lower elevations were dominated by European beech, higher elevations by Norway spruce, and mid elevation areas by a mixture of European beech, Norway spruce and silver fir. This spatial pattern changed under climate change in our simulations, with European beech dominating large parts of the landscape and oak invading the lower reaches of KANP once a dynamic equilibrium between climate and vegetation was reached. These findings are in line with broad-scale studies using species distribution models (SDMs) (e.g., Hanewinkel *et al.*, 2013; Zimmermann *et al.*, 2013), but only emerged after century-long time lags in our spatio-temporally explicit analysis, confirming the hypothesis of a highly protracted tree species adaptation to changing climatic conditions. In this regard it is interesting to note that recent paleoecological work even suggested that forest ecosystems may remain in disequilibrium with climate for several millennia (Herzschuh *et al.*, 2016). Our analysis revealed mean annual change rates in elevation of the most common tree species from -0.02 m asl yr^{-1} to +0.37 m asl yr^{-1} under climate change. These change rates are below the majority of woody species’ change rates reported by Lenoir *et al.* (2008), who investigated elevational optimum shifts of plants in France from 1905 – 2005, but in contrast to our study, they also included ecosystems that have been continuously managed, while we excluded direct human interventions in our analysis. Differences in methodology for determining elevational change rates might also account for some of the divergence, while overall our estimates still fall within the large variation reported empirically (Lenoir *et al.* 2008). Furthermore, for the interpretation of our findings it is important to note that elevational shifts in our analysis were also to some degree limited by the specific topographic conditions of our study landscape. Norway spruce and European larch, for instance, were already occupying the highest elevation areas of the landscape under baseline climate, and were thus no more able to expand their territory upwards.

Our results generally support the expectation of a facilitating effect of disturbance on species adaptation. Because climate change is predicted to intensify future disturbance activity (Seidl *et al.*, 2014a; Millar & Stephenson, 2015), it is likely that disturbances will reduce the climate – vegetation disequilibrium in forest ecosystems. In this regard we here were able to disentangle the effects of changes in disturbance rotation period, severity and size using a factorial simulation experiment. We found that increases in the different characteristics of the disturbance regime affected the compositional maladaptation to climate conditions in distinctly different ways: While increases in disturbance frequency and severity reduced the lag times of autonomous adaptation, increasing disturbance size prolonged the time it took for the landscape to reach a dynamic equilibrium. An increasing disturbance frequency implies an accelerated progression through the adaptive cycle of ecosystem dynamics, and a larger proportion of the landscape in the stages of reorganization and renewal (Gunderson & Holling, 2001). Larger disturbances, on the other hand, result in increased dispersal distances for species, which slows recovery and favors early-seral species over the slowly invading cohort of new late-seral species (Seidl *et al.*, 2014b). This finding on the differential effects of changes in attributes of the disturbance regime suggests that the potential positive effect of intensifying disturbance activity on species adaptation will be contingent on the nature of disturbance change affecting the landscape. While an increase in disturbance frequency, as projected for many areas (Mouillot *et al.*, 2002; Bentz *et al.*, 2010), might aid adaptation, the emergence of "mega-disturbances" (Stephens *et al.*, 2014; Millar & Stephenson, 2015) could further aggravate the maladaptation of vegetation to the emerging climate conditions.

A limitation of our study in this regard was the assumption of equal disturbance sensitivities between species. Wind and bark beetles are the most prominent disturbance agents in Central Europe, and a high share of Norway spruce also implicates a high predisposition of forests to those agents (Thom *et al.*, 2013). This suggests that the abundance of particularly disturbance-sensitive species on the landscape might be overestimated in our analysis. Future work should address this issue by investigating the effects of prominent disturbance agents on landscape trajectories explicitly and account for dynamic feedbacks between vegetation change and the disturbance regime (see e.g. Temperli *et al.*, 2013; Seidl & Rammer, 2016).

Future forests and ecological novelty

In line with previous research, we found early-seral species to benefit from higher levels of disturbance, as they are better able to recolonize disturbed parts of the landscape (Swanson *et al.*, 2011). This suggests that under the changed disturbance regimes expected for the future, early-seral species might play a more prominent role in forest dynamics than in the past. For the landscape investigated here our results suggests a homogenization of the tree species composition as a result of climate change, with European beech-dominated forest types strongly increasing their prevalence over other forest types. This effect is, however, partly offset by disturbances, which foster tree species diversity on the landscape (Silva Pedro *et al.*, 2016). These trends are of particular relevance in the context of biodiversity conservation, as tree species diversity is an important predictor for the diversity of a wide variety of other species groups (see e.g., Díaz *et al.*, 2005; Thom *et al.*, 2016).

In this context another important finding of our analysis is the rise of local novelty as a result of climate change. We found a high turnover of species for the large majority of locations within our study landscape (93.2% of the landscape had a species turnover of >40% (Fig. 5)). While on average species turnover rates were similar in disturbed and undisturbed simulations, we found that neglecting disturbance leads to an overestimation of novelty in high and low elevation areas of KANP (Fig. S3). Furthermore, we found that previous associations of species changed considerably, as tree species responded individually to the emerging climate conditions (see also Hanson & Weltzin, 2000). An aspect we did not account for in the analysis of emerging novel ecosystem composition, however, was the potential for an invasion of alien tree species (see e.g., Radeloff *et al.*, 2015). However, as we here focus on a national park where anthropogenic disturbances are minimized and no exotic tree species will be introduced through management, this omission might be of minor importance for our study system. Nonetheless, specifically the role of disturbances on invasion of alien species requires further attention. While anthropogenic disturbances are generally regarded as catalysts of the invasion of nonnative species (Chytrý *et al.*, 2008; Pysek *et al.*, 2010), only a limited number of studies have assessed the impact of natural disturbances in this regard (see e.g., Davies *et al.*, 2009).

Forest management implications

The uncertainty in future trajectories of forest ecosystems resulting from the rapidly changing environmental conditions poses a key challenge for forest management and conservation (Millar *et al.*, 2007). Our study suggests that disturbance is an important facilitator of the autonomous adaptation of forest ecosystems to changing environmental conditions. We thus suggest that disturbances should be seen as opportunity for forest adaptation in the context of management (see also Seidl *et al.*, 2016). As the slow migration of trees does not allow them to track rapid climatic changes (see also McLachlan *et al.*, 2005), active management should be considered to shorten the extensive lead times, in order to sustain biodiversity and the provisioning of ecosystem services in the future (Seidl *et al.*, 2011). In this regard our results suggest that particularly forests in low and high elevation zones are highly vulnerable to climate change-induced species change, and should thus be in the focus of monitoring and management. However, our findings also showed that changes might be considerably slower than suggested by species distribution models (e.g. Hanewinkel *et al.*, 2013). In fact, our study indicated the absence of strong climate-induced changes in the tree species composition over the next 100 years compared to baseline climate. However, this slow response of forests must not be mistaken for an insensitivity of forests to a changing climate, but rather indicates a growing disequilibrium between forests and climate, and commits forests to strong future alterations in species composition. The effects of this growing maladaptation on biodiversity and ecosystem services provisioning are currently not sufficiently understood, yet will likely be a major factor to consider in the ecosystem management of the coming decades.

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Supporting information captions

Table S1: Relative coefficient of variation (in %) between individual replicates (n=10) in each scenario, displayed for the nine most common tree species at Kalkalpen National Park.

Table S2: Species share in percent of basal area at the end of the simulation period.

Table S3: Sensitivity analysis of the effect of different equilibrium definitions on the time needed to adapt to changing environmental conditions.

Table S4: Sensitivity analysis of the time to reach a dynamic equilibrium to the least and most severe representative concentration pathway of climate change.

Fig. S1: Climate change scenarios for temperature and precipitation change in Austria.

Fig. S2: Spatial distribution of the nine most common tree species under baseline climate and climate change.

Fig. S3: Species turnover as a result of climate change, under undisturbed conditions, and averaged over all scenarios including disturbances.

Supporting information

Table S1: Relative coefficient of variation (in %) between individual replicates (n=10) in each scenario, displayed for the nine most common tree species at Kalkalpen National Park. Values are given for the end of the 1000 year simulation period. B=baseline climate, A=ARPEGE climate change, I=ICTP climate change, R=REMO climate change, dist1–9=disturbance scenarios (see Table 1 for definitions).

	Tree species								
Scenario	*A. alba*	*A. pseudoplatanus*	*B. pendula*	*F. sylvatica*	*L. decidua*	*P. abies*	*P. tremula*	*Q. petraea*	*Q. robur*
B, dist1	0.1	0.1	0.2	0.0	0.1	0.2	0.2	0.2	0.3
A, dist1	0.1	0.1	0.1	0.0	0.1	0.1	0.1	0.2	0.5
I, dist1	0.2	0.2	0.3	0.0	0.1	0.1	0.1	0.1	0.2
R, dist1	0.2	0.2	0.2	0.0	0.1	0.1	0.2	0.2	0.2
B, dist2	0.2	0.2	0.3	0.2	0.2	0.2	0.5	0.4	0.4
A, dist2	0.2	0.4	0.5	0.1	0.2	0.2	0.7	0.2	0.3
I, dist2	0.8	0.5	0.8	0.2	0.4	0.2	0.9	0.2	0.2
R, dist2	0.6	0.5	0.7	0.2	0.2	0.2	0.8	0.2	0.3
B, dist3	1.1	0.4	1.1	0.9	0.5	0.5	1.7	1.0	0.4
A, dist3	0.6	1.9	2.0	0.7	1.0	0.4	2.9	0.5	0.5
I, dist3	1.4	1.2	1.9	0.6	1.0	0.7	2.1	0.5	0.5
R, dist3	0.7	1.0	1.4	0.4	1.2	0.7	2.2	0.6	0.7
B, dist4	0.7	0.3	0.5	0.9	0.3	0.4	0.8	1.1	0.8
A, dist4	0.5	0.6	1.2	0.1	0.5	0.4	1.1	0.3	0.4
I, dist4	1.6	0.7	0.7	0.4	0.4	0.4	0.9	0.5	0.3
R, dist4	1.7	0.8	1.2	0.4	0.5	0.2	1.5	0.3	0.3
B, dist5	1.1	0.9	1.0	1.0	0.8	1.1	0.9	1.4	0.6
A, dist5	1.7	2.3	3.8	1.2	1.0	0.8	4.6	0.8	0.7
I, dist5	3.0	1.9	3.0	1.1	1.4	1.0	4.6	0.7	0.6
R, dist5	1.6	1.2	1.3	0.7	1.2	1.0	2.0	0.9	0.9

B, dist6	0.4	0.3	0.3	0.2	0.3	0.4	0.3	0.5	0.2
A, dist6	0.5	0.3	0.6	0.1	0.3	0.3	0.7	0.2	0.3
I, dist6	0.8	0.3	0.7	0.1	0.3	0.2	0.9	0.3	0.3
R, dist6	0.7	0.3	0.7	0.3	0.4	0.3	0.9	0.3	0.4
B, dist7	0.9	0.5	0.7	0.8	0.4	0.5	1.0	0.7	0.6
A, dist7	0.5	0.5	1.7	0.5	0.6	0.4	1.8	0.4	0.3
I, dist7	1.5	0.9	1.6	0.5	0.9	0.8	2.2	0.8	0.6
R, dist7	1.1	0.8	2.2	0.7	0.6	0.5	2.3	0.7	0.4
B, dist8	0.4	0.2	0.3	0.4	0.5	0.5	0.3	0.6	0.8
A, dist8	1.1	0.2	1.1	0.7	0.5	0.5	1.3	0.7	0.5
I, dist8	0.9	0.4	0.8	0.6	0.6	0.5	1.4	0.6	0.4
R, dist8	1.7	0.3	0.6	0.6	0.3	0.4	0.9	0.4	0.3
B, dist9	1.8	1.0	1.3	1.6	1.4	1.5	1.9	1.1	1.2
A, dist9	1.9	1.4	2.1	1.8	1.1	1.1	3.6	1.6	1.0
I, dist9	3.2	0.9	2.0	1.5	1.0	1.1	3.0	1.5	0.9
R, dist9	3.8	1.2	1.4	1.3	1.0	0.8	2.3	0.6	0.5

Table S2: Species share in percent of basal area at the end of the simulation period of all 29 species considered in this study. Values were aggregated to the mean of the scenario combinations presented in Fig. 2.

	Baseline climate		Climate change	
	Disturbances simulated		Disturbances simulated	
Species	no	yes	no	yes
Abies alba	14.7	8.9	1.2	0.8
Acer campestre	< 0.1	0.1	< 0.1	0.1
Acer platanoides	0.1	0.2	< 0.1	0.3
Acer pseudoplatanus	4.3	8.4	0.6	2.7
Alnus glabra	0.7	1.6	0.1	0.6
Alnus incana	0.4	0.8	0.2	0.9
Alnus viridis	< 0.1	< 0.1	< 0.1	< 0.1
Betula pendula	4.3	10.5	0.4	1.8
Carpinus betulus	< 0.1	0.1	0.5	2.2
Castanea sativa	< 0.1	< 0.1	< 0.1	< 0.1
Corylus avelana	< 0.1	< 0.1	< 0.1	< 0.1
Fagus sylvatica	38.1	24.7	70.3	53.2
Fraxinus excelsior	1.2	3.2	0.2	1.5
Larix decidua	6.0	7.5	1.3	3.5
Picea abies	21.3	19.4	1.9	2.7
Pinus cembra	0.4	0.7	< 0.1	0.1
Pinus nigra	< 0.1	< 0.1	0.2	0.2
Pinus sylvestris	1.9	2.7	1.1	2.8
Populus nigra	< 0.1	0.2	< 0.1	0.1
Populus tremula	1.8	4.8	0.2	1.0
Quercus petraea	0.9	0.7	16.9	17.1
Quercus pubescence	< 0.1	< 0.1	< 0.1	0.1
Quercus robur	0.5	0.5	4.5	7.0
Salix caprea	< 0.1	< 0.1	< 0.1	< 0.1
Sorbus aria	< 0.1	0.1	< 0.1	< 0.1
Sorbus aucuparia	< 0.1	0.1	< 0.1	< 0.1
Tilia cordata	3.2	4.2	0.3	0.7
Tilia platyphyllos	0.1	0.2	< 0.1	< 0.1
Ulmus glabra	0.1	0.3	0.1	0.3

Table S3.1: Sensitivity analysis of the effect of different equilibrium definitions on time needed to adapt to changing environmental conditions. Shown are the average years and standard deviations (SD) per disturbance scenario needed to reach a dynamic equilibrium state defined as ±1.5m²/ha deviance in basal area (default: ±2.0m²/ha). R/S/M provides a summary of the disturbance processes per disturbance scenario: rotation/severity/mean size.

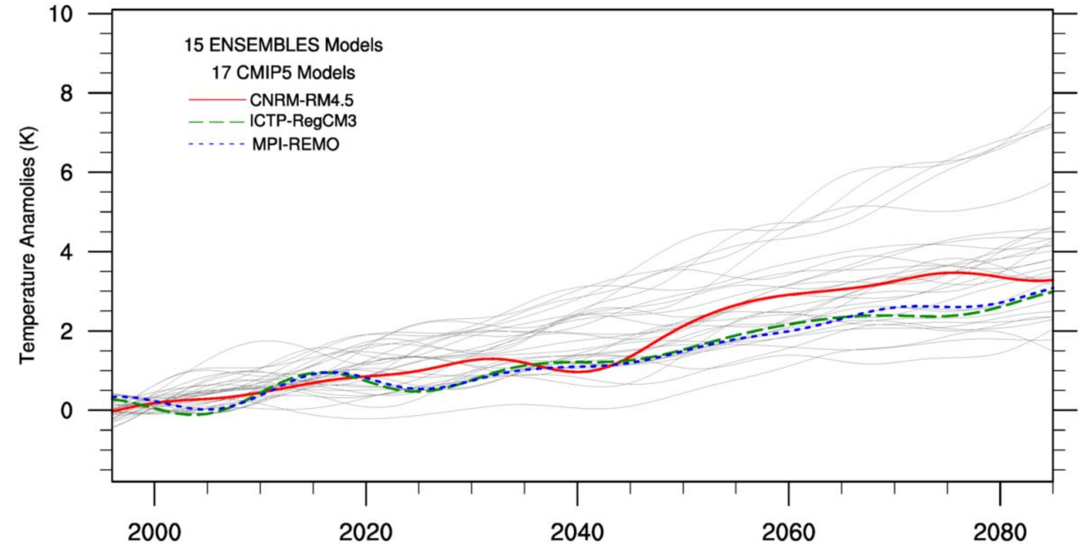
Disturbance scenario		Baseline climate		Climate change	
	R/S/Ms	Mean	SD	Mean	SD
1	∞/0/0	588	0	786	91
2	250/50/5.3	554	9	746	89
3	125/50/5.3	476	7	703	58
4	250/100/5.3	463	11	711	70
5	125/100/5.3	395	6	646	57
6	250/50/53.4	548	24	783	115
7	125/50/53.4	501	30	755	104
8	250/100/53.4	464	39	798	122
9	125/100/53.4	415	19	772	143

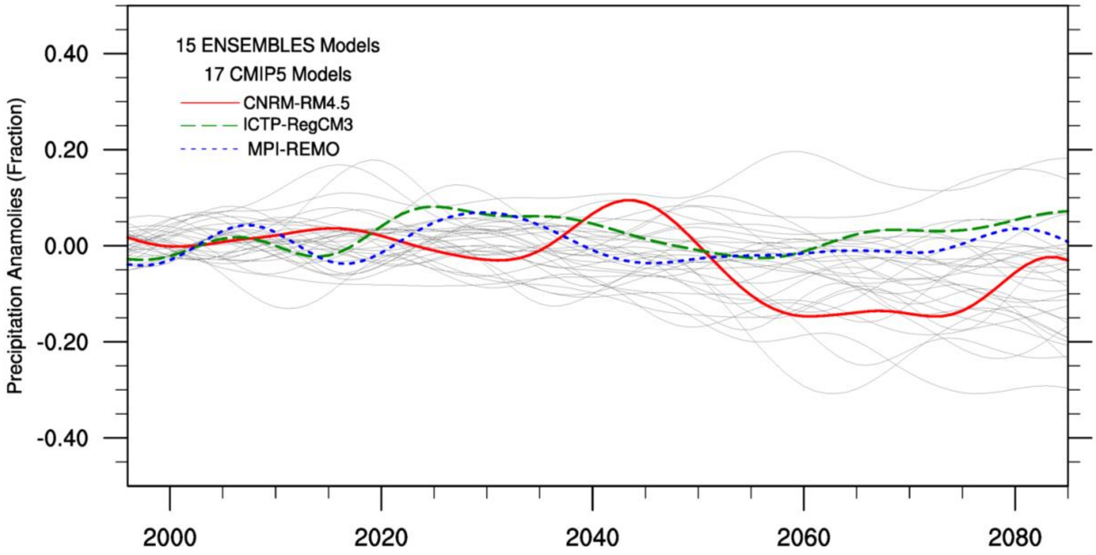
Table S3.2: Sensitivity analysis of the effect of different equilibrium definitions on time needed to adapt to changing environmental conditions. Shown are the average years and standard deviations (SD) per disturbance scenario needed to reach a dynamic equilibrium state defined as ±2.5m²/ha deviance in basal area (default: ±2.0m²/ha). R/S/M provides a summary of the disturbance processes per disturbance scenario: rotation/severity/mean size.

Disturbance scenario		Baseline climate		Climate change	
	R/S/M	Mean	SD	Mean	SD
1	∞/0/0	488	0	548	138
2	250/50/5.3	468	6	531	159
3	125/50/5.3	420	10	535	167
4	250/100/5.3	402	11	571	126
5	125/100/5.3	253	45	373	191
6	250/50/53.4	466	14	596	107
7	125/50/53.4	427	25	600	126
8	250/100/53.4	396	60	597	128
9	125/100/53.4	357	32	540	165

Table S4: Sensitivity analysis of the time to reach a dynamic equilibrium to the least and most severe representative concentration pathway of climate change. We simulated all nine disturbance scenarios using RCP2.6 and RCP8.5, and tested if the time needed to reach dynamic equilibrium falls within the distribution derived for the main scenarios investigated here (A1B). * indicates a significant difference whereas ^{NS} indicates that the result was not significant (α=0.05). Significances in dynamic equilibria between simulated A1B and RCP scenarios were derived using the R package "extremevalues" (van der Loo, 2010).

Disturbance scenario		A1B			
	R/S/Ms	Mean	CI	RCP2.6	RCP8.5
1	∞/0/0	706	218	331*	794^{NS}
2	250/50/5.3	659	99	628 ^{NS}	706^{NS}
3	125/50/5.3	655	100	639^{NS}	695^{NS}
4	250/100/5.3	647	84	631^{NS}	670^{NS}
5	125/100/5.3	495	325	551^{NS}	656^{NS}
6	250/50/53.4	670	152	732^{NS}	721^{NS}
7	125/50/53.4	659	153	730^{NS}	783^{NS}
8	250/100/53.4	675	177	731^{NS}	705^{NS}
9	125/100/53.4	610	215	632^{NS}	660^{NS}


15 ENSEMBLES Models
17 CMIP5 Models
CNRM-RM4.5
ICTP-RegCM3
MPI-REMO
Temperature Anamolies (K)
10
8
6
4
2
0
2000
2020
2040
2060
2080


15 ENSEMBLES Models
17 CMIP5 Models
CNRM-RM4.5
ICTP-RegCM3
MPI-REMO
Precipitation Anamolies (Fraction)
0.40
0.20
0.00
-0.20
-0.40
2000
2020
2040
2060
2080

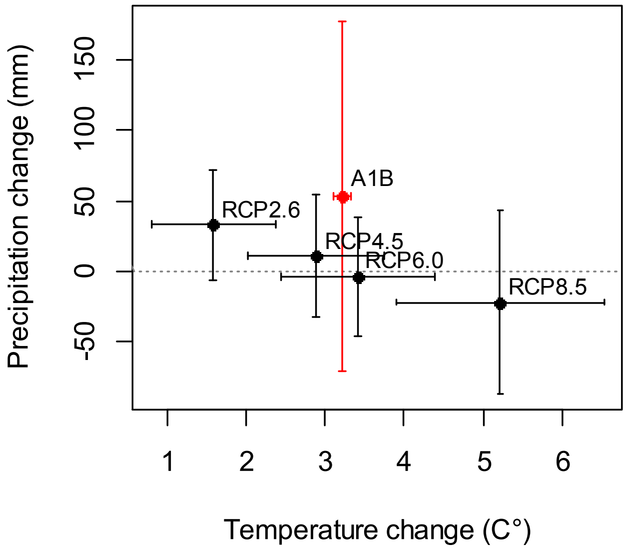

Precipitation change (mm)
150
100
50
0
-50
A1B
RCP2.6
RCP4.5
RCP6.0
RCP8.5
1
2
3
4
5
6
Temperature change (C°)

Fig. S1: Climate change scenarios for temperature and precipitation change in Austria. Top and center panels show the temporal development of the three main scenarios studied here (SRES A1B) relative to the ensemble of CMIP5 scenarios. The bottom panel compares CMIP5 RCPs to A1B for Austria for the period 2080-2099, which was used as reference period for climate stabilization in this analysis (data are from Alder & Hostetler (2013)). Dots represent the mean values, and whiskers indicate the standard deviation of the different models for each scenario (number of models for RCP2.6: n=19, RCP4.5: n=23, RCP6.0: n=15, RCP8.5: n=26).

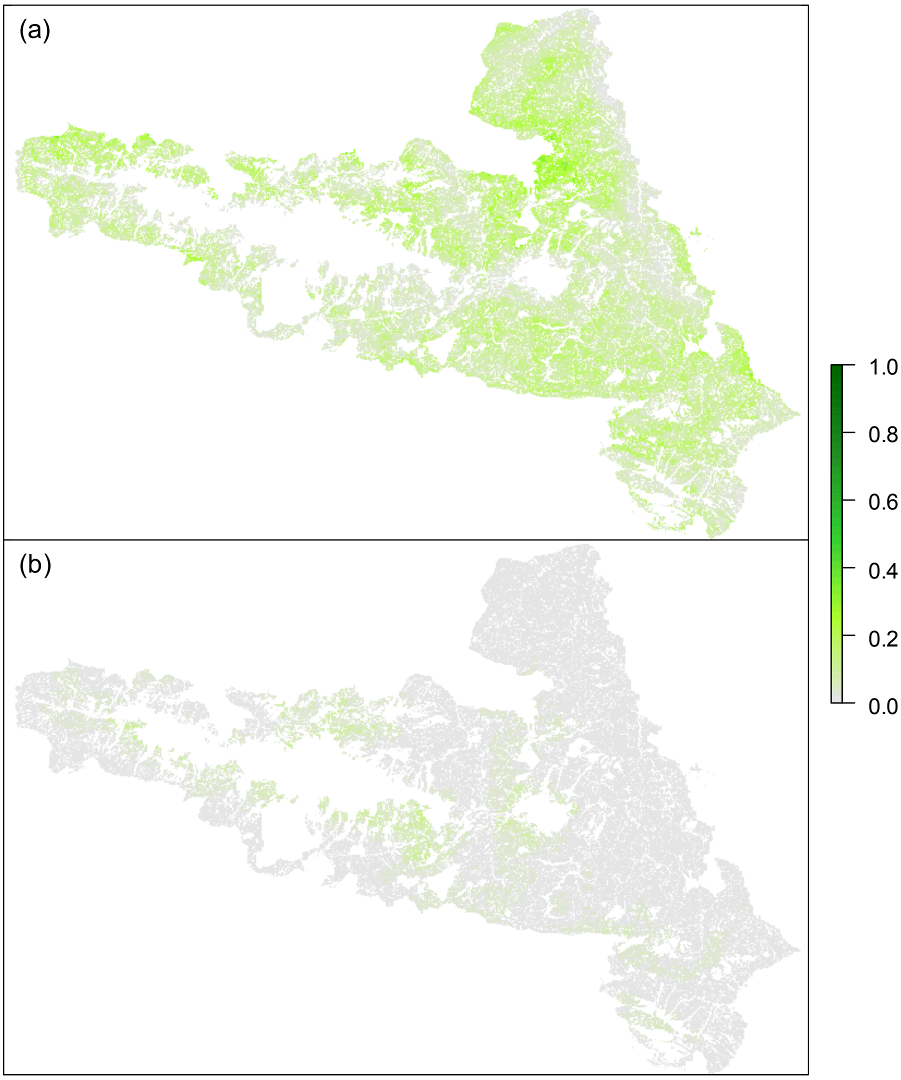


Fig. S2.1: Spatial distribution of *A. alba* at the end of the 1000 year simulation period (a value of 1 indicates a species share of 100%) under (a) baseline climate and (b) climate change scenarios. Both distributions were aggregated to mean values over all disturbance scenarios.

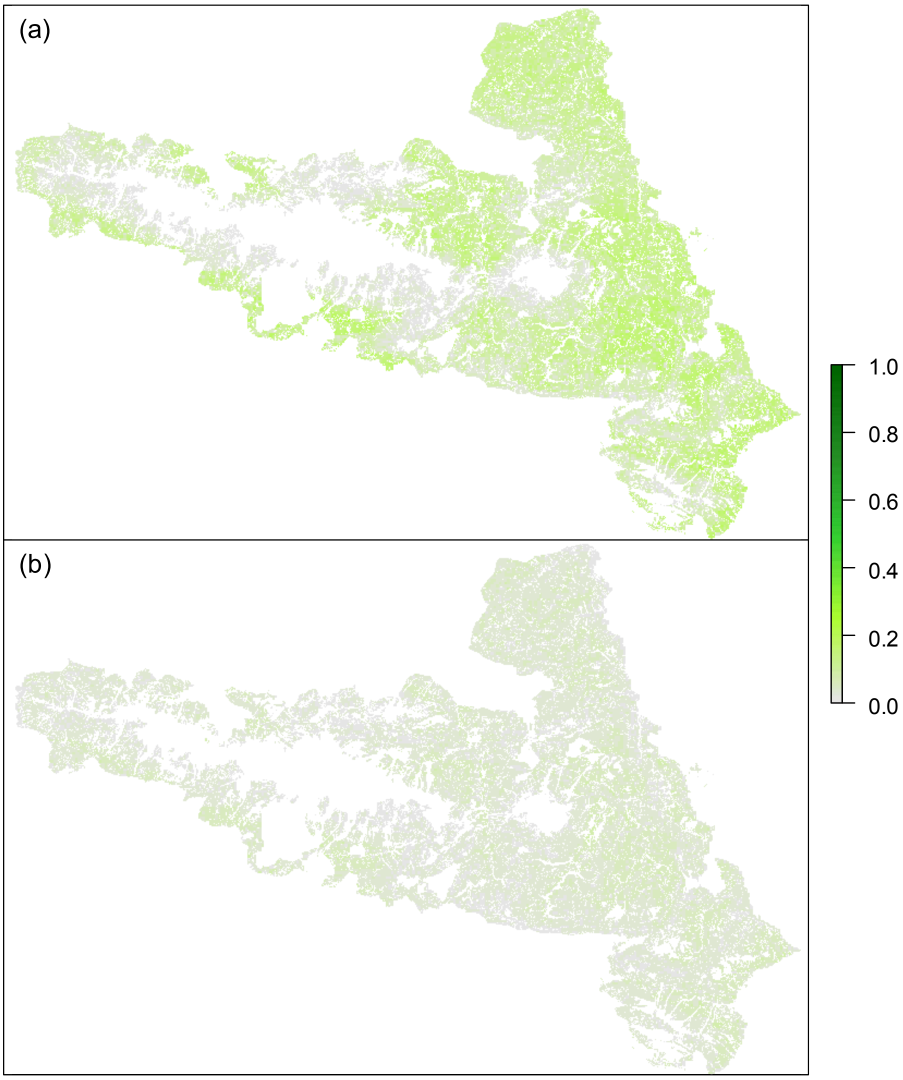


Fig. S2.2: Spatial distribution of *A. pseudoplatanus* at the end of the 1000 year simulation period (a value of 1 indicates a species share of 100%) under (a) baseline climate and (b) climate change scenarios. Both distributions were aggregated to mean values over all disturbance scenarios.

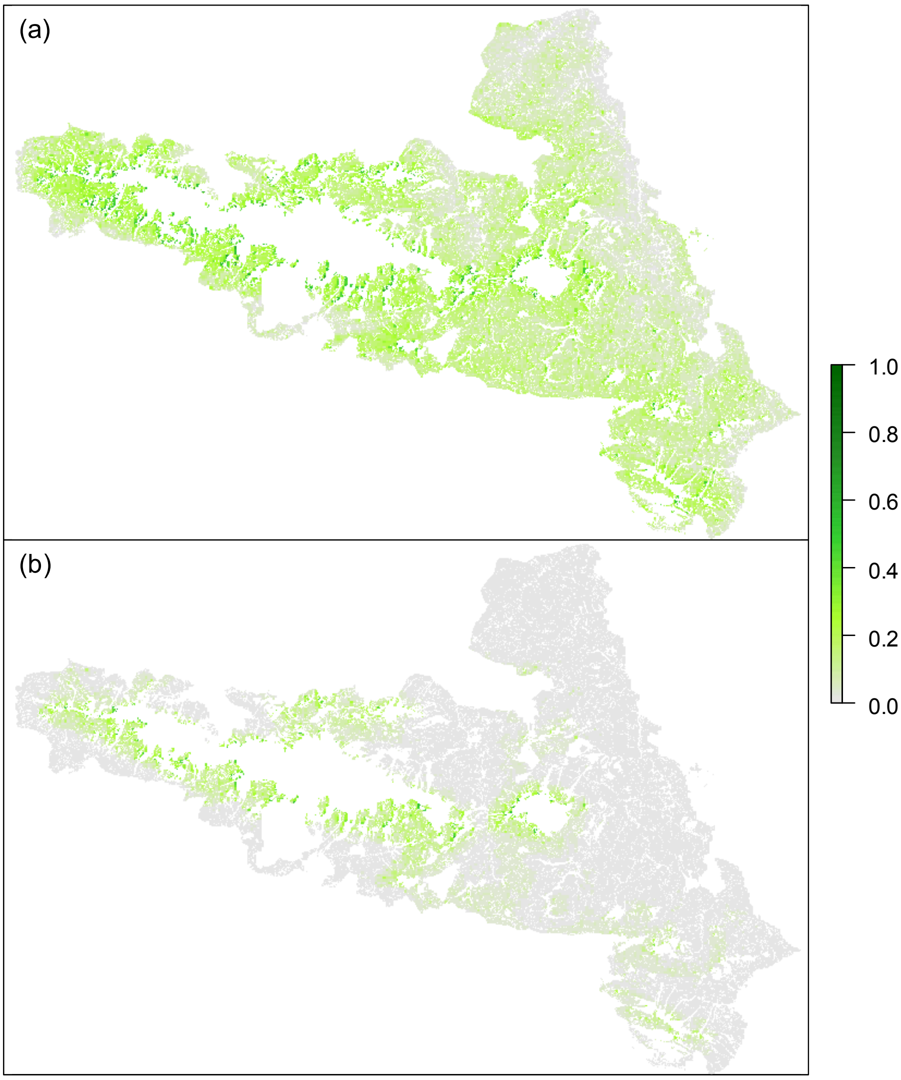


Fig. S2.3: Spatial distribution of *B. pendula* at the end of the 1000 year simulation period (a value of 1 indicates a species share of 100%) under (a) baseline climate and (b) climate change scenarios. Both distributions were aggregated to mean values over all disturbance scenarios.

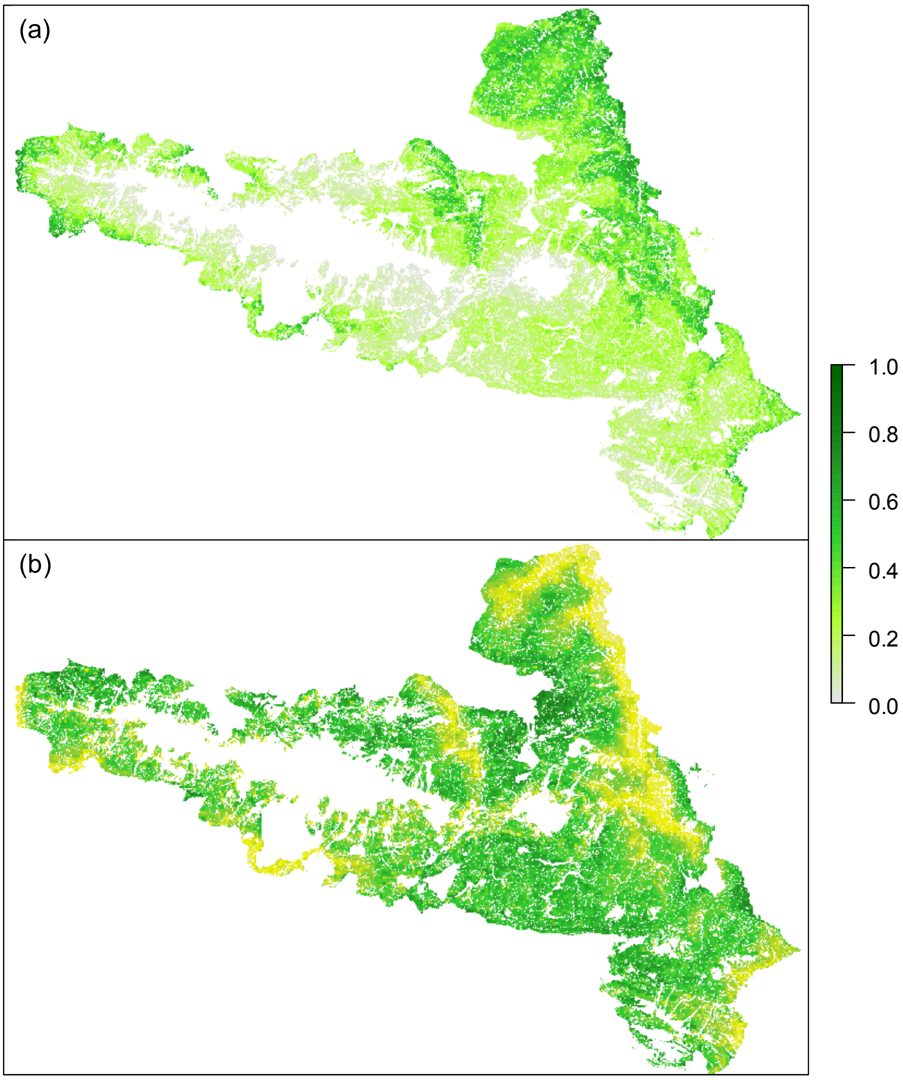


Fig. S2.4: Spatial distribution of *F. sylvatica* at the end of the 1000 year simulation period (a value of 1 indicates a species share of 100%) under (a) baseline climate and (b) climate change scenarios. Both distributions were aggregated to mean values over all disturbance scenarios.

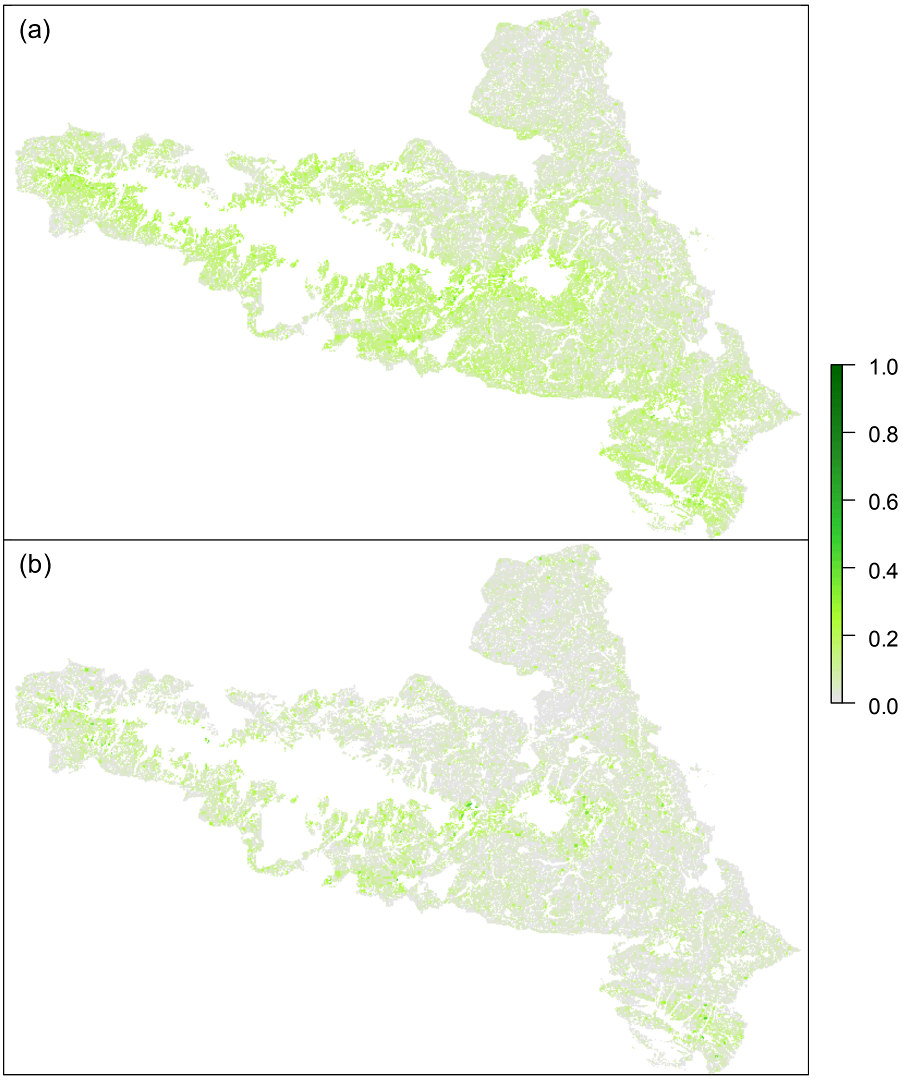


Fig. S2.5: Spatial distribution of *L. decidua* at the end of the 1000 year simulation period (a value of 1 indicates a species share of 100%) under (a) baseline climate and (b) climate change scenarios. Both distributions were aggregated to mean values over all disturbance scenarios.

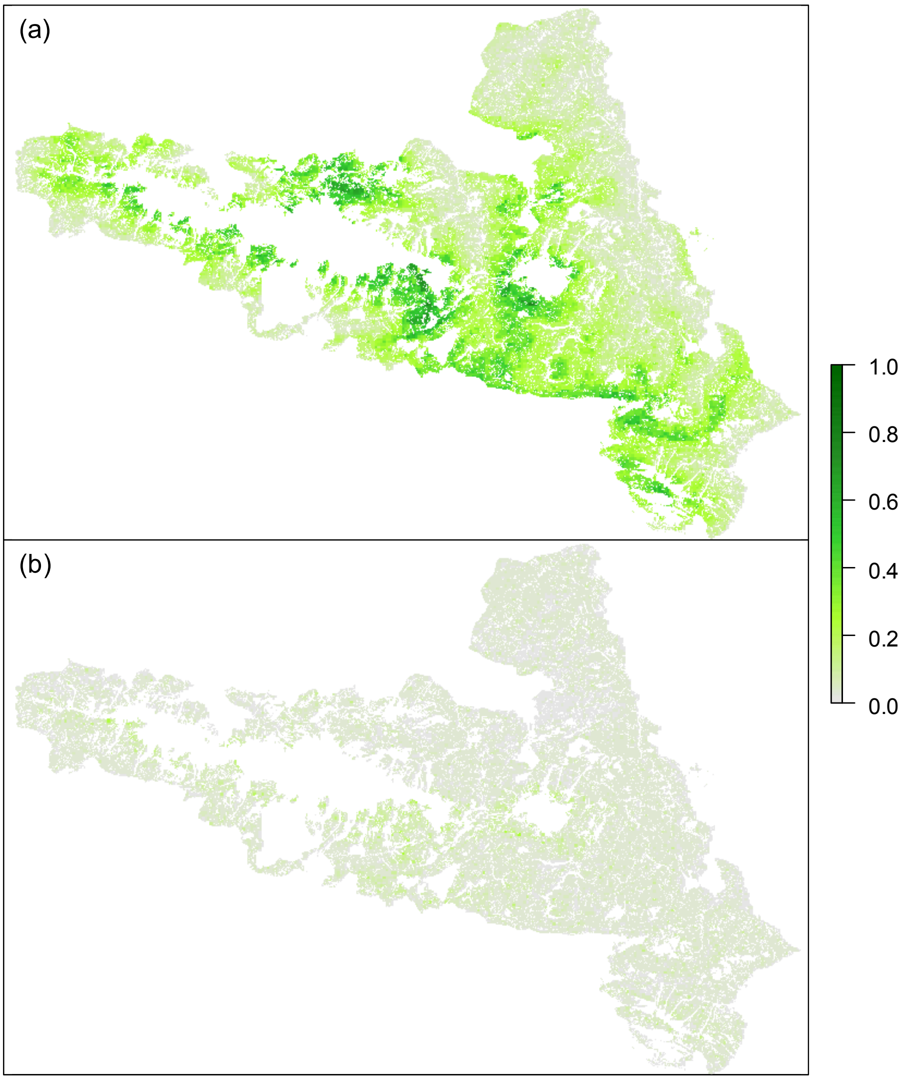


Fig. S2.6: Spatial distribution of *P. abies* at the end of the 1000 year simulation period (a value of 1 indicates a species share of 100%) under (a) baseline climate and (b) climate change scenarios. Both distributions were aggregated to mean values over all disturbance scenarios.

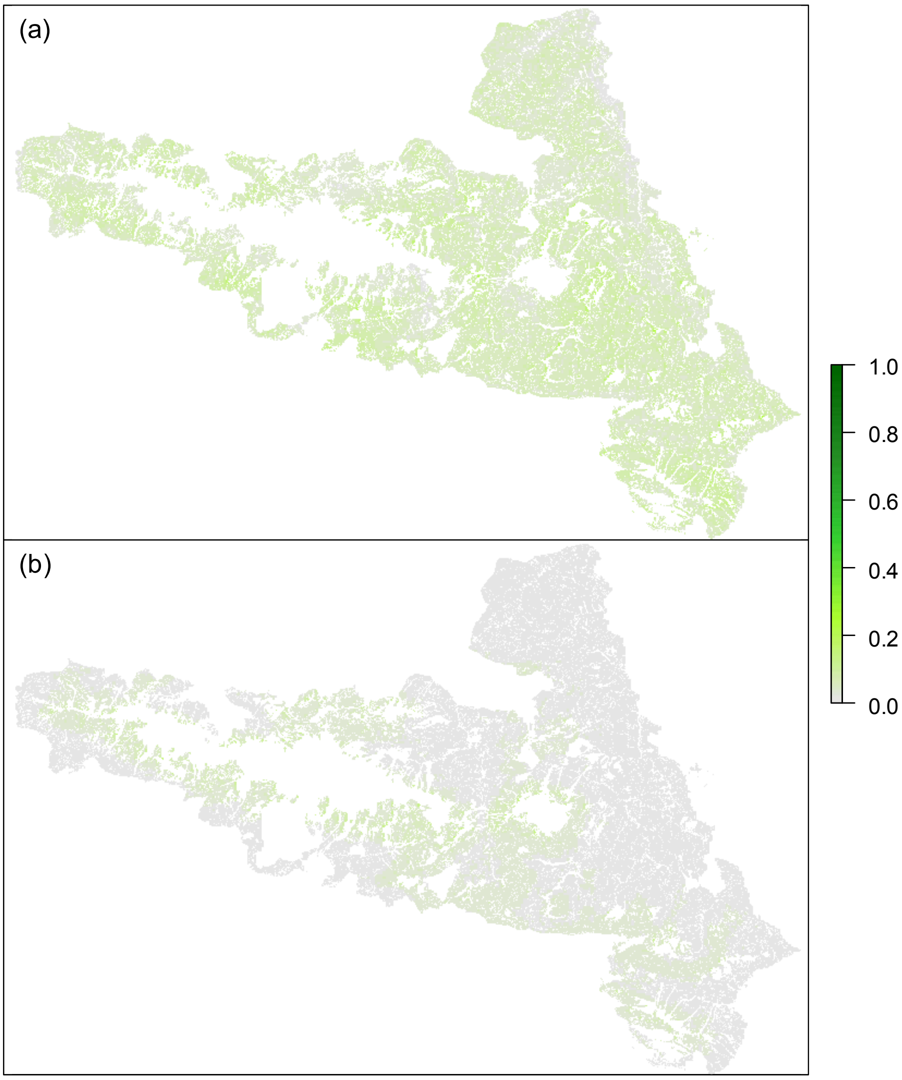


Fig. S2.7: Spatial distribution of *P. tremula* at the end of the 1000 year simulation period (a value of 1 indicates a species share of 100%) under (a) baseline climate and (b) climate change scenarios. Both distributions were aggregated to mean values over all disturbance scenarios.

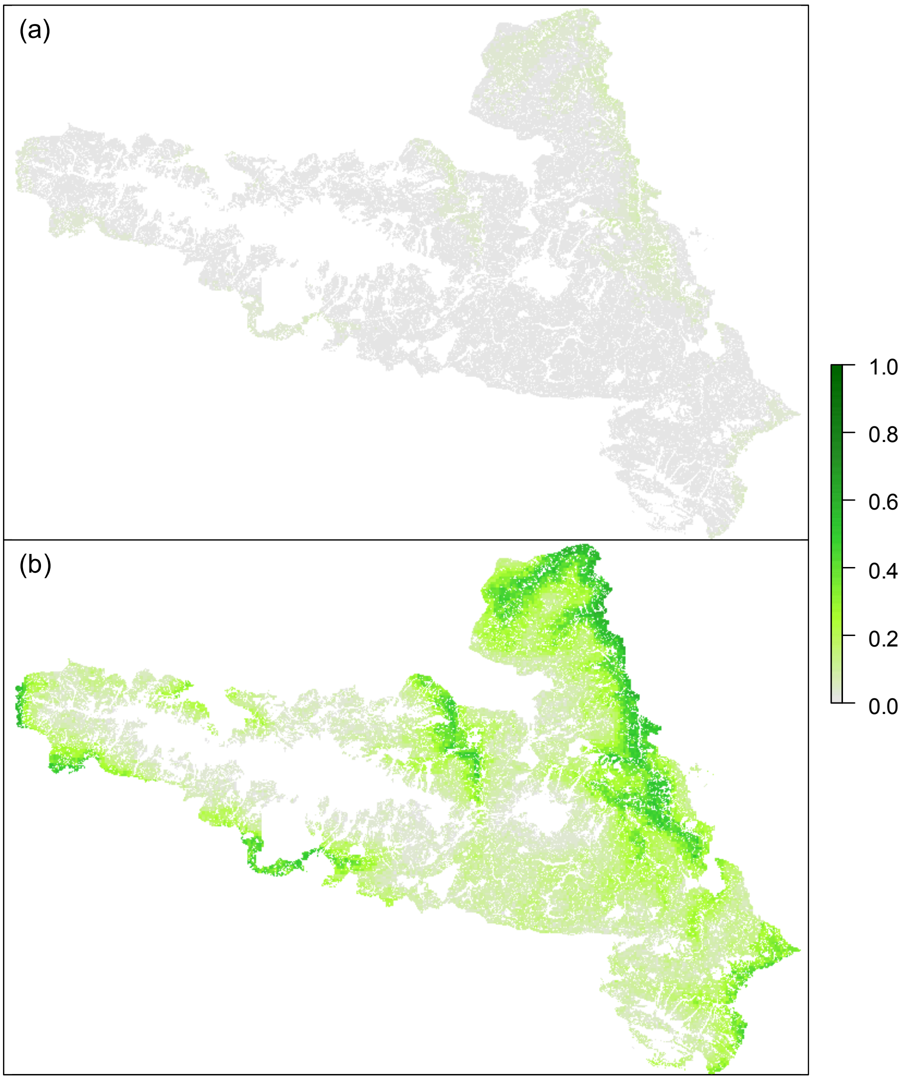


Fig. S2.8: Spatial distribution of *Q. petraea* at the end of the 1000 year simulation period (a value of 1 indicates a species share of 100%) under (a) baseline climate and (b) climate change scenarios. Both distributions were aggregated to mean values over all disturbance scenarios.

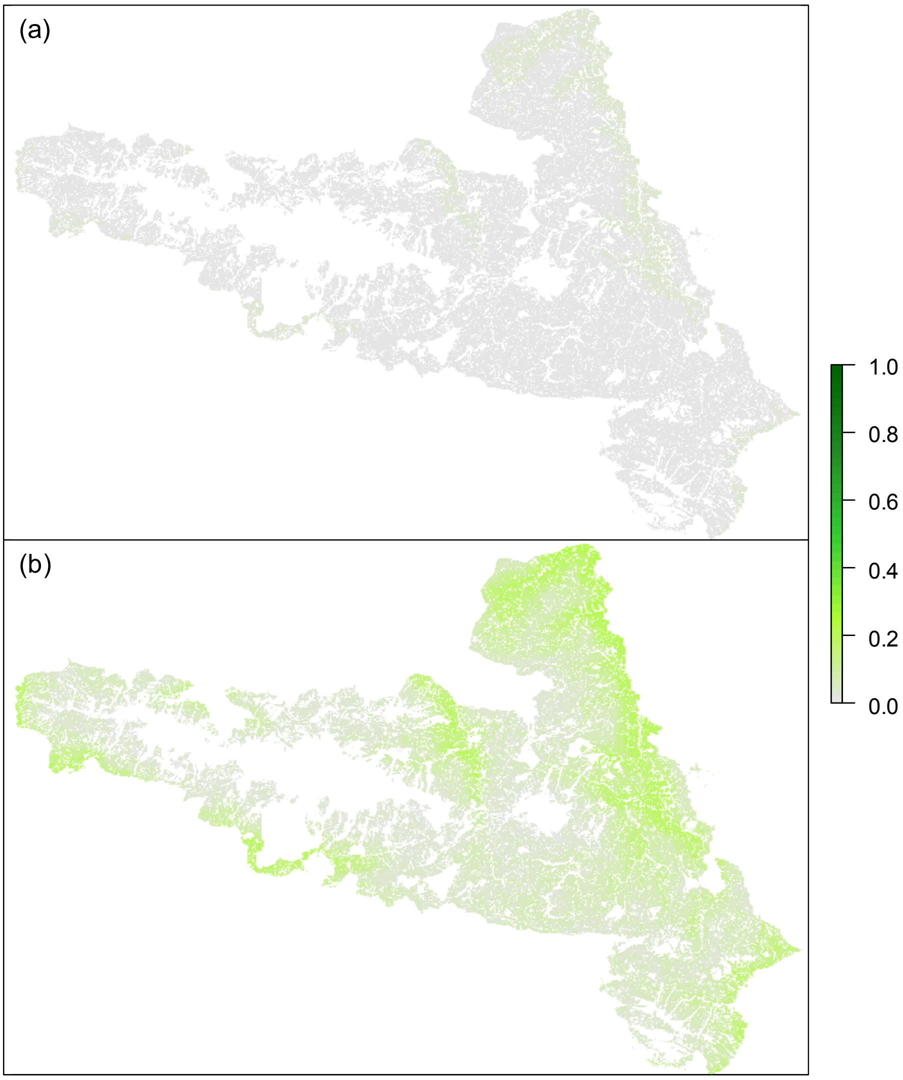


Fig. S2.9: Spatial distribution of *Q. robur* at the end of the 1000 year simulation period (a value of 1 indicates a species share of 100%) under (a) baseline climate and (b) climate change scenarios. Both distributions were aggregated to mean values over all disturbance scenarios.

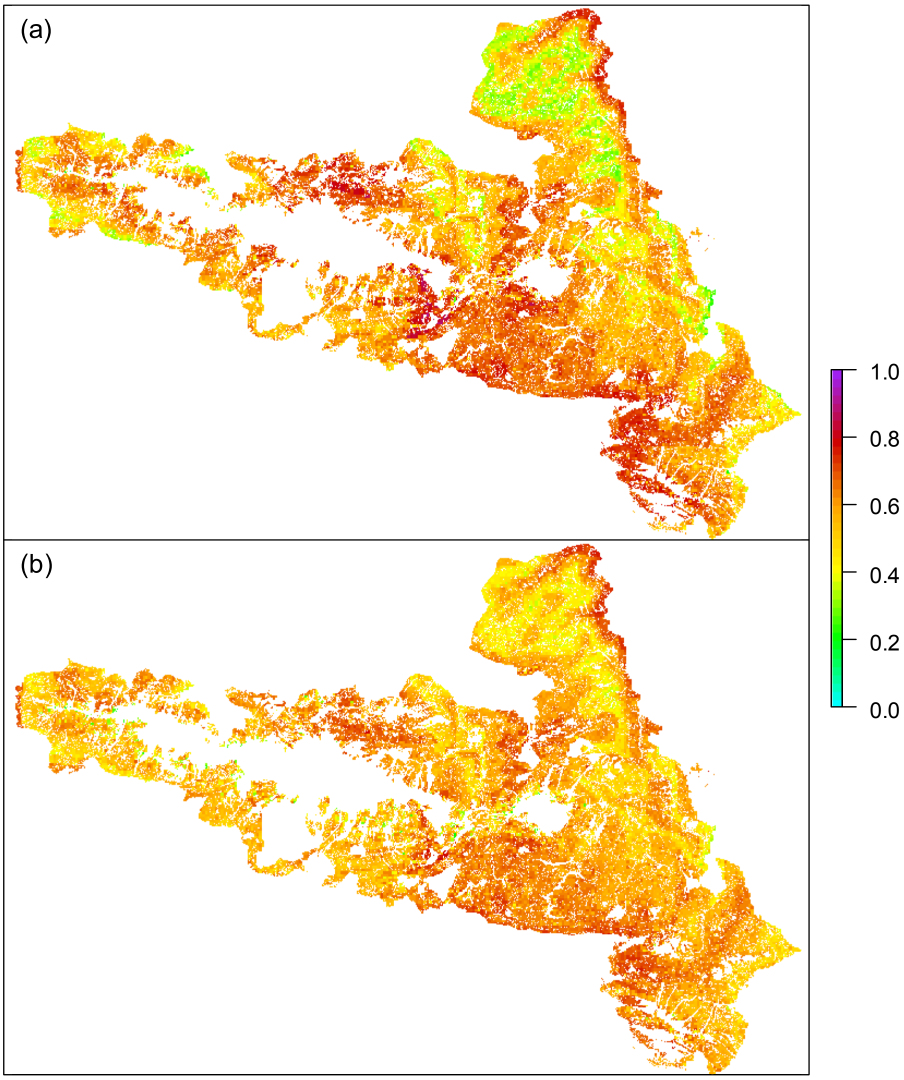


Fig. S3: Species turnover (a value of 1 indicates a turnover of 100% relative to baseline climate) as a result of climate change, under (a) undisturbed conditions, and (b) averaged over all scenarios including disturbances.

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van der Loo MPJ (2010) Distribution based outlier detection for univariate data. *Statistics Netherlands*, **Discussion paper 10003**, 1–14.

9.3 Paper III: The impacts of climate change and disturbance on spatio-temporal trajectories of biodiversity in a temperate forest landscape

Thom, D., Rammer, W., Dirnböck, T., Müller, J., Kobler, J., Katzensteiner, K., Helm, N., Seidl, R., 2016. The impacts of climate change and disturbance on spatio-temporal trajectories of biodiversity in a temperate forest landscape. J. Appl. Ecol., DOI: 10.1111/1365-2664.12644

The impacts of climate change and disturbance on spatio-temporal trajectories of biodiversity in a temperate forest landscape

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Running title: Climate and disturbance effects on biodiversity

Summary

1. The ongoing changes to climate challenge the conservation of forest biodiversity. Yet, in thermally limited systems, such as temperate forests, not all species groups might be affected negatively. Furthermore, simultaneous changes in the disturbance regime have the potential to mitigate climate-related impacts on forest species. Here we (i) investigated the potential long-term effect of climate change on biodiversity in a mountain forest landscape, (ii) assessed the effects of different disturbance frequencies, severities and sizes, and (iii) identified biodiversity hotspots at the landscape scale to facilitate conservation management.

2. We used the model iLand to dynamically simulate the tree vegetation on 13 865 ha of the Kalkalpen National Park in Austria over 1000 years, and investigated 36 unique combinations of different disturbance and climate scenarios. We used simulated changes in tree cover and composition as well as projected temperature and precipitation to predict changes in the diversity of Araneae, Carabidae, ground vegetation, Hemiptera, Hymenoptera, Mollusca, saproxylic beetles, Symphyta, and Syrphidae, using empirical response functions.

3. Our findings revealed widely varying responses of biodiversity indicators to climate change. Five indicators showed overall negative effects, with Carabidae, saproxylic beetles, and tree species diversity projected to decrease by more than 33%. Six indicators responded positively to climate change, with Hymenoptera, Mollusca, and Syrphidae diversity projected to increase more than twofold.

4. Disturbances were generally beneficial for the studied indicators of biodiversity. Our results indicated that an increasing disturbance frequency and severity has a positive effect on biodiversity, while increasing disturbance size has a moderately negative effect. Spatial hotspots of biodiversity were currently found in low- to mid-elevation areas of the mountainous study landscape, but shifted to higher elevation zones under changing climate conditions.

5. *Synthesis and applications*. Our results highlight that intensifying disturbance regimes may alleviate some of the impacts of climate change on forest biodiversity. However, the projected shift in biodiversity hotspots is a challenge for static conservation areas. In this regard

overlapping hotspots under current and expected future conditions highlight priority areas for robust conservation management.

Key-words: biodiversity hotspots, climate change impacts, conservation management, forest ecosystem management, insect diversity, landscape ecology, Kalkalpen National Park, plant diversity

Introduction

Biodiversity has been identified as a key determinant for the quality and functioning of ecosystems worldwide (Díaz & Cabido 2001; Cardinale, Palmer & Collins 2002). The currently ongoing decline in biodiversity threatens the ability of ecosystems to adapt to changing conditions and hampers the provisioning of ecosystem services, and thus represents one of the greatest challenges for humanity (Bellard *et al.* 2012). Changes in land use and climate have been identified as the main drivers of this decline (Sala 2000). Particularly forest ecosystems are under pressure, as climate change may threaten forest-dependent species across a wide range of species groups (Thomas *et al.* 2004). The vulnerability of forest biodiversity along with the fact that the majority of terrestrial species depend on forest ecosystems underlines the key role of forests in conservation management (Myers *et al.* 2000; Parrotta, Wildburger & Mansourian 2012).

The majority of studies on climate change impacts on biodiversity have focused on direct effects of climate change, i.e. effects of changes in temperature and precipitation on biodiversity. Fewer works have also investigated indirect effects, such as the effect of climate-mediated changes in forest structure and composition on species presence and abundance (e.g. De Frenne *et al.* 2013). While forest structure and composition generally respond slowly to environmental changes, they can be altered quickly and profoundly by disturbances, i.e. pulses of tree mortality caused by agents such as bark beetles, fire and wind. Disturbances are climate sensitive and have already intensified during the last decades (Seidl, Schelhaas & Lexer 2011). A further intensification of disturbance regimes in response to ongoing climatic changes is likely (Seidl *et al.* 2014; Millar & Stephenson 2015). While often regarded as undesirable “calamities” in forest management, the resulting increases in biodiversity (e.g. indicated by the number of species) generally reveal a positive impact of disturbances on biodiversity (Müller *et al.* 2008; Thom & Seidl 2015). However, the net effect of changing climate and disturbance regimes on forest biodiversity remains unclear: Will intensifying disturbance regimes offset the predicted negative direct effects of climate change on biodiversity? Or will increasing climate and disturbance change threaten the ecological resilience of ecosystems, and consequently the habitat quality of forest-dependent species?

Future climate change impacts on plant and animal diversity have predominantly been assessed using niche models, i.e. empirical relationships between species presence or abundance and climate variables (Zimmermann *et al.* 2010). Notwithstanding their scientific value (e.g. assessing the climatic suitability of species and their potential range for migration under future climate), such models have major shortcomings in the context of conservation planning and management. For instance, they commonly ignore biotic interactions that strongly affect species composition (but see Thuiller *et al.* (2015)). Moreover, niche models assume that species track changing climatic conditions instantaneously, disregarding time lags and indirect effects of climate change such as habitat changes and disturbance-driven perturbations (Elith & Leathwick 2009). In contrast, process-based forest simulation models project transient pathways of ecosystem change while accounting for the complex and interacting effects of climate change (Kearney & Porter 2009). These approaches, however, usually focus solely on tree vegetation and rarely address other species relevant in the context of biodiversity conservation.

Here we combined landscape-scale forest simulation modelling with empirical climate–diversity relationships to circumvent many of these limitations. Our aim was to address the climate sensitivity of forest biodiversity explicitly in space and time, and particularly study the effect of current and changed climate and disturbance regimes over an extended time frame of 1000 years. Our specific objectives were to (i) investigate the role of climate change on a wide range of indicators of forest biodiversity over time, (ii) assess the effects of different disturbance frequencies, severities, and sizes on biodiversity indicators, and (iii) identify current and future biodiversity hotspots at the landscape scale to facilitate future conservation management. The latter question is of particular relevance as identifying and preserving areas of particular value for biodiversity, e.g. due to their particular richness or habitat value for keystone species (Myers *et al.* 2000), is a cornerstone of current conservation management. Many existing protected areas are centred on such biodiversity hotspots, yet whether these systems also will remain hotspots in a drastically changing climate remains uncertain (see e.g. Hansen *et al.* 2001; Bässler *et al.* 2013). Here, we tested for a shift of biodiversity hotspots along the steep altitudinal gradients of our study landscape to higher elevation areas due to reduced thermal limitations in a future climate. Based on previous large-scale assessments we furthermore hypothesized an overall negative impact of climate change on forest biodiversity (Thomas *et al.* 2004), but a positive effect of natural disturbance (Thom & Seidl 2015). Finally we tested the hypothesis that a slow response of forest composition and structure leads to a considerable time lag in the response of biodiversity to changing climatic conditions (Bertrand *et al.* 2011).

Materials and methods

STUDY AREA

The Kalkalpen National Park (KA-NP) is located at N47.47° E14.22°, in the northern front range of the Austrian Alps (Fig. 1). The landscape is characterized by steep mountainous terrain, with elevations ranging from 385 to 1963 m a.s.l. Soils are predominately shallow with Lithic and Rendzic Leptosols and Chromic Cambisols as the dominant soil types over calcareous bedrock. The climate varies with topography, with temperature decreasing (mean annual temperature range: 3.6–9.0°C) and precipitation increasing (mean annual precipitation range 1205–1741mm) with elevation. With a total size of 20 856 ha mainly consisting of forests, the Kalkalpen National Park is the largest forest wilderness in Austria. It includes a diverse range of forest ecosystems including European beech *Fagus sylvatica* (L.) forests in the lower reaches, mixed forest types of beech, Norway spruce *Picea abies* (L. Karst.), and silver fir *Abies alba* (Mill.) in mid elevations, and subalpine spruce forests in high elevations. Before establishment of the KA-NP in 1997, the area was managed mainly for timber production, but today conforms to IUCN category II (National Park).

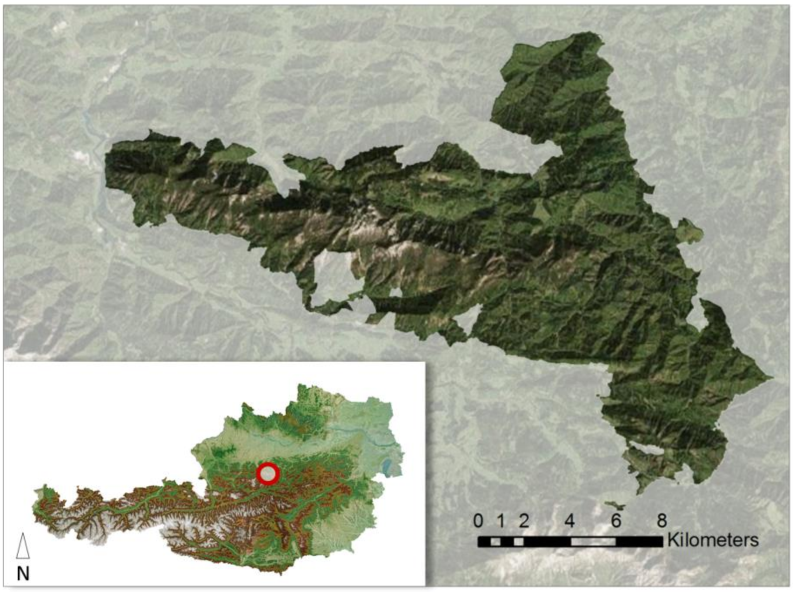

Fig. 1. Location, extent, and topography of the study landscape – Kalkalpen National Park.

SIMULATION MODEL

To simulate forest landscape dynamics at KA-NP we used iLand, the individual-based forest landscape and disturbance model. iLand is a spatially explicit process-based model. It was developed to simulate interactions between environmental drivers (e.g. climate regime, nutrient and water availability), forest vegetation processes (e.g. growth, mortality, and regeneration), and disturbances regimes (e.g. wind storms, wildfires) (Seidl *et al.* 2012a). Processes in iLand interact in a hierarchical multi-scale framework, including processes on the tree (e.g. growth, mortality, competition for resources), stand (availability of water, nutrients), and landscape level (disturbance, seed dispersal). The simulation of primary production in iLand is based on a light-use efficiency approach, with scalar modifiers accounting for the effects of temperature, soil water availability, vapour pressure deficit, nutrient availability as well as atmospheric carbon dioxide (CO_2) concentration. Mortality of trees in iLand considers intrinsic mortality (i.e. age-related causes) and stress-related mortality (using carbon starvation as a physiological proxy for stress) as well as disturbance events such as windstorm or fire. Regeneration is spatially explicit and depends on the availability of seeds as well as favourable light and environmental conditions. A detailed description of iLand is available in Seidl *et al.* (2012a; b) and from an extensive online documentation (http://iLand.boku.ac.at).

For the current study, we evaluated the model’s ability to simulate the KA-NP by testing iLand’s ability to reproduce expected values of productivity (Fig. S1 in Supporting Information), climate sensitivity (Fig. S2), and the potential natural vegetation (Fig. S3). Overall, these tests resulted in good correspondence of the model with independent observations and supported the application of iLand for studying ecosystem dynamics at the KA-NP.

INITIAL CONDITIONS AND DRIVERS

Soil and climate varied at a spatial grain of 100 × 100 m in the simulations (in total 19 200 ha), while the initial vegetation conditions were derived for stand polygons covering the 13 865 ha forest area of the KA-NP (median stand size: 1.4 ha). Soil depth and type (Kobler

2004), texture (from inventory plots) as well as plant available nitrogen (Seidl, Rammer & Lexer 2009) were used to characterize soil conditions. To initialize the current vegetation, we combined data sources from forest inventory and planning data, aerial photo analysis and LiDAR. Altogether, we initialized more than 2 10^6 trees from 17 different species, representing the state of the tree vegetation at KA-NP in the year 1999. Four climate scenarios were studied: A baseline climate scenario where we repeatedly sampled years from the period 1950–2010 for the 1000-year simulation period, and three regionally downscaled climate change scenarios, representing different combinations of global and regional circulation models under A1B forcing. A stabilization of climate conditions at the level of 2080–2099 was assumed for the years beyond 2100 (i.e. *inter alia* 3.1–3.3°C change relative to the baseline period). A more detailed description of the initial conditions and driver data for the simulation is provided in Appendix S1.

LANDSCAPE SIMULATION

We simulated the currently forested 13 865 ha of the KA-NP for 1000 years with 36 unique combinations of climate and disturbance scenarios to derive tree species composition at the level of 100-m grid cells. In addition to the four climate scenarios described above, we investigated all possible combinations of two different disturbance frequencies, severities and size scenarios for every climate scenario. The low-intensity disturbance variant represents the current disturbance regime, with a rotation period of 250 years (Thom *et al.* 2013), and a mean disturbance size of 5.3 ha (based on a disturbance inventory at KA-NP). As moderate disturbance severity we assumed a mortality of 50% of trees with diameter at breast height (d.b.h.) > 10 cm in this variant. At increased disturbance scenarios the disturbance rotation period was halved to 125 years, the size increased 10-fold to 53.4 ha, and the severity doubled to 100%. Additionally, we included a scenario without disturbance, bringing the total number of studied disturbance scenarios to nine (2 frequencies × 2 severities × 2 sizes + 1 no disturbance scenario). Within these disturbance regime definitions, simulated disturbances were implemented stochastically in each scenario, with the actual disturbance size drawn from a negative exponential distribution, and the location of the disturbance assigned randomly to the landscape. Each scenario was replicated ten times to account for stochasticity in the simulation. We tested the sufficiency of using ten replicates per scenario by analysing the coefficients of variation (cv) of our response variables, and found robust results for all indicators at the end of the simulation period (cv < 2% for all indicators and scenarios, Table S1). In total 360 simulations were conducted (4 climate scenarios × 9 disturbance scenarios × 10 replicates). This simulation design was specifically developed (i) to stringently distinguish climate and disturbance effects on biodiversity (due to independence of climate and disturbance scenarios in the simulation), and (ii) to assess which disturbance regime parameters (i.e. size, severity, or frequency) are most influential on biodiversity. To account for the vegetation changes that have occurred between 1999 (the year for which initial vegetation information was available) and 2013 (the initial year of the analysis), we ran the model for these 14 years using the respective climate forcing and recreating the disturbances that were observed during that period. Each simulation was then run over 1000 years starting in the year 2013.

INDICATORS OF BIODIVERSITY

To obtain a comprehensive assessment of the climate and disturbance effects on forest biodiversity we jointly analysed eleven different biodiversity indicators for each simulated 1-ha grid cell. Tree species diversity and canopy complexity were directly derived from iLand simulations. Basal area shares were used to compute tree species diversity, using the exponent of the Shannon-Index ($\exp(H')$) as an indicator for the effective number of tree species. Canopy complexity was described by means of the rumple index (Parker *et al.* 2004), which is the ratio of the canopy surface area to the projected ground surface area, calculated here at 10-m horizontal resolution. With regard to animal diversity, richness data (number of species) on Araneae (web spiders), Carabidae (ground beetles), Hemiptera (true bugs), Hymenoptera (sawflies, wasps, bees and ants), Mollusca (snails and slugs), saproxylic (deadwood-dependent) beetles, Symphyta (sawflies), as well as Syrphidae (hoverflies) were derived from biodiversity inventories (0.1 ha plots) in 52 locations distributed over neighbouring Bavaria (Bässler *et al.* 2008). Furthermore, data on the richness of the ground vegetation (vascular plant species with a height of up to 60 cm) were derived from the FlorAlp-Database (Dullinger *et al.* 2012) by selecting releves with a uniform size of 625 m^2 (n=852). Based on these data we developed empirical response functions for the nine biodiversity indicators not derived directly from simulations, where the response variable (number of species in each group) was related to mean annual precipitation sum (P_{sum}) and mean annual temperature (T_{mean}) (indicators of the climate regime), canopy cover (an indicator for light availability and the local thermal regime), and the relative share of canopy tree species (indicators of species association). We used negative binomial generalized linear models (glms) with a logarithmic link function to predict species diversity of each indicator. Based on ecological theory we hypothesized an optimum relationship of temperature and canopy cover for each indicator, and consequently transformed these predictors using second order polynomial functions (Austin 2002). The transformed variable was retained if the species diversity response was biologically meaningful. To determine the model most strongly supported by the data we used Akaike's information criterion (AIC), Nagelkerke R^2 values as well as *P*-values from chi-square goodness-of-fit tests. Final models were tested for multicollinearity by means of (generalized) variance inflation factors (VIF or GVIF). To further analyse the thus derived empirical models with regard to their response to climate and tree vegetation changes a local sensitivity analysis was conducted.

In a subsequent step we used the fitted glms with the respective climate input and iLand-derived tree layer information to project biodiversity responses for all scenarios. For each of the eleven indicators we derived the effect of climate change at any given point in space and time by relating each simulation under climate change to the mean over the baseline period under the same disturbance scenario. For the analyses of climate change effects over time, we aggregated the 100-m grid cells to landscape-level mean responses. From these comparisons over all scenarios and replicates, the median and 95th percentile range of climate-induced diversity changes were computed. Similarly, the disturbance effect was calculated by relating scenarios of different disturbance frequency, severity and size to the respective undisturbed scenario under any given climate regime. Both climate and disturbance effects were tested against the null hypothesis of no effect by means of Wilcoxon's signed rank sum test.

BIODIVERSITY HOTSPOTS

To also address spatial changes in biodiversity on the landscape we assessed biodiversity hotspots at KA-NP, i.e. we identified areas that support a high diversity across all indicators. To be able to compare across indicators, we used percentiles of diversity estimates for all 360 simulations at the end of the simulation period. In analogy to the assessment of multi-functionality across ecosystem services (e.g. Pasari *et al.* 2013), hotspots were defined as an area where every indicator reaches or exceeds a predefined threshold (here set this at the 25th percentile value). Differences between scenarios were analysed by means of McNemar's chi-squared test, and spatial analysis of hotspots was conducted by mapping at a grain of 100-m grid cells. To evaluate sensitivities of the result to this particular definition of hotspots an alternative hotspot definition was also investigated (see Fig. S4 for details).

Results

SENSITIVITY OF FOREST BIODIVERSITY

The empirical models for predicting diversity in species groups were found to satisfactorily fit the empirical data, with pseudo-R^2 values ranging from 0.23 to 0.96 (Table 1). Chi-square goodness-of-fit tests did not reject the final models. VIF and GVIF, respectively, were all <10, indicating that final models were not strongly affected by multicollinearity (Dormann *et al.* 2013).

Analyses of the fitted parameters and sensitivity analysis indicated that taxonomic groups reacted non-uniformly to modifications in their environment (Table S2). Changes in average temperature, for instance, resulted in a range of responses: while species groups such as Hymenoptera and Syrphidae strongly benefited from increasing temperatures (+71.8% and +49.9% for a +1°C increase), others such as Araneae and saproxylic beetles were clearly negatively affected (-9.3% and -8.8% for the same temperature increase). Compared to this distinct temperature effect, precipitation had a weaker influence on diversity in species groups. Six out of nine models maintained precipitation as covariate though, with Araneae, Carabidae, Hymenoptera and saproxylic beetles showing negative responses while ground vegetation and Syrphidae responding positively to an increase in precipitation. Besides impacts of changing climatic conditions, changes in tree vegetation were also important determinants of diversity in species groups. While the proportion of beech and spruce was found to have negative impacts on biodiversity, the share of oak *Quercus petraea* (Matt.) and *Quercus robur* (L.) and hornbeam *Carpinus betulus* (L.) positively influenced diversity in a range of species groups. An increase in canopy cover was found to have negative effects on the species diversity of most taxonomic groups (between -1.8% and -13.6% for a 10% increase in canopy cover) – only Carabidae and saproxylic beetles were weakly positively related to canopy cover.

Table 1. Parameters and goodness-of-fit of the empirical species diversity models (negative binomial generalized linear models with a logarithmic link function). T_{mean}: mean annual temperature; P_{sum}: sum of annual precipitation; beech, spruce, oak + hornbeam as well as canopy cover are relative shares (%). poly() indicates the polynomial transformation (2. order) of a predictor

Response variable	Predictors	R^2 (Nagelkerke)	*P*-value (Chi^2)
Araneae	T_{mean}, P_{sum}, oak + hornbeam, poly(canopy cover)	0.61	0.179
Carabidae	T_{mean}, P_{sum}, beech, canopy cover	0.26	0.126
Ground vegetation	poly(T_{mean}), P_{sum}, spruce, poly(canopy cover)	0.23	0.176
Hemiptera	T_{mean}, beech, spruce, canopy cover	0.54	0.252
Hymenoptera	T_{mean}, P_{sum}, poly(canopy cover)	0.90	0.174
Mollusca	T_{mean}, spruce, canopy cover	0.87	0.250
Saproxylic beetles	poly(T_{mean}), P_{sum}, oak + hornbeam, poly(canopy cover)	0.96	0.173
Symphyta	T_{mean}, beech, poly(canopy cover)	0.37	0.108
Syrphidae	T_{mean}, P_{sum}, beech, poly(canopy cover)	0.47	0.186

CHANGES IN BIODIVERSITY IN RESPONSE TO CLIMATE CHANGE

Our simulations indicated a pronounced increase in the share of European beech and a decrease in Norway spruce under climate change (Table 2), with changes progressing considerably beyond the assumed point of climate stabilization in 2100. Tree species composition did, however, also change under baseline climate conditions, highlighting past management legacies in the current tree species composition. The combined effects of direct and indirect responses to climate change on the eleven biodiversity indicators were strongly divergent. While six indicators showed overall positive responses, five were negatively affected at the end of the 1000-year simulation period ($P<0.001$). Climate change was beneficial for the diversity of ground vegetation, Hemiptera, Hymenoptera, Mollusca, Symphyta and Syrphidae, but reduced the diversity of Araneae, Carabidae and saproxylic beetles as well as the canopy complexity of forests in the landscape (Fig. 2, Table 3). Tree species diversity was slightly positively affected during the first 100–200 years, but eventually dropped to -35.8% compared to baseline climate conditions. The most drastic changes in a wide range of species groups were found during the first 100 years of the simulation, indicating a prominent direct climate effect. Tree layer-mediated indirect effects were most distinctive for Araneae and saproxylic beetles, where the increase in oak and hornbeam cover in response to warming (positive indirect effect) compensated direct negative impacts of elevated temperature and reduced precipitation over the long term. The opposite signal was found for Hemiptera and Symphyta: While direct climate change effects were beneficial for both species groups, the climate-induced increase in beech negatively influenced species diversity in these groups.

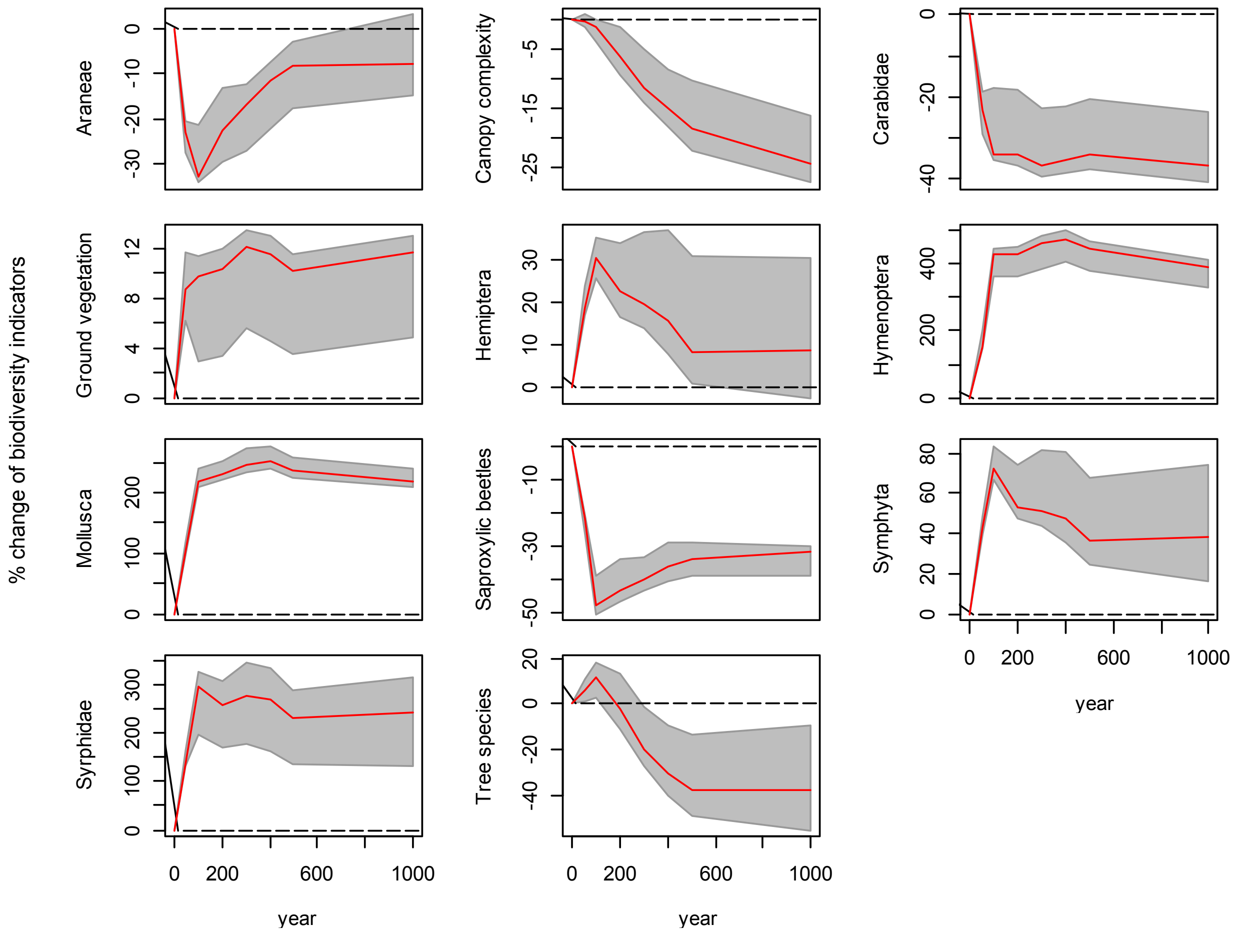

Fig. 2. Landscape-scale response of biodiversity indicators to climate change relative to baseline climate conditions (1950–2010). Red lines present the median, and grey shaded areas illustrate the 95th percentile range. The y-axis indicates the percentage change compared to baseline climate conditions, while the x-axis indicates the simulated year. Note that y-axes are on different scales.

Table 2. The sensitivity of forest composition to climate change and disturbance. Values are based on iLand simulations and indicate means and standard deviations (SD) over averaged landscape values (i.e. average species shares in the landscape) of all respective scenarios

	Disturbance	Initial state	Baseline climate				Climate change			
		year 0	year 100		year 1000		year 100		year 1000	
		mean	mean	SD	mean	SD	mean	SD	mean	SD
A. alba (%)	no	-	3.3	0.0	13.1	0.0	3.6	0.1	1.3	1.0
	yes	2.9	3.4	0.1	7.8	1.8	3.6	0.2	0.9	0.8
C. betulus (%)	no	-	<0.1	0.0	0.0	0.0	0.2	0.1	0.7	0.2
	yes	<0.1	<0.1	0.0	0.1	0.1	0.4	0.3	2.8	1.5
F. sylvatica (%)	no	-	34.7	0.0	34.4	0.0	37.9	1.2	67.3	9.0
	yes	39.3	27.7	4.0	22.2	4.1	31.6	3.8	49.7	11.5
L. decidua (%)	no	-	12.0	0.1	7.9	0.0	12.4	0.9	2.5	0.6
	yes	10.7	12.5	0.3	8.4	0.8	13.0	1.0	4.6	1.2
P. abies (%)	no	-	43.2	0.1	21.5	0.1	36.8	0.7	2.2	0.2
	yes	38.5	39.8	3.0	18.2	2.2	32.7	3.1	2.7	0.2
Q. petraea (%)	no	-	0.1	0.0	0.9	0.0	0.4	0.2	16.3	7.1
	yes	<0.1	0.1	0.0	0.7	0.1	0.6	0.3	15.8	5.9
Q. robur (%)	no	-	0.1	0.0	0.5	0.0	0.3	0.1	4.6	1.3
	yes	<0.1	0.1	0.0	0.5	0.0	0.4	0.2	6.6	1.9
Other tree species (%)	no	-	6.7	0.0	21.8	0.0	8.6	0.3	5.2	0.5
	yes	8.6	16.3	7.0	42.1	8.7	17.7	6.2	16.9	6.6

Table 3. Response of biodiversity indicators to disturbance and climate scenarios for the years 0, 100 and 1000 of the simulation. Mean and standard deviation (SD) are over averaged landscape values (i.e. average species number in the landscape) for the respective scenarios. Presented are richness levels for Araneae, Carabidae, Hemiptera, Hymenoptera, Mollusca, saproxylic beetles, Symphyta and Syrphidae, the effective tree species diversity (exp(H')) as well as the rumple index of forest canopy complexity

	Disturbance	Initial state	Baseline climate				Climate change			
		year 0	year 100		year 1000		year 100		year 1000	
		mean	mean	SD	mean	SD	mean	SD	mean	SD
Araneae	no	-	11.6	0.0	11.8	0.0	8.1	0.7	10.7	0.7
	yes	10.7	11.6	0.0	11.8	0.0	8.2	0.6	11.2	0.7
Canopy complexity	no	-	1.2	0.0	1.5	0.0	1.2	0.0	1.1	0.0
	yes	1.2	1.3	0.0	1.6	0.1	1.3	0.0	1.3	0.0
Carabidae	no	-	8.8	0.0	9.0	0.0	6.2	0.7	5.8	0.6
	yes	7.4	8.9	0.1	9.2	0.0	6.3	0.7	6.1	0.6
Ground vegetation	no	-	33.1	0.0	34.0	0.0	35.6	1.1	37.3	1.2
	yes	37.4	33.4	0.2	34.2	0.2	36.1	1.1	37.6	1.2
Hemiptera	no	-	33.4	0.0	39.5	0.0	43.7	0.9	43.9	4.9
	yes	37.8	37.3	2.6	46.1	2.8	48.8	3.5	52.3	6.7
Hymenoptera	no	-	25.6	0.0	26.3	0.0	129.4	8.2	123.0	7.7
	yes	37.5	26.0	0.3	26.7	0.3	132.7	8.6	127.2	8.4
Mollusca	no	-	10.1	0.0	11.9	0.0	32.7	1.2	38.9	1.3
	yes	12.0	10.3	0.2	12.1	0.1	33.5	1.3	38.9	1.3
Saproxylic beetles	no	-	48.0	0.0	49.9	0.0	25.9	2.4	32.1	1.2
	yes	44.5	48.1	0.1	49.8	0.0	26.0	2.3	33.5	1.2
Symphyta	no	-	11.4	0.0	10.9	0.0	19.7	0.5	14.7	2.0
	yes	14.8	12.2	0.5	12.3	0.6	21.3	1.1	17.8	2.6
Syrphidae	no	-	19.9	0.0	18.9	0.0	73.6	10.2	59.8	12.4

	yes	30.7	21.0	0.6	20.7	0.7	78.3	11.3	68.9	14.1
Tree diversity	no	-	3.1	0.0	5.7	0.0	3.4	0.1	2.8	0.3
	yes	2.5	4.1	0.6	7.4	0.5	4.6	0.7	5.0	1.2

DISTURBANCE EFFECTS ON BIODIVERSITY

While climate change impacts on diversity were ambiguous but strong for each indicator studied, the effect of disturbance was generally positive but less pronounced (Table 3, Fig. 3). Compared to a hypothetical trajectory omitting disturbances for the entire 1000-year simulation period, disturbances increased diversity in all indicators ($P<0.001$). Tree species diversity was affected most strongly by disturbance, followed by the species groups Symphyta, Hemiptera, Syrphidae as well as canopy structure. Increases in both disturbance frequency and severity were positively associated with all biodiversity indicators (Fig. 3). The opposite was the case for disturbance size, where an increase in the mean disturbance size was found to decrease biodiversity.

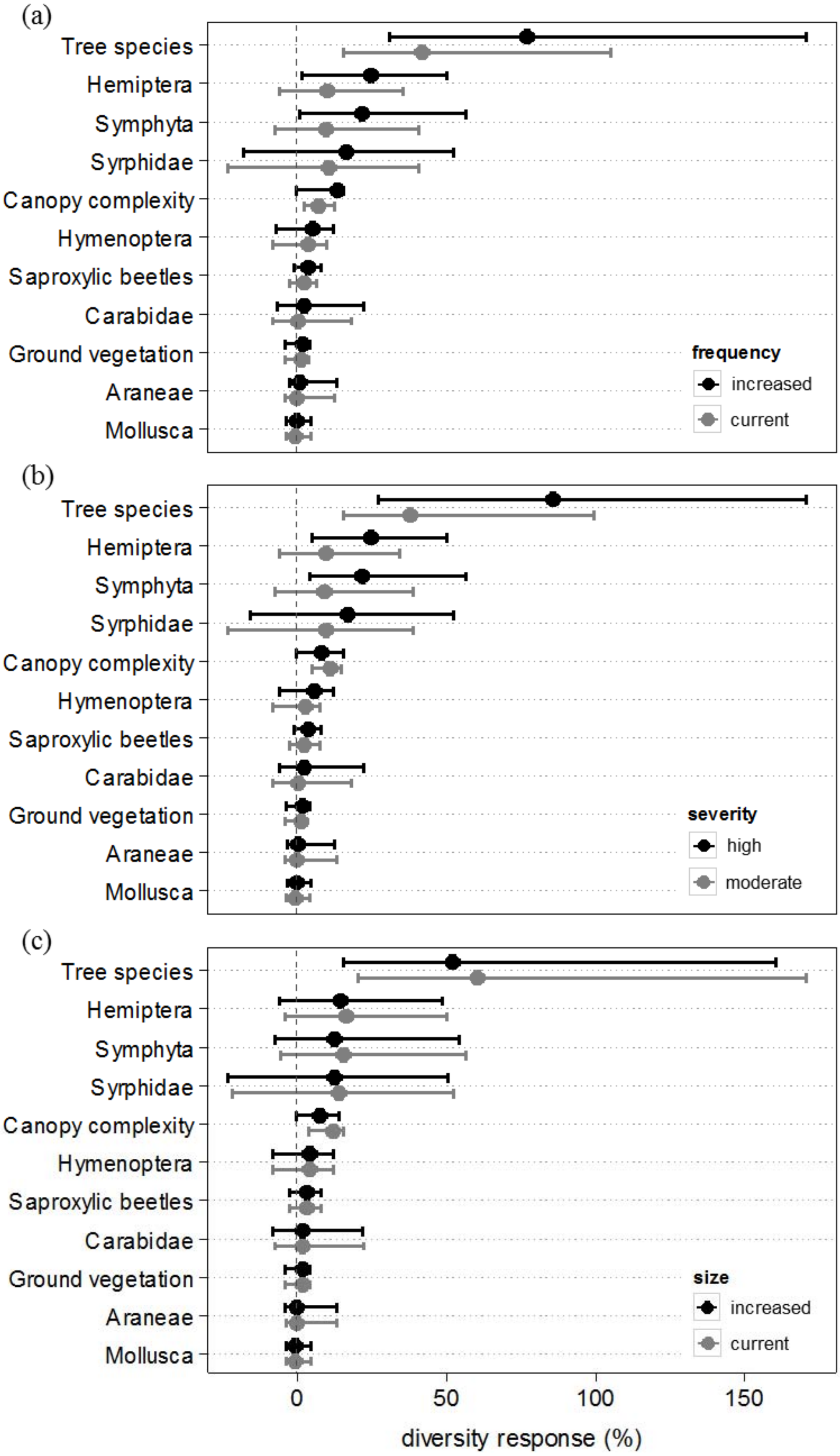
(a)
Tree species
Hemiptera
Symphyta
Syrphidae
Canopy complexity
Hymenoptera
Saproxylic beetles
Carabidae
Ground vegetation
Araneae
Mollusca
frequency
increased
current
(b)
Tree species
Hemiptera
Symphyta
Syrphidae
Canopy complexity
Hymenoptera
Saproxylic beetles
Carabidae
Ground vegetation
Araneae
Mollusca
severity
high
moderate
(c)
Tree species
Hemiptera
Symphyta
Syrphidae
Canopy complexity
Hymenoptera
Saproxylic beetles
Carabidae
Ground vegetation
Araneae
Mollusca
size
increased
current
0
50
100
150
diversity response (%)

Fig. 3. Response of biodiversity indicators to disturbance (a) frequency, (b) severity and (c) size relative to scenarios without disturbance (zero line) at the end of the 1000-year simulation period. Dots are median values and whiskers indicate the 95th percentile range across all scenarios. Positive values indicate an increase in diversity.

SHIFTS IN BIODIVERSITY HOTSPOTS

After 1000 years of simulation, areas identified as hotspots were substantially different when comparing baseline climate and climate change conditions (Fig. 4). While hotspots in the baseline climate scenario were mainly located at low to moderate elevation, climate change supported hotspots in higher elevation zones. The extent of hotspot area strongly decreased under changed climatic conditions ($P<0.001$). Without disturbance and climate change 17.2% of the landscape were hotspots (Fig. 4a), but only a heavily fragmented 0.1% remained under changed climatic conditions (Fig. 4c). Disturbance significantly increased the extent of hotspot areas ($P<0.001$), e.g. by 146.1% under baseline climate (Fig. 4b). Under future climate, the simulations resulted in a total hotspot area of at least 18.4% (Fig. 4d), of which 23.1% overlapped with current hotspots.

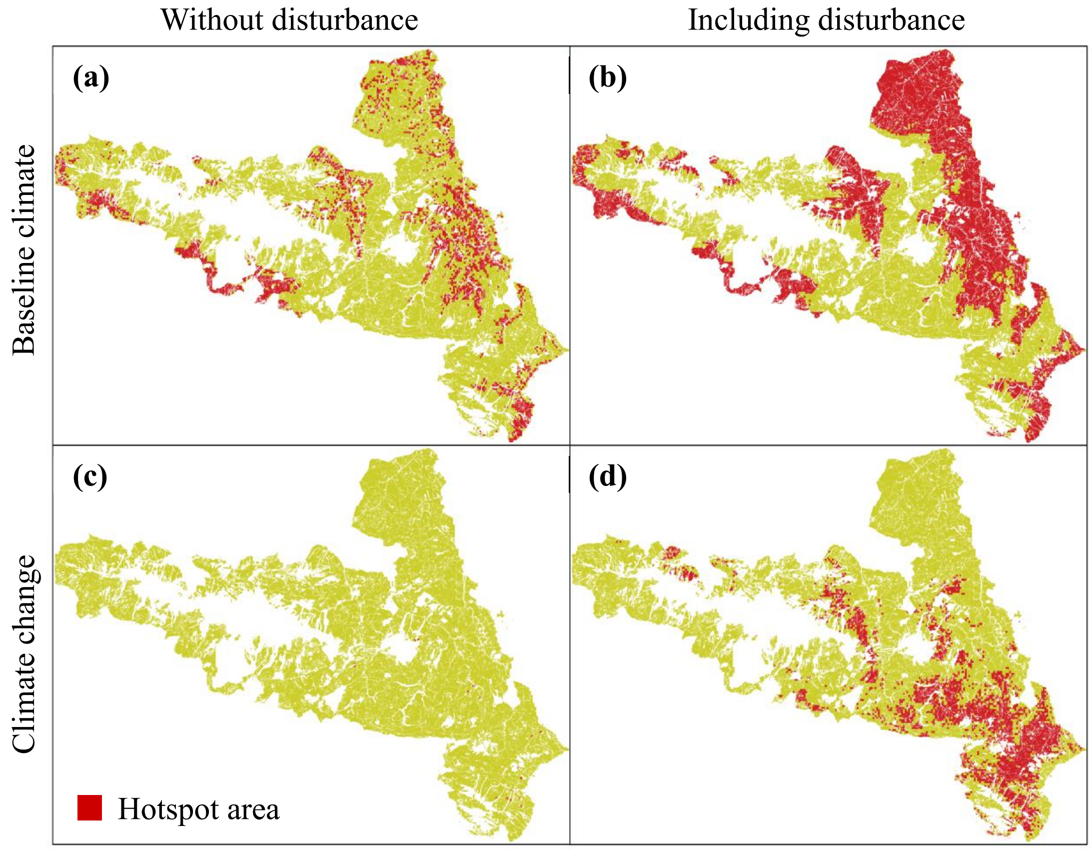

Fig. 4. Biodiversity hotspots of the Kalkalpen National Park after 1000 simulation years. Hotspots are defined as areas where each of the eleven biodiversity indicators studied here exceeds the 25th percentile of its value range.

Discussion

CONSEQUENCES OF CHANGES IN CLIMATE AND DISTURBANCE REGIMES

Based on findings of broad-scale assessments (e.g. Sala 2000; Thomas *et al.* 2004), we had hypothesized a decline in biodiversity in response to climatic changes for the KA-NP. However, our in-depth analyses revealed that climate change effects on forest biodiversity in mountain forest landscapes can be both positive and negative, depending on the indicator and species group assessed. This finding corroborates other studies showing divergent effects among taxonomic groups, and exemplifies the existence of considerable variation in local-scale biodiversity trends (see e.g. Bowler *et al.* 2015). The steep altitudinal gradient of the study landscape (> 1000 m) allows trees to migrate upward, tracking their suitable climate niche. Doing so, European beech increasingly occupies areas dominated by Norway spruce, while giving way to oak and hornbeam at lower elevations. From this setting emanates a specific climate change response in biodiversity, which does not necessarily mirror broad scale biodiversity trends, as species linked to overstorey tree species (e.g. saproxylic beetles associated with oak (Bergman *et al.* 2012)), mainly track the spatio-temporal shifts of these trees.

Another reason for the differentiated result of climate change impacts could be that many previous broad-scale studies have considered the direct effects of climate change only. While individual studies have already incorporated selected indirect climate change effects previously, such as modifications in seed dispersal and biotic interactions (e.g. Brooker *et al.* 2007) or changes in forest structure (e.g. De Frenne *et al.* 2013), here we applied a novel combination of simulation modelling and empirical climate–diversity relationships to comprehensively assess both direct and indirect impacts of climate change. While all species groups indicated a strong direct response to climate, indirect effects also had a distinctive effect on the trajectories of a number of species groups studied (e.g. Araneae, saproxylic beetles, see Fig. S4). In line with our initial hypothesis these indirect effects of climate change were considerably delayed, i.e. forest structure and composition reacted slowly to changes in climatic conditions, resulting in a delayed response of other species groups. Also direct climate change impacts could be delayed, an effect that was not accounted for here. As the species groups investigated here have relatively short life-cycles compared to the pace of climate change, a swift direct response to a changing environment can be assumed (see e.g. Danks 2004), and the lag of direct climate effects might be negligible in our study. Furthermore, our study does not consider biotic interactions within the investigated species groups or any associations with other species groups except trees (see e.g. Thuiller *et al.* 2015).

It is also important to note that the different definitions and focal indicators of biodiversity under consideration in different studies likely account for diverging reports on the climate change sensitivity of biodiversity. For ten out of eleven indicators we here used species diversity as a proxy for biodiversity. Other important aspects of biodiversity not considered here include the abundance of rare species (e.g. red list species) or endemic species (Engler, Guisan & Rechsteiner 2004), as well as the consideration of functional diversity (Thuiller *et al.* 2006) or phylogenetic diversity (Thuiller *et al.* 2011). Moreover, despite the fact that we studied eleven different biodiversity indicators spanning the plant and animal kingdoms it would be desirable to also include, for instance, vertebrate species such as mammals, birds, amphibians or reptiles (see e.g. Maiorano *et al.* 2013) in future assessments.

In contrast to climate change, disturbance had a clear positive effect on the investigated forest biodiversity indicators, supporting our initial hypothesis. This result is in line with a wide range of literature on the impacts of disturbance on biodiversity in forest ecosystems (Thom & Seidl 2015). However, we found different biodiversity responses for changes in the frequency, severity and size of disturbance. While the effect of an increase in disturbance frequency and severity was consistently positive, an increase in disturbance size reduced the positive disturbance effect on biodiversity. High disturbance severity and increasing frequency facilitate edges, and create a complex pattern of open areas and remaining closed canopy forests, increasing the variation in ecological conditions and habitats (Perry *et al.* 2011; Lehnert *et al.* 2013). An increasing disturbance size, however, homogenizes areas and reduces the forest edge density (Hansson 1994). Future changes in climatic conditions are expected to further intensify disturbance regimes in many ecosystems (Seidl *et al.* 2014; Millar & Stephenson 2015), and will thus exert an important indirect impact of climate change on forest biodiversity. Our study suggests that increasing disturbance frequency and severity (at current disturbance sizes) can compensate negative effects of climate change on selected biodiversity indicators (e.g. tree diversity). This underlines that future studies should take a dynamic and integrative perspective on the potential trajectories of biodiversity beyond correlative relationships with temperature and precipitation. The value of such a perspective is furthermore underlined by finding century-long lag times in biodiversity responses to climatic drivers (Menendez *et al.* 2006), and in dampening as well as amplifying feedbacks between direct and indirect influences of climate change.

IMPLICATIONS FOR CONSERVATION MANAGEMENT

Our study indicates that local hotspots of biodiversity can shift significantly under climate change, a fact that should be considered more explicitly in future conservation management. Spatio-temporal analyses as the one presented here can support future conservation planning and foster prospective allocation of resources in conservation management. To increase the robustness of conservation decisions under changing environmental conditions, efforts should focus particularly on areas that are hotspots under both current and changed climatic conditions (see also Rose & Burton 2009). However, it also has to be noted that there are pronounced differences between different hotspot definitions (see Fig. S4), which underline remaining uncertainties in this regard. In the case of the KA-NP, robust hotspots are located in the central and eastern reaches of the park at low to mid elevations in both variants investigated.

Furthermore, addressing a wide range of species groups explicitly is important for conservation management to identify biota particularly at risk from climate change. Based on our analyses these include Araneae, Carabidae and saproxylic beetles at the KA-NP. As tree species diversity was also found to decrease, and many phytophages are host-dependent (Brandle & Brandl 2001), a wide range of indicators might benefit from a coarse filter conservation approach aiming to maintain a diverse forest tree composition. Furthermore, migration corridors as well as temporal connectivity of hotspots on the landscape can help to maintain species threatened by climate change at the regional scale (Fischer, Lindenmayer & Manning 2006). These corridors should be designed particularly to connect current and future hotspots of biodiversity to allow species to relocate in response to changing climatic conditions.

Our findings of positive disturbance impacts on biodiversity underline that intensifying disturbance regimes are congruent with the goals of biodiversity conservation in Central European forests. It is important to note, however, that this positive effect of disturbances can be strongly reduced or even offset by measures such as salvage logging and homogenizing disturbed areas (Lindenmayer & Noss 2006), which is current standard practice in the managed forest ecosystems of Central Europe. For example, the richness of saproxylic beetles as well as wood-inhabiting fungi has been found to increase after disturbance events, but decreased severely when areas were salvage-logged (Thorn *et al.* 2014; Thorn *et al.* 2015). Furthermore, such interventions that are usually performed using heavy machinery compact soils, and consequently reduce soil fauna and microflora (Marshall 2000). In the light of the importance of biodiversity for the adaptive capacity and response diversity of ecosystems (Mori, Furukawa & Sasaki 2013), a more differentiated perspective on disturbance might be necessary in order to ensure the resilience of forest ecosystems in a rapidly changing world.

Acknowledgements

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Data accessibility

The data used in this study are archived in the Dryad Digital Repository http://dx.doi.org/10.5061/dryad.2d6h4 (Thom *et al.* 2016). Additional information on the individual-based forest landscape and disturbance model used in this study can be found on the iLand homepage: http://iland.boku.ac.at/

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Fig. S1. Productivity tests.

Fig. S2. Climate sensitivity test.

Fig. S3. Potential natural vegetation test.

Fig. S4. Additive approach for biodiversity hotspots.

Appendix S1. Initial conditions and drivers add-on.

Table S1. Coefficient of variation of replicates in each scenario for each biodiversity indicator studied at the end of simulation period.

Table S2. Local sensitivity analysis of the empirical species diversity models to changes in climate and tree vegetation.

Supporting Information

INITIAL CONDITIONS AND DRIVERS ADD-ON

Soil

Soil data were derived from inventory plots distributed over the national park on a regular 300 m × 300 m grid. 710 and 688 inventory plots were used to develop statistical models for soil depth (Fig. 1) and soil type (Fig. 2), using linear and logistic regression respectively (Kobler 2004). These relationships were subsequently used to derive wall-to-wall estimate of these parameters for the landscape. Surveys on soil texture (N=622) were aggregated by soil type and resampled for the whole landscape. Plant available nitrogen values were derived from a dataset previously developed for the grid of the Austrian National Forest Inventory (Seidl, Rammer & Lexer 2009), and were imputed to the study area by a stratified sampling over ecoregion, elevation, soil depth, aspect and slope (N=557).

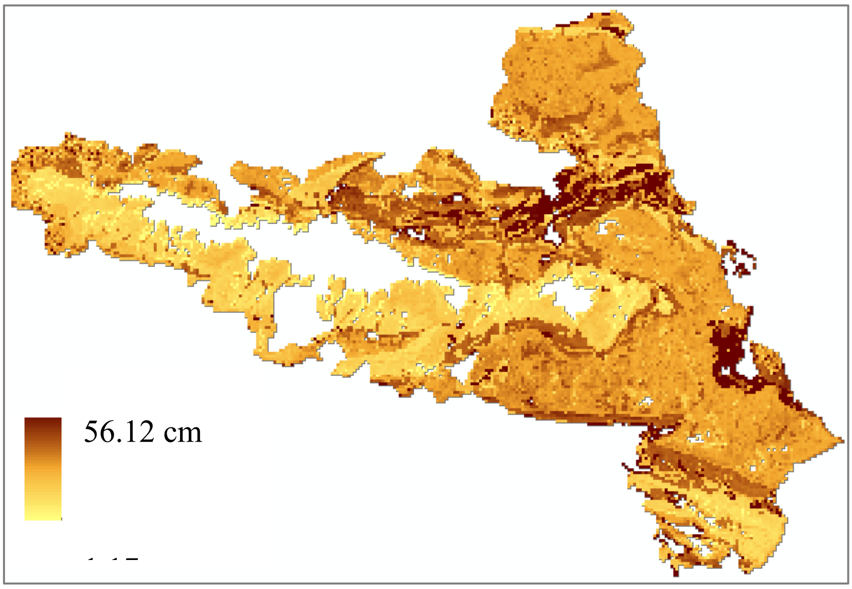

Fig. A1. Effective soil depth according to Kobler (2004).

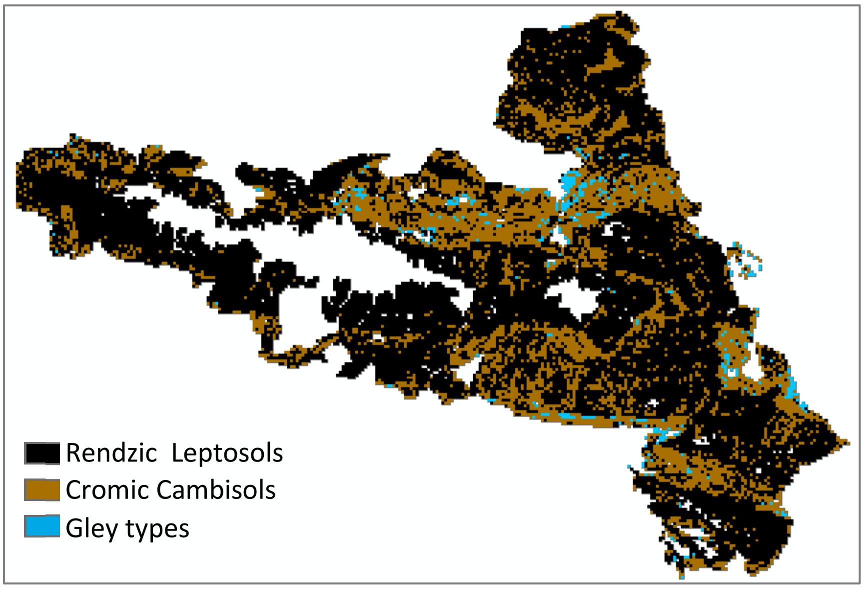

Fig. A2. Soil types according to Kobler (2004).

Climate

The years 1950 – 2010 were selected as the baseline for the analysis of climate change effects (reference period, see examples for climate input parameters in Fig. 4 and Fig. 5). Three regionally downscaled climate change scenarios, representing different combinations of global and regional circulation models under A1B forcing, were studied: CNRM-RM4.5 (Radu, Déqué & Somot 2008) driven by the global climate models (GCM) ARPEGE and MPI-REMO (Jacob 2001) as well as ICTP-RegCM3 (Pal *et al.* 2007) driven by the GCM ECHAM5. Climate changed transiently in these scenarios until the end of the 21st century (temperature change of between 3.1°C and 3.3°C, and precipitation change of between –89 mm and + 141 mm in 2080 – 2099 relative to the baseline period). A stabilization of climate conditions at the level of 2080 – 2099 was assumed for the years beyond 2100.

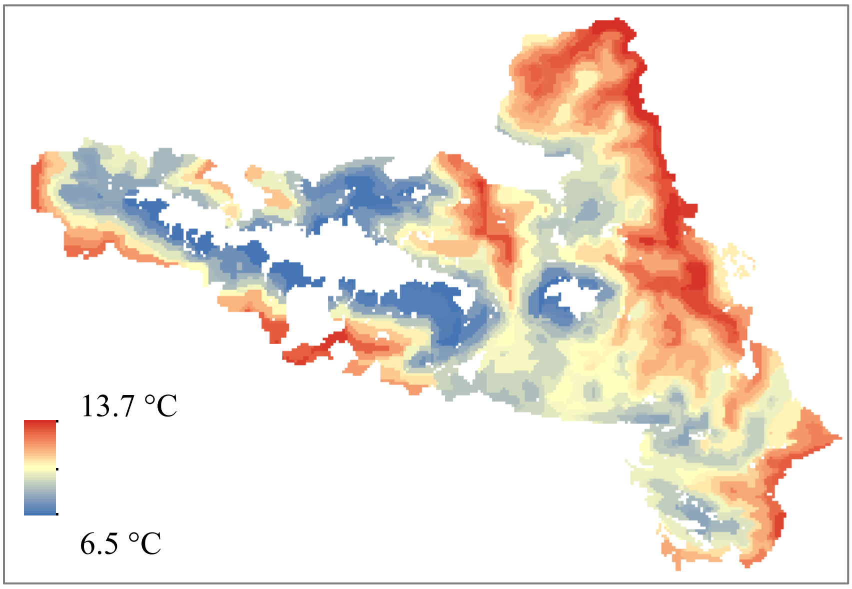

Fig. A3. Mean maximum temperature under baseline climate conditions.

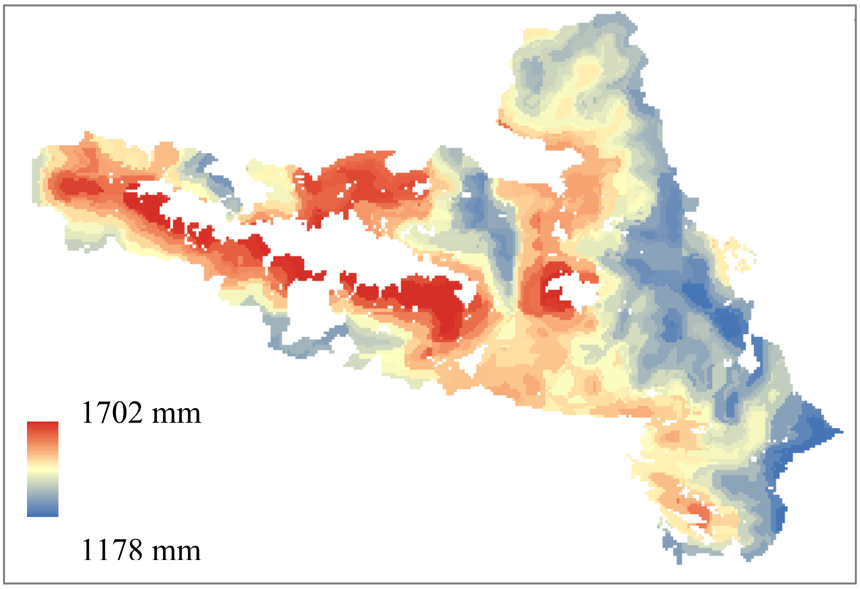

Fig. A4. Annual precipitation sum under baseline climate conditions.

Vegetation

Information on current vegetation was derived via integrating various data sources. First, we defined stand polygons (median stand size: 1.4 ha) based on aerial photo analysis with rough estimates for tree species composition. Then we used terrestrial inventory data (N=1,122) to refine tree species composition as well as to derive diameter at breast height (dbh) and the number of trees per ha within each stand polygons. To establish stand age we used information from forest inventory and planning data. Airborne LiDAR (light detection and ranging) was improved by forest inventory data to estimate tree heights of forest stands (Fig. 6). LiDAR and forest inventories were further used to derive the stockable area within a stand (i.e. based on these data sources, we excluded areas on a 10 m × 10 m where trees cannot grow, for example due to rocks on these areas). LiDAR data also served to determine the position of trees for initialization of the simulation model (i.e. we did not assume a uniform distribution of trees over the stands, but accounted for gaps and lumps of trees within the stands). Altogether, we initialized more than 2 10^6 trees from 17 different species on an area of 13.865 ha. All these data sources pertained to the end of the 1990s or early 2000s, and were combined to determine the state of tree vegetation at KA-NP in the year 1999.

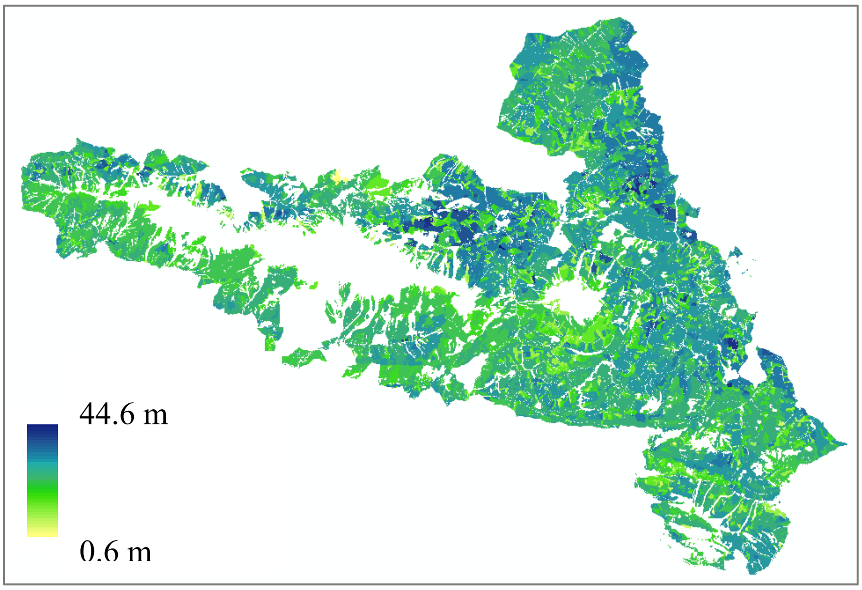

Fig. A5. Dominant tree height within stand polygons.

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