



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

Mountain forest management under changing climate and disturbance regimes

Dissertation

To obtain the doctoral degree (*Dr.nat.techn.*)
at the
University of Natural Resources and Life Sciences
Vienna

DI Julius Johannes Sebald

Institute of Silviculture
Department of Forest- and Soil Sciences

Supervisor: Prof. Dr. Rupert Seidl

***Nothing in life is to be feared, it is only to be understood.
Now is the time to understand more, so that we may fear less.***

Marie Curie

Table of contents

Abstract.....	4
Zusammenfassung.....	5
1 Introduction	7
2 Material and Methods.....	10
2.1 Study Area	10
2.2 How have human and natural disturbances changed in the forests of Austria over the last thirty years (1986-2016)?.....	11
2.2.1 Forest disturbance map.....	11
2.2.2 Structured interviews and field work	13
2.2.3 Landscape metric.....	14
2.3 What are the consequences of changing forest disturbance regimes for the protective function of mountain forests in Austria?	14
2.3.1 Natural hazard database	14
2.3.2 Disturbance regime characterization	15
2.3.3 Bayesian model.....	16
2.4 What can forest managers do to buffer the impacts of changing climate and disturbance regimes?.....	16
2.4.1 Simulation models.....	17
2.4.2 Experimental setup	17
2.4.3 Analyses	18
3 Results.....	19
3.1 How have human and natural disturbances changed in the mountain forests of Austria 1986-2016?	19
3.2 What are the consequences of changing forest disturbance regimes for the protective function of mountain forests in Austria?	19
3.3 Can tree species diversity buffer the impacts of changing climate and disturbance regimes?.....	20
4 Discussion.....	21
4.1 Changing climate and disturbance regimes: a societal and not an ecological problem.....	21
4.2 Mapping and attributing forest disturbances from Landsat data.....	21
4.3 The importance of a landscape perspective for forest scientists and managers	23
4.4 Remote sensing and evidence-based forest management	24
4.5 Computer simulation experiments are complementary to retrospective remote sensing research	25
4.6 Suggestions for management.....	26
5 Acknowledgements	29
6 References.....	30
7 Appendix	43

Abstract

Mountain forests are, compared to forests in the lowland, more exposed to changing climate and increasing disturbances. At the same time, reliable data quantifying the ongoing changes in mountain forests and their consequences for human well-being are missing. These data, however, are necessary to develop appropriate forest management strategies for the future. Covering a broad range of environmental conditions and methods, this thesis provides answers to the following three questions: How have human and natural disturbances changed in the mountain forests of Austria over the last thirty years (1986-2016)? What are the consequences of changing forest disturbance regimes for the protective function of mountain forests in Austria? What can forest managers do to buffer the impacts of changing climate and disturbance regimes? In the first chapter I developed methods to map human and natural disturbances from Landsat satellite data and subsequently quantify changes in Austria's disturbance regimes over the last thirty years. I found that human and natural disturbances can be separated on the basis of the spatial and temporal patterns they create on the landscape (i.e., their spatial and temporal autocorrelation). Further, I estimated that increases in Austria's disturbance rates from 1986 to 2016 were primarily driven by natural causes with wind disturbances increasing by 408% and bark beetle disturbances increasing by 99%. In the second chapter, I assessed the consequences of changing disturbance regimes on the protective function of mountain forests against torrential hazards (i.e., debris flow and flood). I showed that torrential hazard risk decreases with increasing forest cover on the landscape and presented evidence that the disturbance regime of a watershed strongly influences the probability of torrential hazards. Specifically, frequent and large disturbances are strongly detrimental for the protective function of mountain forests. In the third chapter, I employed simulation modelling to test the effects of increasing tree species diversity at different spatial scales (tree = alpha diversity, stand = beta diversity, landscape = gamma diversity) on disturbance impacts under various climate scenarios. I showed that increasing tree species diversity generally reduces disturbance impacts, in particular in conifer-dominated mountain landscapes. Further, I showed that mixing tree species between stands (i.e., increasing beta diversity) is at least as effective as mixing tree species within forest stands (i.e., increasing alpha diversity). This thesis contributes to the development of forest management strategies that foster the integrity of mountain forest ecosystems and their ability to provide ecosystem services to humans in times of rapid environmental change.

Zusammenfassung

Gebirgswälder sind, verglichen mit Wäldern des Flachlandes, stärker vom Klimawandel betroffen, trotzdem fehlen zuverlässige Daten die die aktuellen Veränderungen quantifizieren und deren Konsequenzen abschätzen. Eine solide Datengrundlage ist aber unerlässlich um Strategien zu entwickeln die dabei helfen, dass Gebirgswälder ihre vielfältigen Ökosystemleistungen auch in Zukunft erbringen können. Basierend auf einer großen Vielfalt naturräumlicher Gegebenheiten und Methoden liefert diese Arbeit Antworten auf die folgenden drei Fragen: Wie haben sich menschliche und natürliche Störungen in den österreichischen Gebirgswäldern über die letzten dreißig Jahre (1986-2016) verändert? Was sind die Konsequenzen veränderter Störungsregime für die Schutzfunktion der österreichischen Gebirgswälder? Wie kann die forstliche Bewirtschaftung reagieren um die Auswirkungen von Klimawandel und sich ändernden Störungsregimen abzufedern? Im ersten Kapitel entwickelte ich Methoden, die es erlauben menschliche (Holznutzung) und natürliche (Windwurf oder Borkenkäferbefall) Störungen aus Landsat Satellitendaten zu kartieren und so die Entwicklung von Störungen in Österreich über die letzten dreißig Jahre zu quantifizieren. Ich fand heraus, dass sich menschliche und natürliche Störungen anhand der räumlichen und zeitlichen Muster die sie auf Landschaftsebene erzeugen (i.e., räumliche und zeitliche Autokorrelation) unterscheiden lassen. Darüber hinaus konnte ich zeigen, dass die Zunahme der Störungsraten in Österreich über die letzten dreißig Jahre hauptsächlich von natürlichen Störungen getrieben war. Störungen durch Wind haben in Österreich von 1986 bis 2016 um 408% zugenommen, Störungen durch Borkenkäfer um 99%. Im zweiten Kapitel habe ich den Einfluss der Waldausstattung und des Störungsregimes von Wildbacheinzugsgebieten auf die Wahrscheinlichkeit von Muren und Hochwasser untersucht. Die Daten zeigen, dass die Wahrscheinlichkeit eines Wildbachereignisses mit zunehmender Waldbedeckung eines Einzugsgebietes abnimmt. Gleichzeitig zeigte sich, dass Störungen die Wahrscheinlichkeit von Wildbachereignissen deutlich erhöhen können. Die höchste Wahrscheinlichkeit von Wildbachereignissen wurde in Einzugsgebieten festgestellt, die regelmäßig von großflächigen Störungen betroffen sind. Im dritten Kapitel testete ich Bewirtschaftungsstrategien um die Anfälligkeit von Wäldern gegenüber Störungen zu reduzieren und so die Stabilität von Wäldern zu erhöhen. Ich untersuchte die Störungsanfälligkeit von Baumartenmischungen auf verschiedenen räumlichen Ebenen (Einzelbaumebene = alpha Diversität, Bestandsebene = beta Diversität, Landschaftsebene = gamma Diversität) unter zukünftigen Klima- und Störungsszenarien. Es zeigte sich, dass Wälder mit zunehmender Baumartendiversität grundsätzlich widerstandsfähiger gegenüber Störungen werden, insbesondere in nadelholzdominierten Hochgebirgslandschaften. Darüber hinaus stellte ich fest, dass Baumartendiversität auf Bestandesebene (i.e., beta Diversität) die Störungsanfälligkeit von Waldlandschaften mindestens gleichwertig reduziert wie Baumartendiversität auf

Einzelbaumebene (i.e., alpha Diversität). Die vorliegende Arbeit trägt zur Entwicklung von zukunftsfähigen Bewirtschaftungsstrategien für Gebirgswälder bei, um deren Integrität und Fähigkeit Ökosystemleistungen bereitzustellen in Zeiten rapider Umweltveränderungen zu erhalten.

1 Introduction

Mountain forests are important to human society globally. Forests cover one third of the global land area (i.e., 3,999 billion hectares, Keenan et al., 2015) of which 23% can be found in mountainous regions (Kapos et al., 2000). Mountain forests protect humans against natural hazards (Bebi et al., 2009; Buma and Johnson, 2015; Casteller et al., 2018; Moos et al., 2017), purify drinking water (Abildtrup et al., 2013; Mapulanga and Naito, 2019), store high amounts of carbon (Erb et al., 2018; Nabuurs et al., 2008), and provide natural resources such as timber (Maroschek et al., 2015). Mountain forests are on average older than low elevation forests, are often in very natural conditions and harbor high levels of biodiversity (Hilmers et al., 2018; Kulakowski et al., 2017).

Mountain forests are, compared to forests in the lowland, more exposed to climate change and increasing disturbances. Globally, the rate of temperature change in mountain regions is higher than in lower elevations (Pepin et al., 2015). In the European Alps mean annual temperature has increased by 2 °C over the last century, which is twice as much as the rest of the northern hemisphere (Auer et al., 2007). At the same time the high amount of old and tall trees makes mountain forest ecosystems less resistant to disturbances such as wind-throw (Bebi et al., 2017; Kulakowski and Veblen, 2002) and bark beetle infestation (Kärvemo et al., 2014) which can, due to higher temperatures, expand their habitat to higher elevations (Jakoby et al., 2019; Netherer et al., 2001). While being at high risk of disturbance, the resilience (i.e., the ability of a system to return to its initial state after a perturbation, Nikinmaa et al., 2020) of mountain forests is often limited: Short vegetation periods and harsh environmental conditions in combination with a limited tree species pool can result in very long recovery trajectories (Senf et al., 2019). Under very intense perturbation, these circumstances can cause irreversible changes in the structure and species composition of mountain forests over the upcoming decades (Albrich et al., 2020).

Various studies indicate that forest disturbance regimes in Europe are changing. Early signals of increasing disturbances in Europe were found in 2003 (Schelhaas et al., 2003). More recent remote sensing studies quantified a doubling of disturbance rates for Central Europe from 1986 to 2016 (Senf et al., 2018a) and lately, highest disturbance rates of the past thirty years were attributed to the year 2018 (Senf et al., 2021). While there is clear evidence for changing disturbance regimes in Europe, identifying the drivers behind the observed changes remains challenging. Ecologically defined, disturbances are relatively discrete events in time that disrupt the structure of an ecosystem, community or population and change resource availability (Pickett and White, 1985). As such, forest disturbances include natural processes (e.g., wind-throw and bark beetle outbreaks) as well as human resource use (i.e., timber

harvest). Attributing the observed changes in disturbance activity to either human or natural agents is challenging, as remote sensing methods for separating human and natural disturbances in close spatial and temporal interaction (as it is often the case in Central Europe) are missing. Yet, for forest managers it makes a great difference whether the observed changes are a result of elevated human resource use (and thus a result of active decision making) or a result of increasing natural disturbances (which happen unplanned). In the context of changing disturbance regimes, separating individual agents of disturbance in remote sensing data is the missing link between basic ecological research and applied questions of forest management in Central Europe. Therefore, the first chapter of this dissertation develops methods for separating human and natural disturbances based on Landsat data and investigates to what extent the observed changes in disturbance activity are a result of elevated timber harvest or increasing natural disturbances (i.e., wind-throw and bark beetle outbreaks).

Changing disturbance regimes might impact ecosystem service provisioning, especially the protective function of mountain forests. There is general agreement that forest disturbances can affect the provision of ecosystem services to human societies negatively (e.g., Hlásny et al., 2021; Thom and Seidl, 2016). In mountainous regions, one of the most important ecosystem services is the protection of humans and their infrastructure (houses, roads, railways etc.) against natural hazards (Bradshaw et al., 2007; Brang et al., 2006; Dorren et al., 2004; Moos et al., 2018). Intact forests on steep slopes hold back rockfall (Moos et al., 2017) and avalanches (Feistl et al., 2014; Zurbriggen et al., 2014). Their root systems reinforce the soil and thus increase slope stability (Moos et al., 2016; Scheidl et al., 2020). Disturbances, however, reduce forest cover and – in theory – consequently reduce the protective function of forests in mountain areas. For torrential hazards (i.e., floods and debris flow in steep headwater catchments) the data supporting this relationship is, however, poor. The currently available evidence on the effects of forest cover and disturbance on torrential hazard probability largely stems from local case studies (Brardinoni et al., 2003; Imaizumi et al., 2008; Nyman et al., 2015) and consistent large-scale investigations are missing. To guide forest policy and management decisions, however, generalizable results over extended spatial and temporal scales are necessary. In the second chapter of this dissertation I thus collect data on disturbances and torrential hazards for 10,885 watersheds in Austria. These data allow to investigate how the forest cover of a watershed influences the occurrence of torrential hazards and which disturbance regimes are most detrimental for the protective function of mountain forest in the European Alps.

As disturbances are changing and these changes might impact human well-being, forest managers need appropriate strategies and management approaches for the future. Buffering the already observed and still expected changes in climate and disturbance regimes to

safeguard ecosystem service provisioning is the responsibility of forest ecosystem managers (Seidl, 2014; Seidl et al., 2016b). In the face of great uncertainty regarding future environmental conditions and societal demands, it has been shown that increasing diversity, both regarding forest structure and tree species, is a potent management goal to ensure ecosystem service provisioning of forests (Messier et al., 2015; Silva Pedro et al., 2016; van der Plas et al., 2018). Yet, the implementation of such concepts in operational forest management raised unresolved issues. In particular the question which spatial grain of mixture is most beneficial for robust and stable forests under changing environmental conditions could not be answered yet. Tree species can be mixed on the tree level (alpha diversity), on the stand level (beta diversity) and on the landscape level (gamma diversity) but disentangling the effects of the spatial grain of mixture is difficult. This is because a systematic and consistent investigation calls for extended observation periods (50 – 100 years) and experimental sites with large spatial extent (stand to landscape scale). Therefore, traditional ecological research approaches such as field experiments are impossible due to resource limitations. In the third chapter of this dissertation, I employ two computer simulation models to investigate the effects of tree species diversity under a variety of climate and disturbance regimes. In particular I investigate relationships between tree species diversity, spatial configuration and disturbance impact on the landscape scale.

In summary, the three main research questions of this dissertation are:

- I. How have human and natural disturbances changed in the forests of Austria over the last thirty years (1986-2016)?
- II. What are the consequences of changing forest disturbance regimes for the protective function of mountain forests in Austria?
- III. Can tree species diversity buffer the impacts of changing climate and disturbance regimes? Specifically, what are the effects of tree species diversity at different spatial scales (tree = alpha, stand = beta, landscape = gamma) on disturbance impacts?

2 Material and Methods

This dissertation consists of three papers that are thematically connected and follow a logical flow. The three papers are presented in logical not chronological order since the order of publication is different to the logical order. Paper I (published 2021, Appendix A) is a remote sensing study that lays the empirical groundwork necessary to answer the applied questions of Paper II and Paper III. Paper II (published 2019, Appendix B) combines remote sensing methods with statistical modelling to answer questions related to the protective function of forests in mountainous regions. Paper III (published 2021, Appendix C) is methodological different as the results are based on process-based forest simulation modelling, allowing to investigate potential future trajectories of mountain forests.

2.1 Study Area

All research related to this dissertation was conducted in the European Alps. The European Alps are an east-west running mountain range located in Central Europe. The highest peak (Mount Blanc) is 4,810 m in elevation and the tree line is usually located between 1,800 to 2,300 m (Gehrig-Fasel et al., 2007). The Alps are globally one of the most densely populated mountain ranges, with 14 million permanent residents distributed over 8 countries (Perlik et al., 2001). Almost one third (29%) of the European Alps lie in Austria (Statista.com, 2021), the country where the majority of the research related to this dissertation was conducted. For Central Europe (i.e., Austria, Germany, Poland, Czechia, Slovenia, Slovakia, Hungary) Austria is a very representative study area. According to the forest type classification of the European Environmental Agency six out of the ten Central European forest types occur in Austria (EEA, 2006) and especially the two most frequent (*Hemiboreal forest and nemoral coniferous and mixed broadleaved-coniferous forest* and *Alpine coniferous forest*) account for 89 % of Austria's forest area. Further, the disturbance regime of Austria in terms of patch size and frequency is comparable with other Central European countries (Senf and Seidl, 2021a). Similar to other Central European countries the majority of the forest area (63%) is managed for timber production (BMLRT, 2021) and considerable parts of the forest area are under private ownership (UNECE/FAO, 2009). This makes Austria an ideal study area for investigating forest related questions relevant for Central Europe. Paper I and Paper II investigate the entire forest area of Austria (~4.0 million hectares) whereas Paper III simulates forest development in two landscapes (both ~1,000 hectares in size), one located in Eastern Austria and one located in Switzerland.

2.2 How have human and natural disturbances changed in the forests of Austria over the last thirty years (1986-2016)?

In the first chapter of this dissertation I investigated if and how forest disturbances have changed in Austria over the last thirty years. I attributed patches of an existing forest disturbance map to the three most important disturbance agents in Austria: timber harvest, wind-throw and bark beetle infestation. Subsequently, I analyzed the spatial and temporal patterns of the three disturbance agents and investigated their development in space and time from 1986 to 2016. I gathered reference data conducting structured interviews with forest managers and fieldwork. Further I developed a new metric describing the landscape context of a disturbance patch. I here briefly introduce the main methodological cornerstones of this study, details can be found in the Appendix A.

2.2.1 Forest disturbance map

I used an existing European forest disturbance map (Senf and Seidl, 2021a). The map is based on data of the Landsat satellite family. Landsat satellites are moderate resolution earth observation satellites that fly in an altitude of 705 km over the earth's surface (NASA, 2021). Landsat satellites take images with a size of 185 x 170 km and circle the earth every 16 days. The first Landsat satellite reached its orbit in 1972 and was equipped the Multispectral Scanner (MSS) sensor. This sensor provided data with a spatial resolution of 90x90 m. Since 1983, with the start of Landsat 4, Landsat satellites have sensors that provide images with a spatial resolution of 30x30 m. Landsat 4 and 5 used the Thematic Mapper (TM) as sensor which served in an improved version as Enhanced Thematic Mapper Plus (ETM+) also on Landsat 7. Landsat 8 uses the Operational Earth Imager (OEI) as sensor which provides data also in a spatial resolution of 30x30 m. Unfortunately, there is almost no data for the year 1983 available and disturbances in the first and last two years of a time series are very difficult to detect, thus the disturbance analysis of this dissertation cover the years 1986 to 2016.

The technical details on how forest disturbances can be mapped from Landsat data are extensively described in the corresponding literature (Cohen et al., 2010; Kennedy et al., 2018, 2010; Senf and Seidl, 2021a), however I want to briefly illustrate the basic idea behind this method. The sensors of the Landsat satellites scan the earth's surface and take images with a spatial resolution of 30x30 m. These images are measurements of the earth surface reflectance in seven spectral bands covering, for the human eye, visible and not visible wavelengths of the electromagnetic spectrum. Bands 1-3 measure the visible surface reflectance, (band 1 = blue, band 2 = green, band 3 = red), bands 4-7 measure the non-visible surface reflectance (band 4 = near infrared, band 5 = short-wave infrared, band 6 = thermal infrared, band 7 = short-wave infrared) (Boettinger et al., 2008). These data is openly available in the United States Geological Survey archive (Wulder et al., 2012). Specifically, for every

30x30 m pixel of the earth's surface there is data on the spectral reflectance (imagine as color value) from 1986-2016. In addition to the raw values, spectral indices can be calculated (i.e., quotients or products between values of different spectral bands). For the disturbance maps used in this dissertation, data of two spectral bands (shortwave infrared I and II) and two spectral indices (tasseled cap wetness and normalized burn ratio) were used. These data were filtered to the vegetation period (1st June to 30th September of every year) to exclude phenological changes in the spectral reflectance. Subsequently, it is possible to compare the spectral reflectance (or the spectral index) of a given pixel over multiple years and assess whether the reflectance has changed (for example because of disturbance). This can be done manually (see Cohen et al., 2010 for the method and Senf et al., 2021, 2018b for an application) or via a time series segmentation algorithm called LandTrendr (Kennedy et al., 2010). If the vegetation did not change, the spectral reflectance stays stable over the years. However, disturbances result in breaks or jumps of the spectral signal from one year to the other. Thus, the algorithm searches for these breaks and jumps in the spectral time series of a pixel. Subsequently, it splits the spectral time series of a pixel into linear segments of stable, decreasing or increasing surface reflectance. After this step a random forest classification algorithm is employed that classifies (based on the spectral reflectance and its change over time) each pixel into non-forest, disturbed forest and undisturbed forest. The segment with the greatest change (i.e., the disturbance event) is used to calculate the disturbance year and the particular pixel is marked with the disturbance year. After grouping pixels of the same disturbance year into disturbance patches, the result is a yearly map of all forest disturbances in the study area and over the time period of interest (see figure 1).

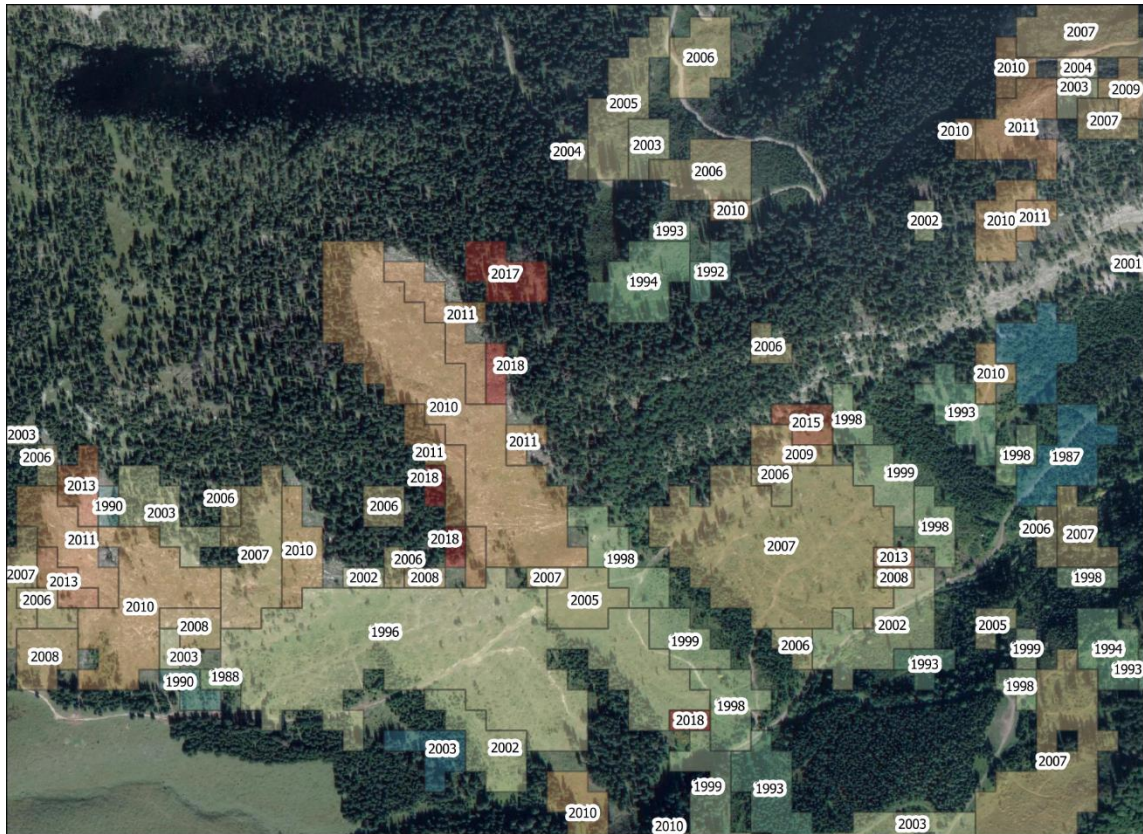


Figure 1: Example for a yearly forest disturbance map based on 30x30 m Landsat data and over multiple years. The map shows all forest canopy disturbances in a given region and for a given time period.

2.2.2 Structured interviews and field work

One of the biggest obstacles in the way of agent-based forest disturbance maps for Central Europe was missing reference data. To train an algorithm that is able to separate disturbance patches caused by humans from those that were caused by natural agents (i.e., wind, bark beetle), it is necessary to gather a reference data set with disturbance patches where the agent that caused the patch is known (Oeser et al., 2017; Schleeweis et al., 2020; Schroeder et al., 2011). However, gathering such a reference data set in Central Europe is difficult, because of obligatory salvage logging (every patch looks like a clear-cut in the end, Leverkus et al., 2018; Thorn et al., 2017), missing historical high-resolution imagery (limiting office-based approaches, Copass et al., 2018) and on average very small disturbance patches (generally complicating agent attribution (Senf et al., 2017a)). For this dissertation I thus made use of the intensive management of Central European forests and gathered reference data with the help of forest managers. I combined methods of qualitative GIS (Cope and Elwood, 2009), participatory mapping (Cadag and Gaillard, 2012; Chambers, 2006) and citizen science (Bonney et al., 2009; Dickinson et al., 2010) to utilize the knowledge of forest managers. I visited nine forest enterprises across Austria and conducted structured interviews with 21 foresters. During the interviews, the forest manager and I went through the disturbance map

and recorded the causal agent (i.e., harvest, wind-throw or bark beetle) of disturbance patches within the management district (1,000 – 5,000 ha in size) of the particular forest manager. Additional to the structured interviews I conducted field work in two Austrian national parks to extend the gradient of the reference data to unmanaged forests. There, I determined the causal agent of disturbance patches directly in the field analyzing the disturbance legacies of a patch (wind = root plates, uprooted trees, broken trees; bark beetle = standing deadwood, red crowns). With these two approaches I gathered reference data on 2,620 disturbance patches during one year.

2.2.3 Landscape metric

Human and natural disturbance agents in Central Europe interact strongly in very close spatial and temporal context, thus the forest ecosystems are coupled human natural systems (Liu et al., 2007; Senf et al., 2017a). Therefore, it was necessary to develop a new approach for separating human and natural disturbances based on Landsat data. I developed a metric that describes the spatial and temporal landscape context of any given disturbance patch. Specifically, I calculated the cumulative forest area in a given radius that was disturbed in the same year as the focal patch. In simple words, this metric describes whether a given disturbance patch is surrounded by many other patches of the same year or if the patch is surrounded by intact forest and/or disturbance patches from other years. The idea behind this approach is that natural disturbances usually happen as pulses of mortality (Senf and Seidl, 2018) while human disturbances create constant disturbance rates over time (White et al., 2017) and is based on the press-pulse dichotomy (Bender et al., 1984).

2.3 What are the consequences of changing forest disturbance regimes for the protective function of mountain forests in Austria?

In the second chapter of this dissertation I investigated the consequences of changing disturbances for the ecosystem service supply of mountain forests. In particular, I studied the effects of forest cover on the protective function of forests against torrential hazards (flood and debris flow). Further, I investigated how different forest disturbance regimes influence the probability of torrential hazards. The methods of chapter II are briefly explained in the following, details can be found in Appendix B.

2.3.1 Natural hazard database

The most important data for this study was the Austrian torrential event catalogue (Heiser et al., 2019; Hübl et al., 2008). This catalogue contains data on torrential hazard events that have happened for 10,885 watersheds distributed over Austria. From 1986 to 2018 3,768 torrential hazards events (2,646 floods and 1,112 debris flows) were recorded. Besides the event data,

the catalogue contains a shapefile of all watersheds in Austria. With this shapefile, a newly developed landcover map (Pflugmacher et al., 2019), a disturbance map (the prototype of the disturbance map described in section 2.2.1) and a digital elevation model I was able to characterize the forest cover and disturbance regime of every watershed, as well as its geographical and geomorphological characteristics. This allowed me to investigate the effects of forest cover and disturbance while controlling for other factors potentially influencing the occurrence of torrential hazards.

2.3.2 Disturbance regime characterization

To characterize the forest cover and disturbance regime I used a similar forest disturbance map as for the first chapter (see 2.2.1) but in an earlier version and created with slightly different methodology (for details see Appendix II). Since I was not able to distinguish between different disturbance agents at this point of my dissertation I characterized the disturbance regime of every watershed based on disturbance extent and disturbance type. The idea inspired the development of the landscape context indicator explained in the first chapter (see 2.2.3) and the approach is comparable. Disturbance extent is the cumulative forest area that was disturbed over the observation period (1986-2016). Disturbance type ranges from press to pulse (Bender et al., 1984) and is expressed as the Gini-Index of the annual disturbed forest area per watershed. A Gini-Index of zero (maximum equality) indicates a press disturbance regime with nearly constant disturbance rates over the years. A Gini-Index of 1 (maximum inequality) indicates a pulse disturbance regime with strongly varying disturbance rates over the years. The combination of disturbance extent and disturbance type allowed to characterize the disturbance regime of a watershed without knowing the agents at play (figure 2).

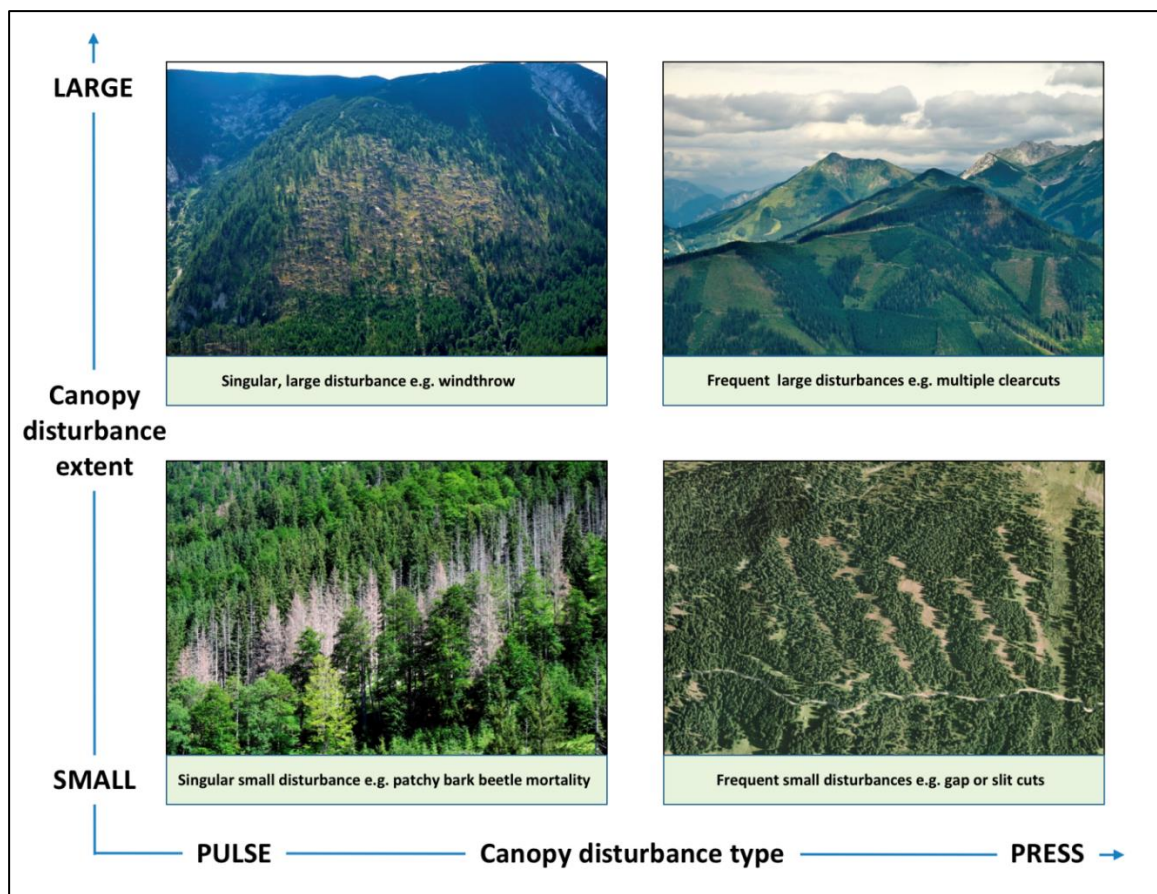


Figure 2: Conceptual figure how the disturbance regime of a watershed can be characterized based on the two indicators disturbance type and disturbance extent (Sebald et al., 2019). These metrics allowed to quantify the disturbance regime of a given watershed without knowing the agents at play.

2.3.3 Bayesian model

The third important methodological aspect that I want to briefly introduce is the statistical model that allowed to quantify the effects of forest cover and disturbance on the occurrence of torrential hazards. In essence the model applied is a generalized linear model that estimates the probability of occurrence (Bernoulli distribution) and the frequency (negative binomial distribution) of torrential hazard events on the watershed scale depending on a set of forest and disturbance related predictors, while controlling for general predisposing factors such as geography and geomorphology. Contrasting to frequentist approaches, however, model results and the effect of the individual predictors are expressed as posterior distribution and not as a point estimate.

2.4 Can tree species diversity buffer the impacts of changing climate and disturbance regimes?

The third chapter of my dissertation contributed to the development of future management strategies for mountain forests. While the first two chapters worked with retrospective

approaches the third chapter employed simulation modelling to investigate future trajectories of mountain forests in Central Europe. In the following I explain the two simulation models employed, the experimental setup and the analysis of the study.

2.4.1 Simulation models

I simultaneously employed two forest landscape models: iLand (Seidl et al., 2012) and LandClim (Schumacher et al., 2004). Both models were developed independently from each other to answer questions related to forest management, disturbances and climate change. Since all of these processes happen at scales larger than an individual stand (1-100 ha), the models simulate the dynamics of entire landscapes (1,000 ha – 100,000 ha). Compared to traditional methods of research in forest ecology (e.g., experiments, field work) simulation models allow for experimental setups that are impossible to realize with traditional methods (Seidl, 2017). While conducting field work or setting up controlled experiments is costly and time consuming, simulation models can – once parametrized and set up – efficiently implement replicated large-scale experiments over long time periods under fully controlled conditions. The models simulate the dynamics of existing landscapes by representing the topography, soil conditions and climate of a given landscape. The model is correctly parametrized once the existing forest structure and known ecological patterns can be reproduced. Examples for such patterns can be the potential natural vegetation of a landscape, the growth dynamics of trees or the change of tree species dominance along an elevational gradient (Honkaniemi et al., 2020; Thom et al., 2017b). Realistic ecological patterns indicate that interactions between topography, soil, climate and vegetation are well represented in the model (Grimm et al., 2005). Once the existing landscapes are set up, modifying parts of the system (e.g., climate, disturbances, forest management) while keeping the other parts constant (e.g., soil, topography, vegetation) allows to gain insights into emergent patterns and future trajectories of forest landscapes.

2.4.2 Experimental setup

I set up the experiment in two landscapes, strongly contrasting in their environmental conditions. The Rosalia landscape is a mid-elevation (374-728 m asl), broadleaved dominated landscape, whereas the Dischma landscape is a high elevation (1,545 - 2,738 m asl) conifer dominated landscape. The idea behind the experimental setup of the third chapter of this dissertation was to systematically investigate the effects of different levels of tree species diversity and configuration on disturbance impacts and temporal stability at the landscape scale. Specifically, I aimed at quantifying the effects of alpha, beta and gamma diversity independently from each other. I therefore divided the two landscapes in standardized 100 x 100 m stands and initialized four different levels of tree species diversity (gamma): no diversity

(1 species), low diversity (2-4 species), high diversity (5-8 species) and high+ diversity (9-10 species). For the alpha-diversity setup I mixed tree species within forest stands (i.e., at the level of individual trees), and for the beta scenario I created single species stands and mixed species between stands on the landscape scale. Subsequently, I exposed the landscapes to a sequence of standardized wind disturbance events over a 200-year simulation period. The whole experiment was replicated under three different climate scenarios (historic climate, representative concentration pathway (RCP) 4.5, RCP 8.5) to find out if effects vary with the intensity of climate change.

2.4.3 Analyses

I quantified disturbance impacts and temporal stability at the landscape scale. I calculated indicators of forest biomass (t ha^{-1}) and forest structure (number of trees $> 30 \text{ cm dbh ha}^{-1}$) over the entire landscape and every ten years of the simulation period (i.e., 20 time steps during a 200-year simulation period). To determine disturbance impacts for individual scenarios I compared landscape values for biomass and forest structure to a simulation run without any disturbances. The difference between the no-disturbance-simulation and the with-disturbance simulation is the disturbance impact. To assess temporal stability of forest biomass stocks and forest structure I calculated the variation (coefficient of variation) of forest structure and forest biomass over the 200-year simulation period.

3 Results

3.1 How have human and natural disturbances changed in the mountain forests of Austria 1986-2016?

I separated disturbances from timber harvest, wind-throw and bark beetle infestation in Austria with an overall accuracy of 63%. Disturbance patches caused by regular timber harvest (i.e., salvage logging not included) were most accurately attributed (producer's accuracy (PA) = 84.6%, user's accuracy (UA) = 67.7%), followed by wind disturbances (PA = 54.8%, UA = 63.0%). Bark beetle patches were most difficult to attribute (PA = 15.0%, UA = 30.6%) and were most often confused with disturbances caused by timber harvest. The newly developed landscape context indicator was key for an improved attribution of causal agents of disturbance as it improved prediction results by up to 26 percentage points. I found that natural disturbance caused by wind and bark beetles have strongly increased in Austria over the last thirty years. The disturbed area caused by wind disturbances increased by 408% and the area caused by bark beetle disturbances by 99% from the 20th (1986-2000) to the 21th (2001-2016) century. However, also disturbances caused by humans increased, yet the increase was not as strong as for natural disturbances (+43%). While the size of individual disturbance patches increased only moderately (wind = +8%, bark beetle = +14%, harvest = +13%), the frequency of disturbance events was the driving force behind the observed increase (wind = +355%, bark beetle = +77%, harvest = +26%).

3.2 What are the consequences of changing forest disturbance regimes for the protective function of mountain forests in Austria?

I modelled the probability of debris flows and flood events depending on 13 watershed attributes. Forest cover was found to be the most important watershed property that reduces the probability of torrential hazards. Specifically, increasing forest cover by 25% points above-average (i.e., from 63% to 88%) reduced the probability of a torrential hazard event by 8.7%. While intact forest cover strongly reduced the probability of torrential hazards, disturbances can decrease the protective function of forests. The probability of flood events was strongly determined by the frequency of disturbances in a watershed, but their extent did not play an important role. Hazard probability increased by 83% when moving from a pulse to a press disturbance regime. The probability of debris flow events was depended on both, disturbance frequency and disturbance size, with regularly occurring large disturbances being most detrimental for debris flow events. Given a press disturbance regime, the probability of a debris flow increased by 248% when moving from 10% (i.e., a disturbance rate of 0.32% year⁻¹) to 50% (i.e., a disturbance rate of 1.61% year⁻¹) of the watershed disturbed.

3.3 Can tree species diversity buffer the impacts of changing climate and disturbance regimes?

I simulated forest dynamics in two contrasting forest landscapes of Central Europe under different climate and disturbance regimes. Specifically, I investigated the effects of varying tree species diversity on disturbance impacts and temporal stability of forest structure and biomass stocks. I found that climate change will strongly increase the pool of potential species (gamma diversity), especially in the alpine landscape (Dischma). Further, I found a general pattern of increasing tree species diversity (gamma diversity) reducing the impacts of wind disturbances on the landscape scale. However, the susceptibility of a landscape to wind disturbances was primarily driven by the susceptibility of the tree species in place (species identity effect) and only to a lesser degree by the level of diversity itself. In simple words: adding a species that is susceptible to windthrow to a landscape that consists of less susceptible tree species will increase disturbance impacts even though tree species diversity increases. Lastly, I did not find a clear difference in disturbance impacts and temporal stability for within-stand mixtures (alpha diversity) and between stand mixtures (beta diversity). Based on the results of this chapter climate change will increase tree species diversity in alpine landscapes. Increasing diversity will reduce disturbance impacts only if the additional tree species are more resistant to wind disturbances than the species already at place, independent from their spatial configuration.

4 Discussion

4.1 Changing climate and disturbance regimes: a societal and not an ecological problem

Forests exist on the earth's surface since 400 million years (Wallace et al., 2017). Since their existence, forest ecosystems have experienced decline and recovery through periods of rapid environmental change (Petit et al., 2008). In Central Europe, the last big wave of forest extinction was marked by the Würm glaciation that lasted from 120,000 years before today to 11,700 years before today (Becker et al., 2017). During this time the Alps and Fennoscandinavia were glaciated and, except from small microrefugia, even in the lowlands no forest existed (Willis and Van Andel, 2004). Over the last 11,700 years, trees have recolonized Central Europe from their refugia in Southern and Eastern Europe. During the recolonization of Central Europe the tree species composition changed drastically several times because of climatic changes (Cheddadi et al., 2006). Forests are thus obviously able to adapt to environmental change. Trees as individuals, however, are immobile and consequently their ability to avoid environmental change through migration is limited. Forests as ecosystems adapt to environmental change through disturbance and recovery (Thom et al., 2017b). After a period of very stable environmental conditions in Central Europe, global mean annual temperature has increased by $\sim 1^{\circ}\text{C}$ over the last century (Hansen et al., 2019, 2006). In the European Alps increases were twice as high ($+2^{\circ}\text{C}$) as the global average (Auer et al., 2007). These changes constitute a fundamental habitat alteration during the life span of a tree, causing physiological stress and reducing vitality. Disturbances reset forest dynamics and the next generation of trees can, from the first day, adapt to the new environmental conditions. From an ecological point of view disturbances are thus elementary to ensure vital forest ecosystems in the future. From a societal point of view, however, it is uncertain if forests can fulfill the human demands of ecosystem services during this phase of reorganization and adaptation. Changing climate and disturbances are thus not an ecological but a societal problem. This dissertation contributes to the development of appropriate management responses to those upcoming challenges. It built scientific groundwork by developing remote sensing methods for investigating forest disturbances and disturbance change. Further it assessed potential consequences of these changes for human well-being. Lastly, it tested various management practices that might buffer the effects of changing climate and disturbance regimes.

4.2 Mapping and attributing forest disturbances from Landsat data

Already at the beginning of the 21th century researchers have pointed towards a potential increase in disturbances due to climate change (Dale et al., 2001) and increases in disturbed

timber volume for Europe have been reported (Schelhaas et al., 2003). These increases will likely continue during the 21st century with far reaching consequences on the carbon dynamics of European forests (Seidl et al., 2014b). However, all of these results were mainly based on grey literature records. The lack of consistent and reliable data on the continental to global scale made a rigorous assessment of disturbance rates and trends difficult.

The opening of the Landsat archive to the public in 2008 (Wulder et al., 2012) and subsequently the development of appropriate methods to analyze this large archive of consistent, global-scale earth observation data (Cohen et al., 2010; Kennedy et al., 2010) built the foundation for accurately quantifying forest disturbance regimes from space. Automatic disturbance detection algorithms were developed and global maps of forest loss followed (Hansen et al., 2013), yet these global analyses were limited to recent years (2000-2012) and reliable estimates on disturbance rates for Europe were still missing. Instead of automatically mapping disturbances, sampling individual Landsat pixels and manually interpreting their disturbance history advanced the quantification of disturbance rates and trends in the US (Cohen et al., 2010). Testing these methods in Europe (Sebold, 2018) allowed to quantify disturbance rates for Central Europe (Senf et al., 2018b) and finally the entire European continent from 1986 to 2018 (Senf et al., 2021).

All of these studies showed significant increases in disturbance activity for Europe, yet whether these increases were driven by human or natural causes remained disputed (Ceccherini et al., 2020; Klein and Hartmann, 2018; Palahí et al., 2021), because of persistent challenges in separating human and natural causes of disturbance based on moderate resolution satellite data (Palahí et al., 2021; Senf et al., 2017b). By testing new approaches for gathering reliable reference data (structured interviews with forest managers, see 2.2.2) and by developing a new predictor class (landscape context metric, see 2.2.3) this dissertation moved the attribution of causal agents of forest disturbances based on Landsat data one step forward. In particular the attribution of human and wind disturbances could be improved (UA = 68% for harvest and 63 % for wind). The landscape context predictors, developed for the first chapter of this dissertation, were recently used to map abiotic (i.e., wind and fire) and human disturbances for the entire European continent from 1986-2016 (Senf and Seidl, 2021b). Collecting a comprehensive dataset on abiotic disturbances has been approached previously (Forzieri et al., 2020; San-Miguel-Ayaz et al., 2012; Schelhaas et al., 2003) but results were never consistent and spatial explicit (Senf and Seidl, 2021b). Thus, the consistent mapping of wind and fire disturbances in Europe was an important step for forest science (Ammer et al., 2018; McDowell et al., 2015). The European map of wind and fire disturbances enables researchers to investigate questions of forest disturbance ecology based on a consistent, reliable and large-scale (temporal and spatial) data set.

A remaining challenge is the attribution of biotic disturbances, which still holds great uncertainties. While biotic disturbances in Europe have, compared to abiotic disturbances, caused less disturbance impact in the past (Schelhaas et al., 2003) their relevance might increase in the future as biotic disturbance agents such as bark beetles benefit from increasing temperatures (Jakoby et al., 2019) and the global trade of goods and services favors the spread of invasive alien disturbance agents (Seidl et al., 2018b). As such, a target for future research is the attribution of biotic disturbances based on satellite data. Besides the need for an improved monitoring of biotic disturbances, improving the understanding of the underlying mechanisms that cause the increase of natural disturbances in European forests is an important research objective for the future. Previous work has already found that changing climate and changing forest structure (i.e., higher shares of old forests, higher shares of conifers, higher timber stocks, more right skewed age class distribution) are both important drivers of increasing disturbances in Europe (Seidl et al., 2011). Recently, drought was identified as important trigger of tree mortality in Europe (Senf et al., 2020). However, none of these studies could rely on spatially explicit agent-based disturbance data (i.e., agent-based disturbance maps). In the future agent-based disturbance maps in combination with increasingly available laser scanning data might help to further understand or even reevaluate the causal relationships between forest structure, climate and disturbances.

4.3 The importance of a landscape perspective for forest scientists and managers

A central finding of this dissertation is the importance of landscape-scale patterns and processes for managing forests in the future. A forested landscape is a mosaic of gaps, stands and watersheds typically between 1,000 and 100,000 hectares in size (Urban et al., 1987). Approaching research questions from the landscape scale is a common denominator of the three chapters of this dissertation. In the first chapter, the spatial and temporal autocorrelation of disturbances on the landscape helped to separate closely interacting human and natural disturbance agents in Landsat data. In the second chapter, the landscape configuration, in particular the overall forest cover and the distribution of forest cover within the landscape, and the disturbance regime of a landscape were linked to the occurrence and frequency of torrential hazards. And finally, in the third chapter, increasing tree species diversity at the landscape scale was found to be at least as effective in buffering disturbance impacts as increasing tree species diversity on the stand scale.

Developing a scientific view that goes beyond the scale of individual or multiple forest stands has been proposed by previous studies (Seidl et al., 2018a, 2016a; Triviño et al., 2017) and the importance of such a perspective was underlined by the results of this dissertation. However, also from the applied view of a forest manager, the landscape scale is an appropriate point-of-view as (i) forest enterprises in Central Europe are typically the size of a landscape,

thus managers actually take decisions on the landscape scale; and (ii) forests are increasingly affected by drivers that operate at landscape (e.g., disturbances) to global (e.g., climate change) scales. Therefore, extending the scope from the individual tree or the stand to the landscape is important for scientists and forest managers in the 21st century.

4.4 Remote sensing and evidence-based forest management

The development of remote sensing methods that allow to quantify disturbance regimes from Landsat data lead to a series of ecological insights in Europe. For example, Senf et al., (2019) found that bark beetle disturbances naturally recover within 30 years and Senf and Seidl, (2018) found disturbances to appear temporally synchronized across Central Europe. Additional to ecological research, Landsat-based forest disturbance maps became increasingly important for tackling applied questions of ecosystem management. Landsat-based disturbance maps were used to monitor illegal logging in protected areas (Kuemmerle et al., 2009; Shchur et al., 2017) and more recent studies quantified how disturbances shape wildlife habitats across space and time (Oeser et al., 2017), or how predisposing factors influence the susceptibility of mountain forests to disturbances (Stritih et al., 2021).

In the case of Austria, a particularly important question of forest management was the influence of forest cover and disturbance on the probability of torrential hazards. The existing results on this question largely stemmed from local case studies (Brardinoni et al., 2003; Imaizumi et al., 2008; Nyman et al., 2015) and large-scale evidence, that is necessary to guide forest policy and formulate management guidelines, was completely missing. I found that intact mountain forests are protecting humans against torrential hazards and that large disturbances erode this protective function, in particular if they occur on a regular basis (Chapter 2). Given the fact that existing guidelines on protection forest management (Frehner et al., 2005) are formulated mainly on the basis of expert opinions and only to a small degree on the basis of empirical data, these results are an important step forward to an evidence-based management of mountain forests.

Remote sensing products are an important source of information that can quantitatively guide decision processes in forest management and policy. However, experienced professionals are necessary to make this data accessible to decision makers on the ground. While remote sensing and GIS methods are already included in forest related study programs, they should become a core discipline of next generation forest professionals in the future to further strengthen evidence-based management decisions in Central European forests.

4.5 Computer simulation experiments are complementary to retrospective remote sensing research

While remote sensing offers great opportunities for the quantification of disturbance regimes and for tackling applied questions, the point-of-view is always retrospective. We are currently facing a situation where environmental conditions change with increasing pace. It is uncertain if patterns, processes and relationships observed in the past will still be valid in the future. Here, computer simulations with process-based forest models offer opportunities to formalize knowledge of the past, gradually change environmental drivers (i.e., climate and disturbances) and thus to get insights into future challenges and opportunities of forest management. With this dissertation I contribute to this process of picturing potential futures and developing appropriate management responses by investigating a topic that has been debated in forest ecology and management already a long time ago (Peterson et al., 1998). The question of diversity – stability relationships in forests has been an important aspect of recent research (Jactel et al., 2021) and has been tackled with various approaches and methods (Griess et al., 2012; Jactel et al., 2017; Knoke et al., 2008; Metz et al., 2016).

In the context of simulation modelling, this dissertation went one step beyond previous studies by simultaneously employing two forest landscape models in two contrasting Central European forest landscapes. While multi-model comparisons have been conducted to investigate the effects of different model formulations and assumptions (Petter et al., 2020), applied questions were previously answered by employing one model in one landscape (e.g. Albrich et al., 2018; Mina et al., 2017; Schumacher et al., 2006; Thom et al., 2017a). However, the multi-model, multi-landscape approach of this dissertation revealed additional insights that would have not been possible with previous approaches. I found that the two models agreed remarkably on the direction of diversity effects, fostering confidence on the robustness of my results. Further, effect sizes differed between the two models opening up a range of realistic values that can be interpreted. While I found clear advantages of such a multi-model approach, this dissertation also revealed drawbacks of investigating research questions with multiple simulation models, such as the necessity of harmonized driver data and a simplified simulation design. In this particular case, the two models have substantially different modules for simulating natural disturbances. I thus used a simplified implementation of wind disturbances, ignoring other important natural disturbance agents and dynamic disturbance interactions. Employing multiple simulation models to answer ecological questions is thus a tradeoff between increasing confidence in the results due to a lower risk of individual model artefacts driving the results and decreasing confidence in the results due to an inherently reduced complexity and level of detail in processes simulated. While employing multiple models brought advantages and disadvantages, simulating in two contrasting landscapes clearly contributed to a more differentiated and comprehensive understanding of the relationship between tree

species diversity and disturbance impacts. Increasing tree species diversity strongly reduced disturbance impacts in the conifer-dominated mountain landscape, while disturbance impacts actually increased with increasing diversity in some cases of the broadleaved dominated lowland landscape. The results of this dissertation thus underline the importance of multi-site studies for drawing generalizable conclusions.

In the context of applied ecology this dissertation went one step beyond previous research by not only investigating effects of tree species diversity within forest stands (alpha diversity) but also between forest stands (beta diversity). The importance of beta diversity for ecosystem functioning (Mori et al., 2018; Schuler et al., 2017), provisioning of multiple ecosystem services (Van Der Plas et al., 2016), ecosystem resilience (Honkaniemi et al., 2020; Lamy et al., 2016) and biodiversity (Schall et al., 2018; Schuler et al., 2019) has been found by previous research. Yet, the effects of spatial configuration on disturbance impacts and temporal stability have not been investigated. I found, that mixing tree species between stands can be as effective or even more effective in buffering disturbance impacts than mixing tree species within stands. This finding opens up opportunities for forest managers to efficiently increase tree species diversity at the landscape scale as efforts to regulate inter-species competition are reduced with between-stand mixtures.

4.6 Suggestions for management

Based on the results and experience of this thesis the following three suggestions for the management of mountain forests under changing climate and disturbance regimes can be formulated.

First, natural disturbances have strongly increased in Europe over the last thirty years (Schelhaas et al., 2003; Seidl et al., 2014b; Senf et al., 2021, 2018a) and will most likely further increase in the future (Dobor et al., 2020; Honkaniemi et al., 2020; Zimová et al., 2020). In Austria increasing natural disturbances were mainly driven by increasing wind disturbances (Chapter 1). The risk of wind-throw exponentially increases with tree heights over 20 meter (Díaz-Yáñez et al., 2019; Schmidt et al., 2010; Suvanto et al., 2019). Thus, the susceptibility of a given landscape to increasing disturbances in Austria increases exponentially with the number of trees over 20 meter height. Besides other management measures, limiting the share of very high trees (> 20 meter) can effectively reduce the risk disturbances. Potential management goals include but are not limited to: reducing rotation period and/or promoting tree species with less height growth.

Second, a quantification of forest ecosystem services beyond wood production is necessary for an evidence-based management of mountain forests in the 21st century. Mountain forests have protected humans from natural hazard processes, including rock fall (Moos et al., 2017),

avalanches (Casteller et al., 2018), debris flows and floods (Chapter 2), very cost efficiently in the past. Frequent disturbances erode this protective function of forests (Chapter 2) and the frequency of disturbances in Austria's forests has strongly increased over the last thirty years (wind = +355%, bark beetle = +77%, harvest = +26%). While the frequency of both human and natural disturbances has increased, human disturbances account for 77 % of all disturbance patches (Chapter 2). Thus, reducing the frequency of management interventions (e.g., timber harvests, salvage logging) in protective forests would strongly decrease the frequency of disturbances and consequently the risk of natural hazards. Further, unmanaged protective forests could store high amounts of carbon (Luyssaert et al., 2008) and natural disturbance patches that are excluded from salvage logging could increase biodiversity (Thorn et al., 2020, 2018). However, without financial incentives for carbon storage, biodiversity enrichment and protection against natural hazards, forest owners are depended on timber harvests. Thus, financial incentives are necessary to enable forest owners to apply new, evidence-based mountain forest management strategies not necessarily including timber harvest. Measures can include but are not limited to: applying continuous cover harvesting systems or no timber harvest at all, avoiding salvage logging where possible, conducting quantitative risk assessment of protection forests (incorporating risk of forest disturbance, risk of natural hazards and resilience of protection forest), applying targeted measures to increase resistance and resilience of protection forests.

Third, in the face of uncertainty, managing for diversity is a promising strategy independent from the spatial scale and the indicator analyzed. It is unclear how climate and disturbance change will exactly play out in a given landscape. Therefore, increasing diversity wherever possible most likely increases chances that forests can cope with future challenges. Increasing the structural diversity (i.e., the diversity in tree height and diameter) of forests fosters resilience to disturbances (Bače et al., 2015; Hupperts et al., 2019). In structurally diverse forests trees of different height and diameter grow next to each other. In the case of disturbance smaller trees often survive disturbances and facilitate recovery (Seidl et al., 2014a) providing ecological and economic advantages (Knoke et al., 2021). Further, structural diversity was found to be a driver of forest productivity (Dănescu et al., 2016). Increasing diversity in tree species also increases forest productivity (Liang et al., 2016; Paquette and Messier, 2011; Pretzsch et al., 2015), buffers biotic (Jactel et al., 2021) and abiotic (Grossiord, 2019; Metz et al., 2016, Chapter 3) disturbances and facilitates ecosystem functioning (Ratcliffe et al., 2017). Further, societal changes (i.e., future demand for ecosystem services) are highly unpredictable and a diverse portfolio of species increases the chances that multiple and varying ecosystem services can be fulfilled (Felipe-Lucia et al., 2018; Knoke et al., 2016). However, increasing diversity is not limited to forest structure and tree species, as genetic diversity (Schaberg et al., 2008; Sgrò et al., 2011) and economic diversity (Knoke et al., 2017)

are considered equally important. Climate change will increase the growth-potential of additional tree species in mountain forests, thus providing opportunities for increasing tree species diversity in mountain landscapes (Chapter III). Forest managers of the 21st century might take up these opportunities and further diversify mountain forests with regard to tree species, forest structure, genetic resources, silvicultural techniques (from no management to selective or single-tree cutting and slit and strip cuts to larger clear-cuts) and management goals (from nature conservation, over timber production, over carbon storage, over protection against natural hazards).

5 Acknowledgements

I want to thank all the colleagues and friends that accompanied me during the journey of my PhD and made the past four years to an exciting experience.

Rupert, I want to thank you for introducing me to the world of science and for true mentorship, in scientific questions and on a personal level.

Cornelius, I want to thank you for all the adventures with skies, with hiking boots and with a laptop on the knees.

Kathi, I want to thank you for being the best office mate I could imagine.

Werner and Dominik, I want to thank you for giving me the feeling that there are no challenges that we as team cannot solve.

Laura, Katja and Johannes, I want to thank you for your endless support, this thesis would have not been possible without you.

6 References

- Abildtrup, J., Garcia, S., Stenger, A., 2013. The effect of forest land use on the cost of drinking water supply: A spatial econometric analysis. *Ecol. Econ.* 92, 126–136. <https://doi.org/10.1016/j.ecolecon.2013.01.004>
- Albrich, K., Rammer, W., Seidl, R., 2020. Climate change causes critical transitions and irreversible alterations of mountain forests. *Glob. Chang. Biol.* 26, 4013–4027. <https://doi.org/10.1111/gcb.15118>
- Albrich, K., Rammer, W., Thom, D., Seidl, R., 2018. Trade-offs between temporal stability and level of forest ecosystem services provisioning under climate change. *Ecol. Appl.* 28, 1884–1896. <https://doi.org/10.1002/eap.1785>
- Ammer, C., Fichtner, A., Fischer, A., Gossner, M.M., Meyer, P., Seidl, R., Thomas, F.M., Annighöfer, P., Kreyling, J., Ohse, B., Berger, U., Feldmann, E., Häberle, K.-H., Heer, K., Heinrichs, S., Huth, F., Krämer-Klement, K., Mölder, A., Müller, J., Mund, M., Opgenoorth, L., Schall, P., Scherer-Lorenzen, M., Seidel, D., Vogt, J., Wagner, S., 2018. Key ecological research questions for Central European forests. *Basic Appl. Ecol.* 1–23. <https://doi.org/10.1016/J.BAAE.2018.07.006>
- Auer, I., Böhm, R., Jurkovic, A., Lipa, W., Orlik, A., Potzmann, R., Schöner, W., Ungersböck, M., Matulla, C., Briffa, K., Jones, P., Efthymiadis, D., Brunetti, M., Nanni, T., Maugeri, M., Mercalli, L., Mestre, O., Moisselin, J.-M., Begert, M., Müller-Westermeier, G., Kveton, V., Bochnicek, O., Stastny, P., Lapin, M., Szalai, S., Szentimrey, T., Cegnar, T., Dolinar, M., Gajic-Capka, M., Zaninovic, K., Majstorovic, Z., Nieplova, E., 2007. HISTALP—historical instrumental climatological surface time series of the Greater Alpine Region. *Int. J. Climatol.* 27, 17–46. <https://doi.org/10.1002/joc.1377>
- Bače, R., Svoboda, M., Janda, P., Morrissey, R.C., Wild, J., Clear, J.L., Čada, V., Donato, D.C., Chen, H.Y.H., 2015. Legacy of pre-disturbance spatial pattern determines early structural diversity following severe disturbance in montane spruce forests. *PLoS One* 10, 1–18. <https://doi.org/10.1371/journal.pone.0139214>
- Bebi, P., Kulakowski, D., Rixen, C., 2009. Snow avalanche disturbances in forest ecosystems—State of research and implications for management. *For. Ecol. Manage.* 257, 1883–1892. <https://doi.org/10.1016/j.foreco.2009.01.050>
- Bebi, P., Seidl, R., Motta, R., Fuhr, M., Firm, D., Krumm, F., Conedera, M., Ginzler, C., Wohlgemuth, T., Kulakowski, D., 2017. Changes of forest cover and disturbance regimes in the mountain forests of the Alps. *For. Ecol. Manage.* 388, 43–56. <https://doi.org/10.1016/j.foreco.2016.10.028>
- Becker, P., Funk, M., Schlüchter, C., Hutter, K., 2017. A study of the Würm glaciation focused on the Valais region (Alps). *Geogr. Helv.* 72, 421–442. <https://doi.org/10.5194/gh-72-421-2017>
- Bender, E.A., Case, T.J., Gilpin, M.E., 1984. *Perturbation Experiments in Community Ecology : Theory and Practice* Author (s): Edward A . Bender , Ted J . Case and Michael E . Gilpin Published by : Ecological Society of America PERTURBATION EXPERIMENTS IN COMMUNITY ECOLOGY : THEORY AND PRACTICE '. *Ecology* 65, 1–13.
- BMLRT, 2021. Waldentwicklungsplan Österreich [WWW Document]. URL <https://www.waldentwicklungsplan.at/map/?b=09X9&layer=ERIWGg&x=1817902&y=6142862&zoom=11>

- Boettinger, J.L., Ramsey, R.D., Bodily, J.M., Cole, N.J., Kienast-Brown, S., Nield, S.J., Saunders, A.M., Stum, A.K., 2008. Landsat spectral data for digital soil mapping. *Digit. Soil Mapp. with Ltd. Data* 193–202. https://doi.org/10.1007/978-1-4020-8592-5_16
- Bonney, R., Cooper, C.B., Dickinson, J., Kelling, S., Phillips, T., Rosenberg, K. V, Shirk, J., 2009. Citizen Science: A Developing Tool for Expanding Science Knowledge and Scientific Literacy 59, 977–984. <https://doi.org/10.1525/bio.2009.59.11.9>
- Bradshaw, C.J.A., Sodhi, N.S., Peh, K.S.H., Brook, B.W., 2007. Global evidence that deforestation amplifies flood risk and severity in the developing world. *Glob. Chang. Biol.* 13, 2379–2395. <https://doi.org/10.1111/j.1365-2486.2007.01446.x>
- Brang, P., Schonenberger, W., Frehner, M., Schwitter, R., Thormann, J.-J., Wasser, B., 2006. Management of protection forests in the European Alps: An overview. *For. Snow Landsc. Res.* 80, 23–44. <https://doi.org/10.1021/pr100686b>
- Brardinoni, F., Hassan, M.A., Slaymaker, H.O., 2003. Complex mass wasting response of drainage basins to forest management in coastal British Columbia. *Geomorphology* 49, 109–124. [https://doi.org/10.1016/S0169-555X\(02\)00166-6](https://doi.org/10.1016/S0169-555X(02)00166-6)
- Buma, B., Johnson, A.C., 2015. The role of windstorm exposure and yellow cedar decline on landslide susceptibility in southeast Alaskan temperate rainforests. *Geomorphology* 228, 504–511. <https://doi.org/10.1016/j.geomorph.2014.10.014>
- Cadag, J.R.D., Gaillard, J.C., 2012. Integrating knowledge and actions in disaster risk reduction: the contribution of participatory mapping. *Area* 44, 100–109. <https://doi.org/10.1111/j.1475-4762.2011.01065.x>
- Casteller, A., Häfelfinger, T., Cortés Donoso, E., Podvin, K., Kulakowski, D., Bebi, P., 2018. Assessing the interaction between mountain forests and snow avalanches at Nevados de Chillán, Chile and its implications for ecosystem-based disaster risk reduction. *Nat. Hazards Earth Syst. Sci.* 18, 1173–1186. <https://doi.org/10.5194/nhess-18-1173-2018>
- Ceccherini, G., Duveiller, G., Grassi, G., Lemoine, G., Avitabile, V., Pilli, R., Cescatti, A., 2020. Abrupt increase in harvested forest area over Europe after 2015. *Nature* 583, 72–77. <https://doi.org/10.1038/s41586-020-2438-y>
- Chambers, R., 2006. Participatory mapping and geographic information systems: whose map? who is empowered and who disempowered? Who gains and who loses? *Electron. J. Inf. Syst. Dev. Ctries.* 25, 1–11.
- Cheddadi, R., Vendramin, G.G., Litt, T., François, L., Kageyama, M., Lorentz, S., Laurent, J.M., de Beaulieu, J.L., Sadori, L., Jost, A., Lunt, D., 2006. Imprints of glacial refugia in the modern genetic diversity of *Pinus sylvestris*. *Glob. Ecol. Biogeogr.* 15, 271–282. <https://doi.org/10.1111/j.1466-822X.2006.00226.x>
- Cohen, W.B., Yang, Z., Kennedy, R., 2010. Detecting trends in forest disturbance and recovery using yearly Landsat time series: 2. TimeSync - Tools for calibration and validation. *Remote Sens. Environ.* 114, 2911–2924. <https://doi.org/10.1016/j.rse.2010.07.010>
- Copass, C., Antonova, N., Kennedy, R., 2018. Comparison of Office and Field Techniques for Validating Landscape Change Classification in Pacific Northwest National Parks. *Remote Sens.* 11, 3. <https://doi.org/10.3390/rs11010003>
- Cope, M., Elwood, S., 2009. *Qualitative GIS: A Mixed Methods Approach*. Sage Publications, Thousand Oaks, CA.

- Dale, V.H., Joyce, L. a, McNulty, S., Neilson, R.P., Ayres, M.P., Flannigan, M.D., Hanson, P.J., Irland, L.C., Lugo, a E., Peterson, C.J., Simberloff, D., Swanson, F.J., Stocks, B.J., Wotton, B.M., 2001. Climate Change and Forest Disturbances 51, 723–734.
- Dănescu, A., Albrecht, A.T., Bauhus, J., 2016. Structural diversity promotes productivity of mixed, uneven-aged forests in southwestern Germany. *Oecologia* 182, 319–333. <https://doi.org/10.1007/s00442-016-3623-4>
- Díaz-Yáñez, O., Mola-Yudego, B., González-Olabarria, J.R., 2019. Modelling damage occurrence by snow and wind in forest ecosystems. *Ecol. Modell.* 408, 108741. <https://doi.org/10.1016/j.ecolmodel.2019.108741>
- Dickinson, J.L., Zuckerberg, B., Bonter, D.N., 2010. Citizen Science as an Ecological Research Tool : Challenges and Benefits. <https://doi.org/10.1146/annurev-ecolsys-102209-144636>
- Dobor, L., Hlásny, T., Rammer, W., Zimová, S., Barka, I., Seidl, R., 2020. Is salvage logging effectively dampening bark beetle outbreaks and preserving forest carbon stocks? *J. Appl. Ecol.* 57, 67–76. <https://doi.org/10.1111/1365-2664.13518>
- Dorren, L.K.A., Berger, F., Imeson, A.C., Maier, B., Rey, F., 2004. Integrity, stability and management of protection forests in the European Alps. *For. Ecol. Manage.* 195, 165–176. <https://doi.org/10.1016/j.foreco.2004.02.057>
- EEA, 2006. European forest types, EEA Technical report No 9/2006.
- Erb, K.H., Kastner, T., Plutzer, C., Bais, A.L.S., Carvalhais, N., Fetzel, T., Gingrich, S., Haberl, H., Lauk, C., Niedertscheider, M., Pongratz, J., Thurner, M., Luyssaert, S., 2018. Unexpectedly large impact of forest management and grazing on global vegetation biomass. *Nature* 553, 73–76. <https://doi.org/10.1038/nature25138>
- Feistl, T., Bebi, P., Teich, M., Bühler, Y., Christen, M., Thuro, K., Bartelt, P., 2014. Observations and modeling of the braking effect of forests on small and medium avalanches. *J. Glaciol.* 60, 124–138. <https://doi.org/10.3189/2014JoG13J055>
- Felipe-Lucia, M.R., Soliveres, S., Penone, C., Manning, P., van der Plas, F., Boch, S., Prati, D., Ammer, C., Schall, P., Gossner, M.M., Bauhus, J., Buscot, F., Blaser, S., Blüthgen, N., de Frutos, A., Ehbrecht, M., Frank, K., Goldmann, K., Hänsel, F., Jung, K., Kahl, T., Nauss, T., Oelmann, Y., Pena, R., Polle, A., Renner, S., Schlöter, M., Schöning, I., Schrupf, M., Schulze, E.D., Solly, E., Sorkau, E., Stempfhuber, B., Tschapka, M., Weisser, W.W., Wubet, T., Fischer, M., Allan, E., 2018. Multiple forest attributes underpin the supply of multiple ecosystem services. *Nat. Commun.* 9. <https://doi.org/10.1038/s41467-018-07082-4>
- Forzieri, G., Pecchi, M., Girardello, M., Mauri, A., Klaus, M., Nikolov, C., Rüetschi, M., Gardiner, B., Tomastik, J., Small, D., Nistor, C., Jonikavicius, D., Spinoni, J., Feyen, L., Giannetti, F., Comino, R., Wolynski, A., Pirotti, F., Maistrelli, F., Savulescu, I., Wurpillot-Lucas, S., Karlsson, S., Zieba-Kulawik, K., Strejczek-Jazwinska, P., Mokroš, M., Franz, S., Krejci, L., Haidu, I., Nilsson, M., Wezyk, P., Catani, F., Chen, Y.Y., Luyssaert, S., Chirici, G., Cescatti, A., Beck, P.S.A., 2020. A spatially explicit database of wind disturbances in European forests over the period 2000-2018. *Earth Syst. Sci. Data* 12, 257–276. <https://doi.org/10.5194/essd-12-257-2020>
- Frehner, M., Schwitler, R., Wasser, B., 2005. Nachhaltigkeit und Erfolgskontrolle im Schutzwald. Wegleitung für Pflegemassnahmen in Wäldern mit Schutzfunktion [Sustainability and controlling in protection forests. Guidelines for tending forests with protective function].

- Gehrig-Fasel, J., Guisan, A., Zimmermann, N.E., 2007. Tree line shifts in the Swiss Alps: Climate change or land abandonment? *J. Veg. Sci.* 18, 571–582. <https://doi.org/10.1111/j.1654-1103.2007.tb02571.x>
- Griess, V.C., Acevedo, R., Härtl, F., Staupendahl, K., Knoke, T., 2012. Does mixing tree species enhance stand resistance against natural hazards? A case study for spruce. *For. Ecol. Manage.* 267, 284–296. <https://doi.org/10.1016/j.foreco.2011.11.035>
- Grimm, V., Revilla, E., Berger, U., Jeltsch, F., Mooij, W.M., Railsback, S.F., Thulke, H.H., Weiner, J., Wiegand, T., DeAngelis, D.L., 2005. Pattern-oriented modeling of agent-based complex systems: Lessons from ecology. *Science* (80-.). 310, 987–991. <https://doi.org/10.1126/science.1116681>
- Grossiord, C., 2019. Having the right neighbors: how tree species diversity modulates drought impacts on forests. *New Phytol.* <https://doi.org/10.1111/nph.15667>
- Hansen, J., Sato, M., Ruedy, R., Lo, K., Lea, D.W., Medina-Elizade, M., 2006. Global temperature change. *Proc. Natl. Acad. Sci. U. S. A.* 103, 14288–14293. <https://doi.org/10.1073/pnas.0606291103>
- Hansen, J., Sato, M., Ruedy, R., Schmidt, G.A., Lo, K., Persin, A., 2019. Global Temperature in 2018 and Beyond 1–4.
- Hansen, M.C.C., Potapov, P. V, Moore, R., Hancher, M., Turubanova, S.A. a, Tyukavina, A., Thau, D., Stehman, S.V. V, Goetz, S.J.J., Loveland, T.R.R., Kommareddy, A., Egorov, A., Chini, L., Justice, C.O.O., Townshend, J.R.G.R.G., Patapov, P.V., Moore, R., Hancher, M., Turubanova, S.A. a, Tyukavina, A., Thau, D., Stehman, S.V. V, Goetz, S.J.J., Loveland, T.R.R., Kommareddy, A., Egorov, A., Chini, L., Justice, C.O.O., Townshend, J.R.G.R.G., 2013. High-Resolution Global Maps of 21st-Century Forest Cover Change. *Science* (80-.). 342, 850–854. <https://doi.org/10.1126/science.1244693>
- Heiser, M., Hübl, J., Scheidl, C., 2019. Completeness analyses of the Austrian torrential event catalog. *Landslides.* <https://doi.org/10.1007/s10346-019-01218-3>
- Hilmers, T., Friess, N., Bässler, C., Heurich, M., Brandl, R., Pretzsch, H., Seidl, R., Müller, J., 2018. Biodiversity along temperate forest succession. *J. Appl. Ecol.* 55, 2756–2766. <https://doi.org/10.1111/1365-2664.13238>
- Hlásny, T., Zimová, S., Merganičová, K., Štěpánek, P., Modlinger, R., Turčáni, M., 2021. Devastating outbreak of bark beetles in the Czech Republic: Drivers, impacts, and management implications. *For. Ecol. Manage.* 490. <https://doi.org/10.1016/j.foreco.2021.119075>
- Honkaniemi, J., Rammer, W., Seidl, R., 2020. Norway spruce at the trailing edge: the effect of landscape configuration and composition on climate resilience. *Landsc. Ecol.* 0123456789. <https://doi.org/10.1007/s10980-019-00964-y>
- Hübl, J., Totschnig, R., Sitter, F., Schneider, A., Krawtschuk, A., Dusl, G., Fischer, N., Swoboda, P., Neckel, N., 2008. Historische Ereignisse — Band 3: Aufarbeitung historischer Ereignisse (VerlagerungsartenWasser und Schnee) in Österreich. Report 111. Institute of Mountain Risk Engineering, University of Life Sciences and Natural Resources, Vienna.
- Hupperts, S.F., Dickinson, Y.L., Webster, C.R., Kern, C.C., 2019. Promoting structural and species diversity in Great Lakes northern hardwoods: A conceptual model and its application. *Forestry* 92, 16–25. <https://doi.org/10.1093/forestry/cpy026>

- Imaizumi, F., Sidle, R.C., Kamei, R., 2008. Effects of forest harvesting on the occurrence of landslides and debris flows in steep terrain of central Japan Fumitoshi. *Earth Surf. Process. Landforms* 34, 155–161. <https://doi.org/10.1002/esp>
- Jactel, H., Bauhus, J., Boberg, J., Bonal, D., Castagneyrol, B., Gardiner, B., Gonzalez-Olabarria, J.R., Koricheva, J., Meurisse, N., Brockerhoff, E.G., 2017. Tree Diversity Drives Forest Stand Resistance to Natural Disturbances. *Curr. For. Reports* 3, 223–243. <https://doi.org/10.1007/s40725-017-0064-1>
- Jactel, H., Moreira, X., Castagneyrol, B., 2021. Tree Diversity and Forest Resistance to Insect Pests: Patterns, Mechanisms and Prospects 1–20.
- Jakoby, O., Lischke, H., Wermelinger, B., 2019. Climate change alters elevational phenology patterns of the European spruce bark beetle (*Ips typographus*), *Global Change Biology*. <https://doi.org/10.1111/gcb.14766>
- Kapos, V., Rhind, J., Edwards, M., Price, M.F., Ravilious, C., 2000. Forests in sustainable mountain development: a state of knowledge report for 2000. Task Force on Forests in Sustainable Mountain Development., in: *Forests in Sustainable Mountain Development: A State of Knowledge Report for 2000. Task Force on Forests in Sustainable Mountain Development*. <https://doi.org/10.1079/9780851994468.0000>
- Kärvemo, S., Van Boeckel, T.P., Gilbert, M., Grégoire, J.C., Schroeder, M., 2014. Large-scale risk mapping of an eruptive bark beetle - Importance of forest susceptibility and beetle pressure. *For. Ecol. Manage.* 318, 158–166. <https://doi.org/10.1016/j.foreco.2014.01.025>
- Keenan, R.J., Reams, G.A., Achard, F., de Freitas, J. V., Grainger, A., Lindquist, E., 2015. Dynamics of global forest area: Results from the FAO Global Forest Resources Assessment 2015. *For. Ecol. Manage.* 352, 9–20. <https://doi.org/10.1016/j.foreco.2015.06.014>
- Kennedy, R.E., Yang, Z., Cohen, W.B., 2010. Detecting trends in forest disturbance and recovery using yearly Landsat time series: 1. LandTrendr - Temporal segmentation algorithms. *Remote Sens. Environ.* 114, 2897–2910. <https://doi.org/10.1016/j.rse.2010.07.008>
- Kennedy, R.E., Yang, Z., Gorelick, N., Braaten, J., Cavalcante, L., Cohen, W.B., Healey, S., 2018. Implementation of the LandTrendr algorithm on Google Earth Engine. *Remote Sens.* 10, 1–10. <https://doi.org/10.3390/rs10050691>
- Klein, T., Hartmann, H., 2018. Climate change drives tree mortality. *Science* (80-.). 362, 758.1-758. <https://doi.org/10.1126/science.aav6508>
- Knoke, T., Ammer, C., Stimm, B., Mosandl, R., 2008. Admixing broadleaved to coniferous tree species: A review on yield, ecological stability and economics. *Eur. J. For. Res.* 127, 89–101. <https://doi.org/10.1007/s10342-007-0186-2>
- Knoke, T., Messerer, K., Paul, C., 2017. The Role of Economic Diversification in Forest Ecosystem Management. *Curr. For. Reports* 3, 93–106. <https://doi.org/10.1007/s40725-017-0054-3>
- Knoke, T., Paul, C., Gosling, E., Jarisch, I., Mohr, J., Seidl, R., 2021. Assessing the Economic Resilience of Different Management Systems to Severe Forest Disturbance. *SSRN Electron. J.* 1–48. <https://doi.org/10.2139/ssrn.3844645>
- Knoke, T., Paul, C., Hildebrandt, P., Calvas, B., Castro, L.M., Hartl, F., Dollerer, M., Hamer, U., Windhorst, D., Wiersma, Y.F., Curatola Fernández, G.F., Obermeier, W.A., Adams,

- J., Breuer, L., Mosandl, R., Beck, E., Weber, M., Stimm, B., Haber, W., Fürst, C., Bendix, J., 2016. Compositional diversity of rehabilitated tropical lands supports multiple ecosystem services and buffers uncertainties. *Nat. Commun.* 7. <https://doi.org/10.1038/ncomms11877>
- Kuemmerle, T., Chaskovskyy, O., Knorn, J., Radeloff, V.C., Kruhlov, I., Keeton, W.S., Hostert, P., 2009. Forest cover change and illegal logging in the Ukrainian Carpathians in the transition period from 1988 to 2007. *Remote Sens. Environ.* 113, 1194–1207. <https://doi.org/10.1016/j.rse.2009.02.006>
- Kulakowski, D., Seidl, R., Holeksa, J., Kuuluvainen, T., Nagel, T.A., Panayotov, M., Svoboda, M., Thorn, S., Vacchiano, G., Whitlock, C., Wohlgemuth, T., Bebi, P., 2017. A walk on the wild side: Disturbance dynamics and the conservation and management of European mountain forest ecosystems. *For. Ecol. Manage.* 388, 120–131. <https://doi.org/10.1016/j.foreco.2016.07.037>
- Kulakowski, D., Veblen, T.T., 2002. Influences of fire history and topography on the pattern of a severe wind blowdown in a Colorado subalpine forest. *J. Ecol.* 90, 806–819. <https://doi.org/10.1046/j.1365-2745.2002.00722.x>
- Lamy, T., Liss, K.N., Gonzalez, A., Bennett, E.M., 2016. Landscape structure affects the provision of multiple ecosystem services. *Environ. Res. Lett.* 11, 1–9. <https://doi.org/10.1088/1748-9326/11/12/124017>
- Leverkus, A.B., Lindenmayer, D.B., Thorn, S., Gustafsson, L., 2018. Salvage logging in the world's forests: Interactions between natural disturbance and logging need recognition. *Glob. Ecol. Biogeogr.* 27, 1140–1154. <https://doi.org/10.1111/geb.12772>
- Liang, J., Crowther, T.W., Picard, N., Wiser, S., Zhou, M., Alberti, G., Schulze, E.D., McGuire, A.D., Bozzato, F., Pretzsch, H., De-Miguel, S., Paquette, A., Hérault, B., Scherer-Lorenzen, M., Barrett, C.B., Glick, H.B., Hengeveld, G.M., Nabuurs, G.J., Pfautsch, S., Viana, H., Vibrans, A.C., Ammer, C., Schall, P., Verbyla, D., Tchebakova, N., Fischer, M., Watson, J. V., Chen, H.Y.H., Lei, X., Schelhaas, M.J., Lu, H., Gianelle, D., Parfenova, E.I., Salas, C., Lee, E., Lee, B., Kim, H.S., Bruijnzeel, H., Coomes, D.A., Piotto, D., Sunderland, T., Schmid, B., Gourlet-Fleury, S., Sonké, B., Tavan, R., Zhu, J., Brandt, S., Vayreda, J., Kitahara, F., Searle, E.B., Neldner, V.J., Ngugi, M.R., Baraloto, C., Frizzera, L., Bałazy, R., Oleksyn, J., Zawila-Niedzwiecki, T., Bouriaud, O., Bussotti, F., Finžgar, L., Jaroszewicz, B., Jucker, T., Valladares, F., Jagodzinski, A.M., Peri, P.L., Gonmadje, C., Marthy, W., O'Brien, T., Martin, E.H., Marshall, A.R., Rovero, F., Bitariho, R., Niklaus, P.A., Alvarez-Loayza, P., Chamuya, N., Valencia, R., Mortier, F., Wortel, V., Engone-Obiang, N.L., Ferreira, L. V., Odeke, D.E., Vasquez, R.M., Lewis, S.L., Reich, P.B., 2016. Positive biodiversity-productivity relationship predominant in global forests. *Science* (80-.). 354. <https://doi.org/10.1126/science.aaf8957>
- Liu, J., Dietz, T., Carpenter, S.R., Folke, C., Alberti, M., Redman, C.L., Schneider, S.H., Ostrom, E., Pell, A.N., Lubchenco, J., Taylor, W.W., Ouyang, Z., Deadman, P., Kratz, T., Provencher, W., 2007. Coupled Human and Natural Systems. *Bioscience* 36, 639–649.
- Luyssaert, S., Schulze, E.D., Börner, A., Knohl, A., Hessenmöller, D., Law, B.E., Ciais, P., Grace, J., 2008. Old-growth forests as global carbon sinks. *Nature* 455, 213–215. <https://doi.org/10.1038/nature07276>
- Mapulanga, A.M., Naito, H., 2019. Effect of deforestation on access to clean drinking water. *Proc. Natl. Acad. Sci. U. S. A.* 116, 8249–8254. <https://doi.org/10.1073/pnas.1814970116>
- Maroschek, M., Rammer, W., Lexer, M.J., 2015. Using a novel assessment framework to

- evaluate protective functions and timber production in Austrian mountain forests under climate change. *Reg. Environ. Chang.* 15, 1543–1555. <https://doi.org/10.1007/s10113-014-0691-z>
- McDowell, N.G., Coops, N.C., Beck, P.S.A., Chambers, J.Q., Gangodagamage, C., Hicke, J.A., Huang, C. ying, Kennedy, R., Krofcheck, D.J., Litvak, M., Meddens, A.J.H., Muss, J., Negrón-Juarez, R., Peng, C., Schwantes, A.M., Swenson, J.J., Vernon, L.J., Williams, A.P., Xu, C., Zhao, M., Running, S.W., Allen, C.D., 2015. Global satellite monitoring of climate-induced vegetation disturbances. *Trends Plant Sci.* 20, 114–123. <https://doi.org/10.1016/j.tplants.2014.10.008>
- Messier, C., Puettmann, K., Chazdon, R., Andersson, K.P., Angers, V.A., Brotons, L., Filotas, E., Tittler, R., Parrott, L., Levin, S.A., 2015. From Management to Stewardship: Viewing Forests As Complex Adaptive Systems in an Uncertain World. *Conserv. Lett.* 8, 368–377. <https://doi.org/10.1111/conl.12156>
- Metz, J., Annighöfer, P., Schall, P., Zimmermann, J., Kahl, T., Schulze, E.D., Ammer, C., 2016. Site-adapted admixed tree species reduce drought susceptibility of mature European beech. *Glob. Chang. Biol.* 22, 903–920. <https://doi.org/10.1111/gcb.13113>
- Mina, M., Bugmann, H., Cordonnier, T., Irauschek, F., Klopčič, M., Pardos, M., Cailleret, M., 2017. Future ecosystem services from European mountain forests under climate change. *J. Appl. Ecol.* 54, 389–401. <https://doi.org/10.1111/1365-2664.12772>
- Moos, C., Bebi, P., Graf, F., Mattli, J., Rickli, C., Schwarz, M., 2016. How does forest structure affect root reinforcement and susceptibility to shallow landslides? *Earth Surf. Process. Landforms* 41, 951–960. <https://doi.org/10.1002/esp.3887>
- Moos, C., Bebi, P., Schwarz, M., Stoffel, M., Sudmeier-Rieux, K., Dorren, L., 2018. Ecosystem-based disaster risk reduction in mountains. *Earth-Science Rev.* 177, 497–513. <https://doi.org/10.1016/j.earscirev.2017.12.011>
- Moos, C., Dorren, L., Stoffel, M., 2017. Quantifying the effect of forests on frequency and intensity of rockfalls. *Nat. Hazards Earth Syst. Sci.* 17, 291–304. <https://doi.org/10.5194/nhess-17-291-2017>
- Mori, A.S., Isbell, F., Seidl, R., 2018. β -Diversity, Community Assembly, and Ecosystem Functioning. *Trends Ecol. Evol.* xx, 1–16. <https://doi.org/10.1016/j.tree.2018.04.012>
- Nabuurs, G.J., Thürig, E., Heidema, N., Armolaitis, K., Biber, P., Cienciala, E., Kaufmann, E., Mäkipää, R., Nilsen, P., Petritsch, R., Pristova, T., Rock, J., Schelhaas, M.J., Sievanen, R., Somogyi, Z., Vallet, P., 2008. Hotspots of the European forests carbon cycle. *For. Ecol. Manage.* 256, 194–200. <https://doi.org/10.1016/j.foreco.2008.04.009>
- NASA, 2021. Landsat Science [WWW Document]. URL <https://landsat.gsfc.nasa.gov/>
- Netherer, S., Grasser, G., Schopf, A., Stauffer, C., 2001. Untersuchungen u“ber die Bereitschaft zur Geschwisterbrutanlage des Buchdruckers *Ips typographus* (Coleoptera; Scolytidae) aus verschiedenen Ho“henstufen. *Cent. für das gesamte Forstwes.* 118, 163–174.
- Nikinmaa, L., Lindner, M., Cantarello, E., Jump, A.S., Seidl, R., Winkel, G., Muys, B., 2020. Reviewing the Use of Resilience Concepts in Forest Sciences. *Curr. For. Reports* 6, 61–80. <https://doi.org/10.1007/s40725-020-00110-x>
- Nyman, P., Smith, H.G., Sherwin, C.B., Langhans, C., Lane, P.N.J., Sheridan, G.J., 2015. Geomorphology Predicting sediment delivery from debris fl ows after wild fi re 250, 173–

186. <https://doi.org/10.1016/j.geomorph.2015.08.023>

- Oeser, J., Pflugmacher, D., Senf, C., Heurich, M., Hostert, P., 2017. Using intra-annual Landsat time series for attributing forest disturbance agents in Central Europe. *Forests* 8. <https://doi.org/10.3390/f8070251>
- Palahí, M., Valbuena, R., Senf, C., Acil, N., Pugh, T.A.M., Sadler, J., Seidl, R., Potapov, P., Gardiner, B., Hetemäki, L., Chirici, G., Francini, S., Hlásny, T., Lerink, B.J.W., Olsson, H., Olabarria, J.R.G., Ascoli, D., Asikainen, A., Bauhus, J., Berndes, G., Donis, J., Fridman, J., Hanewinkel, M., Jactel, H., Lindner, M., Marchetti, M., Marušák, R., Sheil, D., Tomé, M., Trasobares, A., Verkerk, P.J., Korhonen, M., Nabuurs, G.J., 2021. Concerns about reported harvested area and biomass loss in European forests. *Nature* in press.
- Paquette, A., Messier, C., 2011. The effect of biodiversity on tree productivity: From temperate to boreal forests. *Glob. Ecol. Biogeogr.* 20, 170–180. <https://doi.org/10.1111/j.1466-8238.2010.00592.x>
- Pepin, N., Bradley, R.S., Diaz, H.F., Baraer, M., Caceres, E.B., Forsythe, N., Fowler, H., Greenwood, G., Hashmi, M.Z., Liu, X.D., Miller, J.R., Ning, L., Ohmura, A., Palazzi, E., Rangwala, I., Schöner, W., Severskiy, I., Shahgedanova, M., Wang, M.B., Williamson, S.N., Yang, D.Q., 2015. Elevation-dependent warming in mountain regions of the world. *Nat. Clim. Chang.* 5, 424–430. <https://doi.org/10.1038/nclimate2563>
- Perlik, M., Messerli, P., Bätzing, W., 2001. Towns in the Alps. *Mt. Res. Dev.* 21, 243–252. [https://doi.org/10.1659/0276-4741\(2001\)021\[0243:tita\]2.0.co;2](https://doi.org/10.1659/0276-4741(2001)021[0243:tita]2.0.co;2)
- Peterson, G., Allen, C.R., Holling, C.S., 1998. Ecological resilience, biodiversity, and scale. *Ecosystems* 1, 6–18. <https://doi.org/10.2307/3658701>
- Petit, R.J., Hu, F.S., Dick, C.W., 2008. Forests of the Past: A Window to Future Changes. *Science* (80-.). 320, 1450–1452. <https://doi.org/10.1126/science.1155457>
- Petter, G., Mairota, P., Albrich, K., Bebi, P., Bruna, J., Bugmann, H., Haffenden, A., Scheller, R.M., Schmatz, D.R., Seidl, R., Speich, M., Vacchiano, G., Lischke, H., 2020. How robust are future projections of forest landscape dynamics? Insights from a systematic comparison of four forest landscape models. *Environ. Model. Softw.* 134, 104844. <https://doi.org/10.1016/j.envsoft.2020.104844>
- Pflugmacher, D., Rabe, A., Peters, M., Hostert, P., 2019. Mapping pan-European land cover using Landsat spectral-temporal metrics and the European LUCAS survey. *Remote Sens. Environ.* 221, 583–595. <https://doi.org/10.1016/j.rse.2018.12.001>
- Pickett, S.T.A., White, P.S., 1985. *The Ecology of Natural Disturbance and Patch Dynamics*. Academic Press. <https://doi.org/10.1016/C2009-0-02952-3>
- Pretzsch, H., del Río, M., Ammer, C., Avdagic, A., Barbeito, I., Bielak, K., Brazaitis, G., Coll, L., Dirnberger, G., Drössler, L., Fabrika, M., Forrester, D.I., Godvod, K., Heym, M., Hurt, V., Kurylyak, V., Löf, M., Lombardi, F., Matović, B., Mohren, F., Motta, R., den Ouden, J., Pach, M., Ponette, Q., Schütze, G., Schweig, J., Skrzyszewski, J., Sramek, V., Sterba, H., Stojanović, D., Svoboda, M., Vanhellefont, M., Verheyen, K., Wellhausen, K., Zlatanov, T., Bravo-Oviedo, A., 2015. Growth and yield of mixed versus pure stands of Scots pine (*Pinus sylvestris* L.) and European beech (*Fagus sylvatica* L.) analysed along a productivity gradient through Europe. *Eur. J. For. Res.* 134, 927–947. <https://doi.org/10.1007/s10342-015-0900-4>
- Ratcliffe, S., Wirth, C., Jucker, T., van der Plas, F., Scherer-Lorenzen, M., Verheyen, K., Allan, E., Benavides, R., Bruelheide, H., Ohse, B., Paquette, A., Ampoorter, E., Bastias, C.C.,

- Bauhus, J., Bonal, D., Bouriaud, O., Bussotti, F., Carnol, M., Castagneyrol, B., Češko, E., Dawud, S.M., Wandeler, H. De, Domisch, T., Finér, L., Fischer, M., Fotelli, M., Gessler, A., Granier, A., Grossiord, C., Guyot, V., Haase, J., Hättenschwiler, S., Jactel, H., Jaroszewicz, B., Joly, F.X., Kambach, S., Kolb, S., Koricheva, J., Liebersgesell, M., Milligan, H., Müller, S., Muys, B., Nguyen, D., Nock, C., Pollastrini, M., Purschke, O., Radoglou, K., Raulund-Rasmussen, K., Roger, F., Ruiz-Benito, P., Seidl, R., Selvi, F., Seiferling, I., Stenlid, J., Valladares, F., Vesterdal, L., Baeten, L., 2017. Biodiversity and ecosystem functioning relations in European forests depend on environmental context. *Ecol. Lett.* 20, 1414–1426. <https://doi.org/10.1111/ele.12849>
- San-Miguel-Ayanz, J., Schulte, E., Schmuck, G., Camia, A., Strobl, A., Liberta, Giorgio Giovando, Cristiano Boca, R., Sedano, Fernando Kempeneers, P., McInerney, D., Withmore, C., Santos de Oliveira, S., Rodrigues, M., Durrant, T., Corti, P., Oehler, F., Vilar, L., Amatulli, G., 2012. Comprehensive Monitoring of Wildfires in Europe: The European Forest Fire Information System (EFFIS). *Eur. Comm. Jt. Res. Cent.*
- Schaberg, P.G., DeHayes, D.H., Hawley, G.J., Nijensohn, S.E., 2008. Anthropogenic alterations of genetic diversity within tree populations: Implications for forest ecosystem resilience. *For. Ecol. Manage.* 256, 855–862. <https://doi.org/10.1016/j.foreco.2008.06.038>
- Schall, P., Gossner, M.M., Heinrichs, S., Fischer, M., Boch, S., Prati, D., Jung, K., Baumgartner, V., Blaser, S., Böhm, S., Buscot, F., Daniel, R., Goldmann, K., Kaiser, K., Kahl, T., Lange, M., Müller, J., Overmann, J., Renner, S.C., Schulze, E.D., Sikorski, J., Tschapka, M., Türke, M., Weisser, W.W., Wemheuer, B., Wubet, T., Ammer, C., 2018. The impact of even-aged and uneven-aged forest management on regional biodiversity of multiple taxa in European beech forests. *J. Appl. Ecol.* 55, 267–278. <https://doi.org/10.1111/1365-2664.12950>
- Scheidt, C., Heiser, M., Kamper, S., Thaler, T., Klebinder, K., Nagl, F., Lechner, V., Markart, G., Rammer, W., Seidl, R., 2020. Science of the Total Environment The influence of climate change and canopy disturbances on landslide susceptibility in headwater catchments. *Sci. Total Environ.* 742, 140588. <https://doi.org/10.1016/j.scitotenv.2020.140588>
- Schelhaas, M.-J., Nabuurs, G.-J., Schuck, A., 2003. Natural disturbances in the European forests in the 19th and 20th centuries. *Glob. Chang. Biol.* 9, 1620–1633. <https://doi.org/10.1046/j.1529-8817.2003.00684.x>
- Schleeweis, K.G., Moisen, G.G., Schroeder, T.A., Toney, C., Freeman, E.A., Goward, S.N., Huang, C., Dungan, J.L., 2020. US national maps attributing forest change: 1986–2010. *Forests* 11, 1–20. <https://doi.org/10.3390/F11060653>
- Schmidt, M., Hanewinkel, M., Kändler, G., Kublin, E., Kohnle, U., 2010. An inventory-based approach for modeling singletree storm damage - experiences with the winter storm of 1999 in southwestern Germany. *Can. J. For. Res.* 40, 1636–1652. <https://doi.org/10.1139/X10-099>
- Schroeder, T.A., Wulder, M.A., Healey, S.P., Moisen, G.G., 2011. Mapping wildfire and clearcut harvest disturbances in boreal forests with Landsat time series data. *Remote Sens. Environ.* 115, 1421–1433. <https://doi.org/10.1016/j.rse.2011.01.022>
- Schuler, L.J., Bugmann, H., Petter, G., Snell, R.S., 2019. How multiple and interacting disturbances shape tree diversity in European mountain landscapes. *Landsc. Ecol.* 34, 1279–1294. <https://doi.org/10.1007/s10980-019-00838-3>

- Schuler, L.J., Bugmann, H., Snell, R.S., 2017. From monocultures to mixed-species forests: is tree diversity key for providing ecosystem services at the landscape scale? *Landsc. Ecol.* 32, 1499–1516. <https://doi.org/10.1007/s10980-016-0422-6>
- Schumacher, S., Bugmann, H., Mladenoff, D.J., 2004. Improving the formulation of tree growth and succession in a spatially explicit landscape model. *Ecol. Modell.* 180, 175–194. <https://doi.org/10.1016/j.ecolmodel.2003.12.055>
- Schumacher, S., Reineking, B., Sibold, J., Bugmann, H., 2006. Modeling the impact of climate and vegetation on fire regimes in mountain landscapes. *Landsc. Ecol.* 21, 539–554. <https://doi.org/10.1007/s10980-005-2165-7>
- Sebald, J., Senf, C., Heiser, M., Scheidl, C., Pflugmacher, D., Seidl, R., 2019. The effects of forest cover and disturbance on torrential hazards: Large-scale evidence from the Eastern Alps. *Environ. Res. Lett.* <https://doi.org/10.1088/1748-9326/ab4937>
- Sebald, J.J., 2018. Störungsanalyse für Österreichs Wald anhand von Satellitenbildern der Jahre 1985 bis 2016 Masterarbeit Institut für Waldbau 66.
- Seidl, R., 2017. To Model or not to Model, That is no Longer the Question for Ecologists. *Ecosystems* 20, 222–228. <https://doi.org/10.1007/s10021-016-0068-x>
- Seidl, R., 2014. The shape of ecosystem management to come: Anticipating risks and fostering resilience. *Bioscience* 64, 1159–1169. <https://doi.org/10.1093/biosci/biu172>
- Seidl, R., Albrich, K., Thom, D., Rammer, W., 2018a. Harnessing landscape heterogeneity for managing future disturbance risks in forest ecosystems. *J. Environ. Manage.* 209, 46–56. <https://doi.org/10.1016/j.jenvman.2017.12.014>
- Seidl, R., Klonner, G., Rammer, W., Essl, F., Moreno, A., Neumann, M., Dullinger, S., 2018b. Invasive alien pests threaten the carbon stored in Europe's forests. *Nat. Commun.* 9, 1–10. <https://doi.org/10.1038/s41467-018-04096-w>
- Seidl, R., Müller, J., Hothorn, T., Bässler, C., Heurich, M., Kautz, M., 2016a. Small beetle, large-scale drivers: How regional and landscape factors affect outbreaks of the European spruce bark beetle. *J. Appl. Ecol.* 53, 530–540. <https://doi.org/10.1111/1365-2664.12540>
- Seidl, R., Rammer, W., Scheller, R.M., Spies, T.A., 2012. An individual-based process model to simulate landscape-scale forest ecosystem dynamics. *Ecol. Modell.* 231, 87–100. <https://doi.org/10.1016/j.ecolmodel.2012.02.015>
- Seidl, R., Rammer, W., Spies, T.A., 2014a. Disturbance legacies increase the resilience of forest ecosystem structure, composition, and functioning. *Ecol. Appl.* 24, 2063–2077. <https://doi.org/10.1890/14-0255.1>
- Seidl, R., Schelhaas, M.J., Lexer, M.J., 2011. Unraveling the drivers of intensifying forest disturbance regimes in Europe. *Glob. Chang. Biol.* 17, 2842–2852. <https://doi.org/10.1111/j.1365-2486.2011.02452.x>
- Seidl, R., Schelhaas, M.J., Rammer, W., Verkerk, P.J., 2014b. Increasing forest disturbances in Europe and their impact on carbon storage. *Nat. Clim. Chang.* 4, 806–810. <https://doi.org/10.1038/nclimate2318>
- Seidl, R., Spies, T.A., Peterson, D.L., Stephens, S.L., Hicke, J.A., 2016b. Searching for resilience: Addressing the impacts of changing disturbance regimes on forest ecosystem services. *J. Appl. Ecol.* 53, 120–129. <https://doi.org/10.1111/1365-2664.12511>

- Senf, C., Buras, A., Zang, C.S., Rammig, A., Seidl, R., 2020. Excess forest mortality is consistently linked to drought across Europe. *Nat. Commun.* 11, 1–8. <https://doi.org/10.1038/s41467-020-19924-1>
- Senf, C., Müller, J., Seidl, R., 2019. Post-disturbance recovery of forest cover and tree height differ with management in Central Europe. *Landsc. Ecol.* 9, 2837–2850. <https://doi.org/10.1007/s10980-019-00921-9>
- Senf, C., Pflugmacher, D., Hostert, P., Seidl, R., 2017a. Using Landsat time series for characterizing forest disturbance dynamics in the coupled human and natural systems of Central Europe. *ISPRS J. Photogramm. Remote Sens.* 130, 453–463. <https://doi.org/10.1016/j.isprsjprs.2017.07.004>
- Senf, C., Pflugmacher, D., Hostert, P., Seidl, R., 2017b. Using Landsat time series for characterizing forest disturbance dynamics in the coupled human and natural systems of Central Europe. *ISPRS J. Photogramm. Remote Sens.* 130, 453–463. <https://doi.org/10.1016/j.isprsjprs.2017.07.004>
- Senf, C., Pflugmacher, D., Zhiqiang, Y., Sebal, J., Knorn, J., Neumann, M., Hostert, P., Seidl, R., 2018a. Canopy mortality has doubled in Europe's temperate forests over the last three decades. *Nat. Commun.* 9, 4978. <https://doi.org/10.1038/s41467-018-07539-6>
- Senf, C., Pflugmacher, D., Zhiqiang, Y., Sebal, J., Knorn, J., Neumann, M., Hostert, P., Seidl, R., 2018b. Canopy mortality has doubled in Europe's temperate forests over the last three decades. *Nat. Commun.* 9, 4978. <https://doi.org/10.1038/s41467-018-07539-6>
- Senf, C., Sebal, J., Seidl, R., 2021. Increasing canopy mortality affects the future demographic structure of Europe's forests II Increasing canopy mortality affects the future demographic structure of Europe's forests. *One Earth* 1–7. <https://doi.org/https://doi.org/10.1016/j.oneear.2021.04.008>
- Senf, C., Seidl, R., 2021a. Mapping the forest disturbance regimes of Europe. *Nat. Sustain.* 4, 63–70. <https://doi.org/10.1038/s41893-020-00609-y>
- Senf, C., Seidl, R., 2021b. Storm and fire disturbances in Europe: distribution and trends. *Glob. Chang. Biol.* 0–2. <https://doi.org/10.1111/gcb.15679>
- Senf, C., Seidl, R., 2018. Natural disturbances are spatially diverse but temporally synchronized across temperate forest landscapes in Europe. *Glob. Chang. Biol.* 24, 1201–1211. <https://doi.org/10.1111/gcb.13897>
- Sgrò, C.M., Lowe, A.J., Hoffmann, A.A., 2011. Building evolutionary resilience for conserving biodiversity under climate change. *Evol. Appl.* 4, 326–337. <https://doi.org/10.1111/j.1752-4571.2010.00157.x>
- Shchur, A., Bragina, E., Sieber, A., Pidgeon, A.M., Radeloff, V.C., 2017. Monitoring selective logging with Landsat satellite imagery reveals that protected forests in Western Siberia experience greater harvest than non-protected forests. *Environ. Conserv.* 44, 191–199. <https://doi.org/10.1017/S0376892916000576>
- Silva Pedro, M., Rammer, W., Seidl, R., 2016. A disturbance-induced increase in tree species diversity facilitates forest productivity. *Landsc. Ecol.* 31, 989–1004. <https://doi.org/10.1007/s10980-015-0317-y>
- Statista.com, 2021. Fläche des alpinen Raums in den Alpenanrainerstaaten im Jahr 2013 [WWW Document]. URL <https://de.statista.com/statistik/impressum/>

- Stritih, A., Senf, C., Seidl, R., Grêt-Regamey, A., Bebi, P., 2021. The impact of land-use legacies and recent management on natural disturbance susceptibility in mountain forests. *For. Ecol. Manage.* 484. <https://doi.org/10.1016/j.foreco.2021.118950>
- Suvanto, S., Peltoniemi, M., Tuominen, S., Strandström, M., Lehtonen, A., 2019. High-resolution mapping of forest vulnerability to wind for disturbance-aware forestry. *For. Ecol. Manage.* 453, 117619. <https://doi.org/10.1016/j.foreco.2019.117619>
- Thom, D., Rammer, W., Dirnböck, T., Müller, J., Kobler, J., Katzensteiner, K., Helm, N., Seidl, R., 2017a. The impacts of climate change and disturbance on spatio-temporal trajectories of biodiversity in a temperate forest landscape. *J. Appl. Ecol.* 54, 28–38. <https://doi.org/10.1111/1365-2664.12644>
- Thom, D., Rammer, W., Seidl, R., 2017b. Disturbances catalyze the adaptation of forest ecosystems to changing climate conditions. *Glob. Chang. Biol.* 23, 269–282. <https://doi.org/10.1111/gcb.13506>
- Thom, D., Seidl, R., 2016. Natural disturbance impacts on ecosystem services and biodiversity in temperate and boreal forests. *Biol. Rev. Camb. Philos. Soc.* 91, 760–781. <https://doi.org/10.1111/brv.12193>
- Thorn, S., Bässler, C., Brandl, R., Burton, P.J., Cahall, R., Campbell, J.L., Castro, J., Choi, C.Y., Cobb, T., Donato, D.C., Durska, E., Fontaine, J.B., Gauthier, S., Hebert, C., Hothorn, T., Hutto, R.L., Lee, E.J., Leverkus, A.B., Lindenmayer, D.B., Obrist, M.K., Rost, J., Seibold, S., Seidl, R., Thom, D., Waldron, K., Wermelinger, B., Winter, M.B., Zmihorski, M., Müller, J., 2018. Impacts of salvage logging on biodiversity: A meta-analysis. *J. Appl. Ecol.* 55, 279–289. <https://doi.org/10.1111/1365-2664.12945>
- Thorn, S., Bässler, C., Svoboda, M., Müller, J., 2017. Effects of natural disturbances and salvage logging on biodiversity – Lessons from the Bohemian Forest. *For. Ecol. Manage.* 388, 113–119. <https://doi.org/10.1016/j.foreco.2016.06.006>
- Thorn, S., Chao, A., Georgiev, K.B., Müller, J., Bässler, C., Campbell, J.L., Castro, J., Chen, Y.-H., Choi, C.-Y., Cobb, T.P., Donato, D.C., Durska, E., Macdonald, E., Feldhaar, H., Fontaine, J.B., Fornwalt, P.J., Hernández, R.M.H., Hutto, R.L., Koivula, M., Lee, E.-J., Lindenmayer, D., Mikusiński, G., Obrist, M.K., Perlík, M., Rost, J., Waldron, K., Wermelinger, B., Weiß, I., Žmihorski, M., Leverkus, A.B., 2020. Estimating retention benchmarks for salvage logging to protect biodiversity. *Nat. Commun.* (in press), 1–8. <https://doi.org/10.1038/s41467-020-18612-4>
- Triviño, M., Pohjanmies, T., Mazziotta, A., Juutinen, A., Podkopaev, D., Le Tortorec, E., Mönkkönen, M., 2017. Optimizing management to enhance multifunctionality in a boreal forest landscape. *J. Appl. Ecol.* 54, 61–70. <https://doi.org/10.1111/1365-2664.12790>
- UNECE/FAO, 2009. Private Forest Ownership in Europe. *For. Prod. Annu. Mark. Rev.* 2008-2009 24, 186.
- Urban, D.L., Neill, R.V.O., Shugart, H.H., 1987. Ecology Landscape spatial patterns. *Bioscience* 37, 119–127.
- Van Der Plas, F., Manning, P., Soliveres, S., Allan, E., Scherer-Lorenzen, M., Verheyen, K., Wirth, C., Zavala, M.A., Ampoorter, E., Baeten, L., Barbaro, L., Bauhus, J., Benavides, R., Benneter, A., Bonal, D., Bouriaud, O., Bruelheide, H., Bussotti, F., Carnol, M., Castagneyrol, B., Charbonnier, Y., Coomes, D.A., Coppi, A., Bestias, C.C., Dawud, S.M., De Wandeler, H., Domisch, T., Finér, L., Gessler, A., Granier, A., Grossiord, C., Guyot, V., Hättenschwiler, S., Jactel, H., Jaroszewicz, B., Joly, F.X., Jucker, T., Koricheva, J., Milligan, H., Mueller, S., Muys, B., Nguyen, D., Pollastrini, M., Ratcliffe, S., Raulund-

- Rasmussen, K., Selvi, F., Stenlid, J., Valladares, F., Vesterdal, L., Zielinski, D., Fischer, M., Schlesinger, W.H., 2016. Biotic homogenization can decrease landscape-scale forest multifunctionality. *Proc. Natl. Acad. Sci. U. S. A.* 113, 3557–3562. <https://doi.org/10.1073/pnas.1517903113>
- van der Plas, F., Ratcliffe, S., Ruiz-Benito, P., Scherer-Lorenzen, M., Verheyen, K., Wirth, C., Zavala, M.A., Ampoorter, E., Baeten, L., Barbaro, L., Bastias, C.C., Bauhus, J., Benavides, R., Benneter, A., Bonal, D., Bouriaud, O., Bruelheide, H., Bussotti, F., Carnol, M., Castagneyrol, B., Charbonnier, Y., Cornelissen, J.H.C., Dahlgren, J., Checko, E., Coppi, A., Dawud, S.M., Deconchat, M., De Smedt, P., De Wandeler, H., Domisch, T., Finér, L., Fotelli, M., Gessler, A., Granier, A., Grossiord, C., Guyot, V., Haase, J., Hättenschwiler, S., Jactel, H., Jaroszewicz, B., Joly, F.X., Jucker, T., Kambach, S., Kaendler, G., Kattge, J., Koricheva, J., Kunstler, G., Lehtonen, A., Liebergesell, M., Manning, P., Milligan, H., Müller, S., Muys, B., Nguyen, D., Nock, C., Ohse, B., Paquette, A., Peñuelas, J., Pollastrini, M., Radoglou, K., Raulund-Rasmussen, K., Roger, F., Seidl, R., Selvi, F., Stenlid, J., Valladares, F., van Keer, J., Vesterdal, L., Fischer, M., Gamfeldt, L., Allan, E., 2018. Continental mapping of forest ecosystem functions reveals a high but unrealised potential for forest multifunctionality. *Ecol. Lett.* 21, 31–42. <https://doi.org/10.1111/ele.12868>
- Wallace, M.W., Hood, A., Shuster, A., Greig, A., Planavsky, N.J., Reed, C.P., 2017. Oxygenation history of the Neoproterozoic to early Phanerozoic and the rise of land plants. *Earth Planet. Sci. Lett.* 466, 12–19. <https://doi.org/10.1016/j.epsl.2017.02.046>
- White, J.C., Wulder, M.A., Hermosilla, T., Coops, N.C., Hobart, G.W., 2017. A nationwide annual characterization of 25 years of forest disturbance and recovery for Canada using Landsat time series. *Remote Sens. Environ.* 194, 303–321. <https://doi.org/10.1016/j.rse.2017.03.035>
- Willis, K.J., Van Andel, T.H., 2004. Trees or no trees? The environments of central and eastern Europe during the Last Glaciation. *Quat. Sci. Rev.* 23, 2369–2387. <https://doi.org/10.1016/j.quascirev.2004.06.002>
- Wulder, M.A., Masek, J.G., Cohen, W.B., Loveland, T.R., Woodcock, C.E., 2012. Opening the archive: How free data has enabled the science and monitoring promise of Landsat. *Remote Sens. Environ.* 122, 2–10. <https://doi.org/10.1016/j.rse.2012.01.010>
- Zimová, S., Dobor, L., Hlásny, T., Rammer, W., Seidl, R., 2020. Reducing rotation age to address increasing disturbances in Central Europe: Potential and limitations. *For. Ecol. Manage.* 475, 118408. <https://doi.org/10.1016/j.foreco.2020.118408>
- Zurbriggen, N., Nabel, J.E.M.S., Teich, M., Bebi, P., Lischke, H., 2014. Explicit avalanche-forest feedback simulations improve the performance of a coupled avalanche-forest model. *Ecol. Complex.* 17, 56–66. <https://doi.org/10.1016/j.ecocom.2013.09.002>

7 Appendix

A: Human or natural? Landscape context improves the attribution of forest disturbances mapped from Landsat in Central Europe

B: The effects of forest cover and disturbance on torrential hazards: large-scale evidence from the Eastern Alps

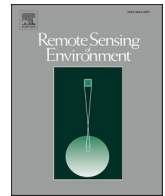
C: Mixing tree species at different spatial scales: the effect of alpha, beta and gamma diversity on disturbance impacts under climate change

D: Academic Curriculum Vitae

Appendix A: Human or natural? Landscape context improves the attribution of forest disturbances mapped from Landsat in Central Europe

Published 2021 in *Remote Sensing of Environment*

Impact factor 2019: 9.763



Human or natural? Landscape context improves the attribution of forest disturbances mapped from Landsat in Central Europe

Julius Sebald^{a,b,*}, Cornelius Senf^b, Rupert Seidl^{a,b,c}

^a Institute of Silviculture, Department of Forest- and Soil Sciences, University of Natural Resources and Life Sciences (BOKU) Vienna, Peter-Jordan-Straße 82, 1190 Vienna, Austria

^b Ecosystem Dynamics and Forest Management Group, School of Life Sciences, Technical University of Munich, Hans-Carl-von-Carlowitz-Platz 2, 85354 Freising, Germany

^c Berchtesgaden National Park, Doktorberg 6, 83471 Berchtesgaden, Germany

ARTICLE INFO

Editor name: Marie Weiss

ABSTRACT

Disturbances have increased in Central Europe's forests, but whether changes in disturbance regimes are driven by natural or human causes remains unclear. Satellite-based remote sensing provides an important data source for quantifying forest disturbance change. Separating causes of forest disturbance is challenging, however, particularly in areas such as Central Europe where disturbance patches are small and disturbance agents interact strongly. Here we present a novel approach for the causal attribution of forest disturbance agents and illustrate its utility for 1.01 million disturbance patches mapped from Landsat data in Austria for the period 1986–2016. We gathered reference data on 2620 disturbance patches by conducting targeted field observations and structured interviews with 21 forest managers. We developed a novel indicator class characterizing the landscape context of a disturbance patch (i.e., the spatio-temporal autocorrelation of disturbance patches on the landscape), and combined it with other predictor variables describing the spectral signal, topography, and patch form of each disturbance patch. We used these predictors to identify the causal agents for disturbances mapped in Austria using Random Forest classification. Landscape context was the most important predictor of disturbance agent, improving model performance by up to 26 percentage points. Wind, bark beetles and timber harvesting were separated with an overall accuracy of 63%. Bark beetle patches were most difficult to identify correctly (producer's accuracy = 15%, user's accuracy = 30%), while regular timber harvesting was classified with highest certainty (producer's accuracy = 68%, user's accuracy = 82%). Harvesting dominates the disturbance regime of Austria's forests, with 70.5% of the disturbed area (76.7% of the disturbed patches) attributed to human causes and 29.5% (23.3%) to natural causes (wind: 23.0% [14.8%], bark beetles: 6.5% [8.5%]). Increases in disturbance since 1986 were driven by natural causes, with wind increasing by 408% and bark beetles increasing by 99% between the first and the second half of the observation period. Wind-disturbed patches were also considerably larger than those caused by bark beetles and harvesting (+102% and +67%, respectively). Our novel approach to mapping causal agents of forest disturbance, applicable also to highly complex and interactive disturbance regimes, provides an important step towards a comprehensive monitoring and management of forest disturbances in a changing world.

1. Introduction

Disturbance is an important process in forest ecosystem dynamics. Disturbances are relatively discrete events in time that disrupt the structure of an ecosystem, community or population and change resource availability (Pickett and White, 1985). As such, disturbances

shape the structure, species composition and demography of forests for decades to centuries (Schuler et al., 2019; Schurman et al., 2018; Senf et al., 2021; Thom et al., 2018). Besides their ecological importance, disturbances directly affect human well-being through their impact on the supply of ecosystem services (Thom and Seidl, 2016), such as timber production (Seidl et al., 2008), protection against natural hazards

* Corresponding author at: Institute of Silviculture, Department of Forest- and Soil Sciences, University of Natural Resources and Life Sciences (BOKU) Vienna, Peter-Jordan-Straße 82, 1190 Vienna, Austria.

E-mail address: julius.sebald@tum.de (J. Sebald).

<https://doi.org/10.1016/j.rse.2021.112502>

Received 26 November 2020; Received in revised form 4 May 2021; Accepted 11 May 2021

Available online 20 May 2021

0034-4257/© 2021 The Author(s). Published by Elsevier Inc. This is an open access article under the CC BY license (<http://creativecommons.org/licenses/by/4.0/>).

(Sebold et al., 2019), or carbon storage (Dobor et al., 2018; Pugh et al., 2019; Seidl et al., 2014). Forest disturbances also affect wildlife habitat (Kortmann et al., 2018; Thom et al., 2017; Thorn et al., 2017), and are a strong driver of the prevalence of many forest-dwelling species (Hilmers et al., 2018). Given their relevance for both humans and the environment, there is increasing interest in monitoring forest disturbances from local to global scales (Griffiths et al., 2014; Hansen et al., 2013; Masek et al., 2013; White et al., 2017), especially because forest disturbances are highly sensitive to climate change (Seidl et al., 2020, 2017; Sommerfeld et al., 2018).

Disturbances have increased over the past thirty years in Central Europe, but the causes of this increase remain unresolved. Since 1986, disturbance rates have doubled in Central Europe (Senf et al., 2018) with the highest disturbance rate of the period 1986–2018 observed in 2018 (Senf et al., 2021). Increases in disturbance rates resulted primarily from increasing disturbance frequency rather than increasing patch size, while disturbance severity generally decreased in Central Europe (Senf and Seidl, 2021). Yet, the root causes of disturbance and the contribution of individual disturbance agents to the observed increase remain disputed. While some studies identify forestry to be the driving force behind increasing disturbances in Central Europe (Ceccherini et al., 2020; Curtis et al., 2018), others suggest that climate change and increased natural disturbances are a major driver (Klein and Hartmann, 2018). It remains unclear whether the increases in forest disturbance reported for Central Europe are due to elevated human resource use (i.e., timber harvest) or increased natural disturbances (e.g., wind-throw and bark beetle outbreaks, the two most important agents of natural disturbance in Central Europe, Thom et al., 2013). It is of central relevance for policy and resource management to understand the drivers underlying recent changes in Europe's forests (McDowell et al., 2015). While human disturbances are the result of active decision making – their occurrence, frequency, extent and severity are directly controlled by managers on the ground – the dynamics of natural disturbances remain difficult to control, especially under climate change (Seidl et al., 2017). Natural disturbances frequently upend management plans and challenge the stable and continuous supply of ecosystem services to society (Albrich et al., 2018). Further, natural disturbances are expected to intensify due to climate change (McDowell et al., 2020), potentially exceeding the ecological resilience of forests and resulting in regime shifts (Hughes et al., 2013). Therefore, it is necessary to accurately identify the causes of forest disturbance in order to develop appropriate response strategies to the ongoing changes in Europe's forests.

Remote sensing using moderate-resolution sensors has evolved as a key tool for forest disturbance ecology. Since the opening of the Landsat archive in 2008, numerous studies have utilized the long and dense time series of Landsat for mapping forest disturbances in a variety of different ecosystems (e.g., Neigh et al., 2014a; Schroeder et al., 2017; White et al., 2017; Zhu, 2017). While mapping forest disturbances from Landsat data is thus quasi-operational (e.g., Hansen et al., 2013; Senf and Seidl, 2021), the attribution of causal agents of disturbance remains a major challenge (Anderegg et al., 2020). Previous attempts have jointly used spectral information, topography and patch metrics (e.g., the size and shape of a disturbance patch) to identify causal agents of forest disturbance (Hermosilla et al., 2015; Kennedy et al., 2015; Schroeder et al., 2017). Reference data has often been collected via the interpretation of high-resolution imagery (e.g., Shimizu et al., 2017). While such approaches led to satisfactory results in some regions of the world (e.g., Canada: Hermosilla et al., 2015, USA: Kennedy et al., 2015; Schroeder et al., 2017), its application in Central Europe revealed a number of challenges (Oeser et al., 2017; Senf et al., 2017; Senf and Seidl, 2021): First, patch sizes are generally much smaller in Central Europe, compared to the US or Canada, inherently reducing the diversity of patch forms at a given pixel size and limiting the inferential potential of patch metrics for distinguishing causal agents of disturbance. Hermosilla et al. (2015), for example, report an average size of 98 ha for disturbance patches caused by timber logging in Canada, while patches created by

wildfire were on average more than three times larger (324 ha). In contrast, approximately 99% of all disturbances patches from both natural and human causes are smaller than 10 ha in Central Europe (Senf and Seidl, 2021), limiting the use of patch metrics to distinguish between disturbance agents. Second, the forests of Central Europe are intensively managed and salvage logging after natural disturbance is a common practice (Leverkus et al., 2018; Thorn et al., 2020, 2017). Consequently, the spectral signal of natural disturbances is frequently inseparable to that of human disturbances, especially when working with annual resolution Landsat time series (Senf et al., 2017). Third, freely available high-resolution imagery is often limited to recent years, underlies access restrictions, and/or has low temporal resolution. This, in combination with immediate salvage logging, limits the instances where the causal agent of a forest disturbance can be determined with confidence from high resolution imagery in Central Europe.

The fact that the forests of Central Europe are coupled human and natural systems might also provide an advantage for disturbance attribution. In particular, planned logging traditionally aims at sustainable timber supply, which leads to largely constant disturbance rates in space and time (Sebold et al., 2019; White et al., 2017). In contrast, natural disturbances often occur in localized pulses (Kennedy et al., 2015; Schroeder et al., 2017, 2011; Senf and Seidl, 2018). For example, cyclonic storm events leave distinct tracks of spatially autocorrelated disturbance patches visible at the landscape-scale (Forzieri et al., 2020; Turner and Gardner, 2015). Similarly, bark beetles only disperse for a few tens to hundreds of meters, and infestations are thus spatially autocorrelated (Seidl et al., 2016b; Turner et al., 1989). Consequently, natural disturbances create a distinctly different landscape pattern surrounding a given disturbance patch compared to planned harvest. Here, we hypothesized that the landscape context (e.g., how a disturbance patch relates to disturbances in the landscape surrounding it) holds important information for identifying the causal agent of a disturbance. Additionally, we aimed at taking advantage of the intensive management of Central Europe's forests for creating a reliable reference database for disturbance attribution. Forest managers are an excellent source of information on causal agents of disturbance, because they are the ones planning and implementing management interventions, and because they usually have good knowledge of the natural disturbances affecting their management district. In Central Europe, management districts are typically small (1000–5000 ha), and managers often spend their entire professional life in the same district. They thus have detailed local knowledge on disturbances. Yet this information can be difficult to integrate with remote sensing data because it is distributed across many individuals and hard to quantify. Here we combine established methods of qualitative GIS (Cope and Elwood, 2009), participatory mapping (Cadag and Gaillard, 2012; Chambers, 2006) and citizen science (Bonney et al., 2009; Dickinson et al., 2010) to tap into the available knowledge of forest managers.

We present a novel approach harnessing managers' knowledge and information on landscape context for improving the attribution of forest disturbances mapped from satellite data to causal agents. Our main motivation was to improve our understanding of the drivers of recent increases in disturbance rates in Central Europe, i.e., to determine whether elevated timber harvesting or increased natural disturbances are behind recent changes in the forest disturbance regime. We focused on Austria, a country representing several important European forest types because of its high environmental variation. Our specific objectives were to:

- (1) establish a local reference database on the causal agents of forest disturbance through conducting structured interviews with forest managers;
- (2) investigate the discriminating power of landscape context indicators (i.e., the spatial-temporal autocorrelation of disturbances) for the attribution of causal agents, focusing on (planned) harvest, wind and bark beetle disturbances;

- (3) attribute a total of 1.01 million disturbance patches in Austria for the period 1986–2016 to either harvest, wind or bark beetles, and quantify their patterns, prevalence and trends; and
- (4) compare the prevalence and trends of disturbance agents to official statistics, testing the applicability of our approach in the context of the forest disturbance regimes of Central Europe.

2. Methods

2.1. Study area

Austria is a topographically diverse country located in Central Europe. It is characterized by high mountains in the west and south, while plains dominate the east and uplands characterize the north of the country. A total of 48% (~4,000,000 ha) of the land area is forested, with forests extending over an elevation gradient from the natural tree line at between 1800 and 2300 m a.s.l. to forests near the lower tree line at 100 m a.s.l. Forests are dominated by conifers (80.2% of growing stock, BFW, 2020), with Norway spruce (*Picea abies* (L.) Karst), European larch (*Larix decidua* L.), Scots pine (*Pinus sylvestris* L.) and Silver fir (*Abies alba* Mill.) being the most important tree species (BFW, 2020). The most common broadleaved tree species are European beech (*Fagus sylvatica* L.) and pedunculate oak (*Quercus robur* L.) (BFW, 2020). The natural disturbance regime of Austria is dominated by wind and bark beetle infestations (Thom et al., 2013). Forest fires do not play an important role in Austria at the moment, but might become more important in the future (Müller et al., 2013).

Austria's forests are intensively managed, with a high ratio of professional forestry staff per forest area (7.8 professional forest managers per 10,000 ha forest area, BMFLUW, 2008). Forest owners with a property larger than 1000 ha are required by law to hire professional staff for managing their forest. Further, the law strictly regulates forestry operations such as clearcutting, replanting and salvage logging. For example, the clear-cut size is restricted to <2 ha, standing or uprooted trees that are infested by bark beetles have to be salvage logged within two weeks after detection, and both natural disturbances and clear-cuts must be restocked within five years. Consequently, mean patch sizes are small and regeneration periods are short, making causal agent attribution from satellite data challenging (Senf et al., 2017).

2.2. Forest disturbance map

We used an existing Landsat-based European forest disturbance map to identify disturbance patches (Senf and Seidl, 2021, available from doi://doi.org/10.5281/zenodo.4570157; version 1.0.0). The disturbance map was created at a spatial grain of 30 m and identifies disturbances at annual resolution for the period from 1986 to 2016. It is based on all available Collection 1 Level 1 surface reflectance images from the USGS Landsat archive and a well-established disturbance detection algorithm (Kennedy et al., 2010) implemented in the Google Earth Engine cloud computing platform (Gorelick et al., 2017a; Kennedy et al., 2018). Disturbances in Europe were mapped with an overall accuracy of 92.5%, a commission error of 14.6% and an omission error of 32.8%. Disturbance patches were defined annually using rook-contiguity. The mean absolute error of the mapped disturbance year is 3 years and 77% of disturbance years were classified within this range (Senf and Seidl, 2021).

2.3. Reference data

For attributing causal agents of disturbance, we collected reference data across Austria from March to December of 2019. The data was collected in nine forest enterprises and two national parks (Fig. 1, Table 1). Forest enterprises in Central Europe are the administrative entities responsible for management, and are comprised by multiple forest management units. We contacted ten forest enterprises distributed

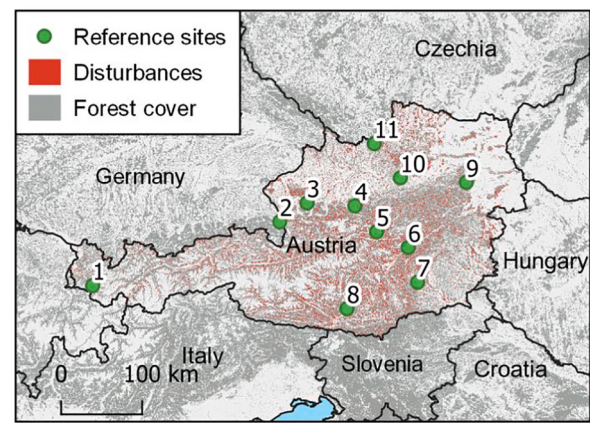


Fig. 1. Disturbance map showing the study area (Austria) and the sites for which reference data on disturbance agents were collected. Disturbances (canopy removal) were mapped from Landsat data at a spatial grain of 30×30 m (Senf and Seidl, 2021). Reference site 4 and 5 are National parks, reference site 1–3 and 6–11 are forest enterprises.

across Austria, of which nine agreed to contribute to our analysis. Contact information for all forest enterprises managing a forest area larger than 500 ha in Austria is publicly available in a forestry yearbook. In each forest enterprise we conducted structured interviews with professional foresters, obtaining local expert information on the occurrence of harvest, bark beetle and wind disturbances (comparable to participatory mapping approaches see Cadag and Gaillard, 2012; Chambers, 2006). In addition to these three major disturbance agents we also recorded patches caused by fire, gravitational events and land use change. Their frequency was too low, however, to be included in our analysis (fire $n = 1$, gravitational events $n = 114$, land use change $n = 74$, of the 2809 patches recorded). Enterprises were typically structured into management units with a size between 1000 and 5000 ha. Each of these management units had a responsible forest manager, in charge of the executive management decisions in the district (e.g. timber harvesting, replanting, salvage logging). Managers thus have detailed, first-hand knowledge on all harvesting operations and natural disturbances that happen in their area of responsibility. During the interviews, the interviewer and the forest manager went through patches of the Landsat-based disturbance map (Senf and Seidl, 2021) and determined the causal agent of disturbance patches. Patches for which forest managers were not able to identify the causal agent with certainty were skipped. If more than one agent was responsible for a disturbance patch, the agent that had caused the largest proportion of the patch was recorded. We preferably interviewed experienced foresters who had been in charge of their district for more than 20 years, thus covering the majority of the time span covered by the European forest disturbance map (1986 to 2016). In total, we interviewed 21 foresters, managing a forest area of ~37,000 ha, accessing the combined knowledge of 501 cumulative years of professional experience (Table 1). The distribution of reference data over time is displayed in the Appendix (SI 1).

In addition to structured interviews with forest managers we collected reference data in two Austrian national parks to extend our reference dataset also to unmanaged forests. In contrast to forest companies, national parks do not conduct planned timber harvesting operations, and their core zones are excluded from the legal obligation to salvage log natural disturbances. Wind-thrown and bark beetle infested trees thus remain on site, allowing an experienced field crew to distinguish wind disturbance (root plates, uprooted trees, broken trees) from bark beetle patches (standing deadwood, red crowns) for several years after the disturbance event (Copass et al., 2018). Field crews were equipped with disturbance maps and GPS devices to identify specific disturbance patches in the field. After a close inspection of the

Table 1

Summary of the reference data on disturbance agents collected. We recorded reference data on the causal agents of forest disturbance in nine forest enterprises and two national parks throughout Austria. We conducted structured interviews with 21 forest managers, harnessing 501 years of cumulative professional experience. Further, we collected reference data in the field for the two national parks. From both data sources we gathered information on the causal agents of disturbance for 2620 disturbed patches. For the location of each reference site see ids in Fig. 1.

Id	Type		Elevation [m a.s.l.]				Number of foresters / cumulative years of experience	Forest area [ha]	Attributed patches	
	Forest enterprise	National park	Min	Max	Mean	SD			Number	Hectares
1	x		677	2051	1415	227	4/120	7500	390	309
2	x		434	1499	793	251	2/52	4400	204	311
3	x		489	810	629	80	3/75	2628	242	361
4		x	541	1546	1138	204	–	15,629	309	319
5		x	603	1303	885	151	–	9676	91	72
6	x		609	1497	1001	236	3/70	6650	194	347
7	x		385	1709	1099	414	2/55	3290	82	142
8	x		1154	1731	1471	138	1/33	1850	135	150
9	x		231	1422	465	161	3/64	4860	285	299
10	x		246	688	379	82	1/34	1600	211	311
11	x		773	1022	897	53	2/32	4400	477	483
Overall	9	2	161	2051	924	385	21/501	62,298	2620	3240

disturbance patch and the available on-site disturbance legacies, field crews determined the causal agent of disturbance. Patches that were inconclusive were not included in the reference database. The core zones of the two National parks are 15,629 ha (Kalkalpen National Park) and 9676 ha (Gesäuse National Park) in size. Over both parks, disturbance agents were determined in the field for 400 patches. From both sources (i.e., national parks and forest enterprises), we determined agent information for 2620 disturbance patches in our reference database, of which 455 were caused by bark beetles, 760 by wind, and 1405 by timber harvest.

2.4. Attribution model

We utilized the reference data to train a Random Forest classifier (Breiman, 2001), predicting the causal agent of all disturbance patches mapped for Austria between 1986 and 2016, based on predictors describing the spectral signal, topography, patch form, and landscape context of each patch (Table 2). To identify the importance of individual predictors and to test our hypothesis on the importance of landscape context for attributing agents we built three models and compared their predictive performance. The first model only included predictors describing shape, topography and spectral properties of a patch; the

Table 2

List of all predictors that were considered for attributing causal agents of disturbance in Austria. Those with the highest predictive power were included in the final model (underlined). For additional information on all predictors see Table SI 2.

Domain	Predictors (included in final model)
Topography	Easternness, Northernness, Slope, Topographic ruggedness index
Patch	Area, Core area Index, Related circumscribing circle, Contiguity index, Core area, Euclidean nearest neighbor distance, Fractal dimension index, Radius of gyration, Number of core areas, Perimeter-area ratio, Patch perimeter, Shape index
Spectral	
Pre-disturbance mean	B1, B2, B3, B4, B5, B7, NBR, NBR2, NDMI, NDVI, SAVI
Change magnitude	B1, B2, B3, B4, B5, B7, NBR, NBR2, NDMI, NDVI, SAVI
Post disturbance minimum	B1, B2, B3, B4, B5, B7, NBR, NBR2, NDMI, NDVI, SAVI
Landscape context	Same year, one year before, two years before, three years before

second model additionally included four predictors describing the landscape context of a disturbance patch. For the third model, we removed all predictors of the second model that became redundant by adding the landscape context predictors. In the following, we describe the predictor variables in detail, followed by details on the Random Forest model, variable selection, the application of the model, and the evaluation of our results.

2.4.1. Predictor variables

We calculated three metrics describing the spectral characteristics of a disturbance: the pre-disturbance spectral mean, the spectral change magnitude during disturbance, and the post-disturbance spectral minimum (Fig. 2). The pre-disturbance mean describes the “normal” spectral reflectance of the surface before a disturbance has happened. The change magnitude describes the “disturbance impact”, that is how strongly the spectral signal changes in response to the disturbance. The

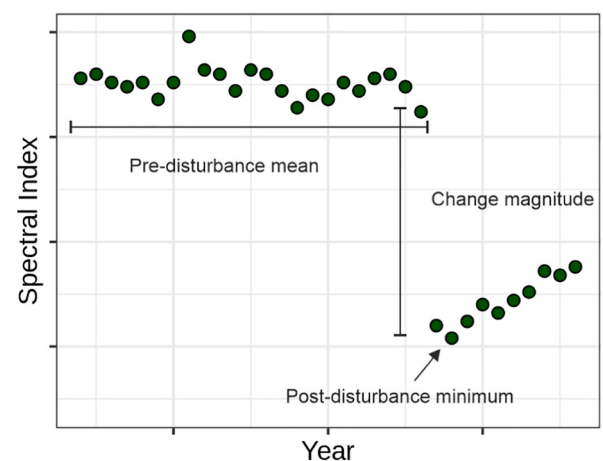


Fig. 2. Conceptual figure explaining how we quantified the spectral signal of a disturbance using three metrics: the pre-disturbance spectral mean, the spectral change magnitude, and the post-disturbance spectral minimum. We calculate all three metrics for the six spectral bands of Landsat (excluding the Cirrus band for Landsat 8) and five spectral indices: The Normalized Burn Ratio (NBR), the Normalized Burn Ratio 2 (NBR2), the Normalized Difference Moisture Index (NDMI), the Normalized Difference Vegetation Index (NDVI), and the Soil-Adjusted Vegetation Index (SAVI). All metrics were calculated per Landsat pixel and then averaged over all pixels of a disturbed patch. For the distributions of predictor values and correlations among final predictors see SI 2, SI 3 and SI 4.

post disturbance minimum describes the spectral reflectance after the disturbance event. Spectral variation after disturbance is often high and recovery trajectories can quickly resemble pre-disturbance spectral characteristics, especially if understory vegetation is present (Hais et al., 2009). We therefore used the minimum value over the mean to depict the spectral characteristics directly after disturbance, instead of the mean spectral characteristics of the post-disturbance recovery trajectory. Metrics were derived from annual medoid composites (see Flood, 2013), which were created from all Tier-1 surface reflectance images available between 1st of June and 30th of September. Data from TM/ETM+ and OLI were spectrally aligned using coefficients provided by Roy et al. (2016) prior to compositing, and clouds, cloud shadows and snow observations were filtered using the quality flags accompanying the Tier-1 products. The image acquisition, processing and compositing was done with help of the Google Earth Engine cloud computing environment (Gorelick et al., 2017b). We calculated the three spectral metrics (pre-disturbance mean, change magnitude, and the post-disturbance minimum) for all six spectral bands (excluding the Cirrus band for Landsat 8) as well as for five spectral indices: The Normalized Burn Ratio (NBR), the Normalized Burn Ratio 2 (NBR2), the Normalized Difference Moisture Index (NDMI), the Normalized Difference Vegetation Index (NDVI), and the Soil-Adjusted Vegetation Index (SAVI). These indices have been employed for causal agent attribution in the US and Canada in previous studies (Hermosilla et al., 2015; Kennedy et al., 2015) and we here test their inferential power in Central Europe. The three metrics were calculated at the pixel-level for each index (i.e., 30 m Landsat resolution) and were subsequently averaged at the patch-level. This resulted in a total of 21 predictor variables.

In addition to spectral characteristics we included a set of topographic metrics found to be important in previous studies (Kennedy et al., 2015; Oeser et al., 2017; Shimizu et al., 2017), including two indicators describing the exposition of a patch (i.e., easternness and northernness), one indicator quantifying the average slope of a disturbance patch, and one indicator expressing terrain ruggedness (Terrain Ruggedness Index, TRI, Riley, 1999) within a disturbance patch. Previous research also suggested patch form (e.g., rectangle, round, strip, highly complex) to hold relevant information for distinguishing disturbance agents (e.g., Kennedy et al., 2015; Shimizu et al., 2017). We consequently also included a comprehensive set of 12 patch metrics (Hesselbarth et al., 2019), describing both the size and form of a disturbance patch (Table 2). Patch metrics were calculated using the *landscapemetrics* package (Hesselbarth et al., 2019) in the R software environment for statistical computing (R Core Team, 2020).

In addition to these established predictors used in past studies we here propose a new metric describing the landscape context of a disturbance patch. Specifically, we calculated the cumulative forest area that was disturbed in the same year as the focal patch within a given radius around the focal patch (see Fig. 3). The new metric is based on the press-pulse dichotomy of disturbance (Bender et al., 1984) and follows the assumption that wind and bark beetle disturbances occur in pulses (Senf and Seidl, 2018), while human resource use leads to relatively stable harvesting rates over time (White et al., 2017), thus creating a press disturbance regime (Sebold et al., 2019). Our metric also accounts for the fact that natural disturbances are often spatially clustered (Kautz et al., 2011; Pasztor et al., 2014; Seidl et al., 2016b; Turner et al., 1989). In simple terms, we expected a disturbance patch that is surrounded by many disturbance patches occurring in the same year to be more likely caused by a natural disturbance agent (i.e., wind or bark beetle) compared to a patch that is surrounded by disturbance patches occurring in many different years (see Fig. 3). Wind disturbances increase the amount of suitable breeding material for bark beetles on the landscape, frequently triggering mass outbreaks (Marini et al., 2013; Seidl et al., 2016b). Consequently, the years after a wind disturbance are often characterized by severe bark beetle outbreaks in adjacent forests of wind thrown patches (Stadelmann et al., 2014; Wermelinger, 2004). We accounted for these spatio-temporal interactions between wind and bark

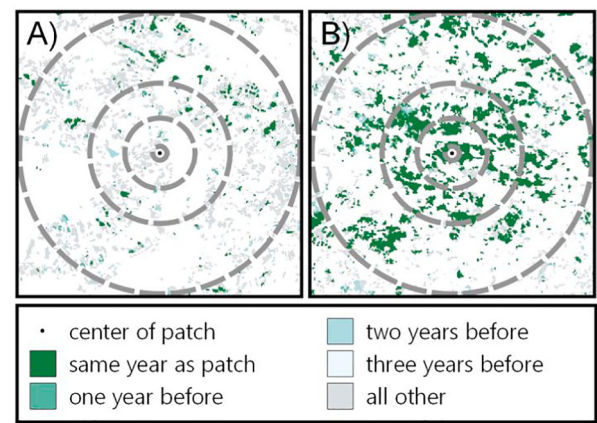


Fig. 3. Example of how landscape context - quantified in a certain radius around a focal patch - was used to distinguish between natural and human disturbances. A) focal patch is caused by regular harvesting, B) focal patch is caused by windthrow. The underlying assumption is that natural disturbances occur in pulses and are spatially clustered, while human resource use aims for stable harvesting rates over time, thus creating a press disturbance regime with lower spatio-temporal clustering. To characterize landscape context, we calculated the cumulative forest area disturbed in the same year as the focal patch within a fixed radius. The dashed circles correspond to different radii tested (i.e., 500 m, 2500 m, 5000 m, 10,000 m). We also calculated the cumulative disturbed area in the three years preceding the disturbance of the focal patch in order to account for temporal autocorrelation.

beetle disturbances by not only including the cumulative disturbed area of the same year as the focal patch in our new metric, but also accounting for the disturbed area of the three previous years. The landscape context metric was calculated on the level of patches. We measured the radius around a patch from its centroid, thus if the centroid of the patch fell within the radius the entire patch was included. The landscape context predictors were only weakly correlated among each other (see SI 5). As no a priori information on landscape size (i.e., here the radius around a focal patch within which context information is considered) was available, we tested different radii from 500 to 10,000 m (but see also Section 2.4.2).

2.4.2. Variable selection

Important variables were selected using the VSURF package based on the variable importance measure of the Random Forest package (Genuer et al., 2015, 2010). Variable importance is calculated from the difference in out-of-bag accuracy for different models with varying variables expressed as mean decrease in Gini index. The VSURF packages selects influential variables in three steps. In a first step ("thresholding step") it computes 50 Random Forests and sorts variables according to their mean variable importance, in decreasing order. Next, a threshold is computed, which is the minimum predicted value of a pruned CART tree fitted to the curve of the standard deviations of variable importance. Finally, the actual "thresholding step" is performed: only variables with a mean variable importance larger than the threshold are kept. The second step ("interpretation step") considers only variables selected by the first step and computes again 25 Random Forest models, starting with the Random Forest build with only the most important variable and ending with all variables selected in the first step. Then, the minimum mean out-of-bag (OOB) error of these models and its associated standard deviations are computed. Finally, the model with the lowest error (and hence its corresponding variables) is selected. In a third step ("prediction step") the starting point is the same than in the second step. However, now the variables are added to the model in a stepwise manner. A mean jump value is calculated using variables that have been left out by the second step. A variable is included in the model if the mean OOB error decrease is larger than the mean jump value. The idea is that the

OOB error decrease must be significantly greater than the average variation obtained by adding noisy variables.

2.4.3. Random forest model

The parametrization of the Random Forest models was based on the recommended default values of the *randomForest* package in R (ntrees = 500, cutoff = $1/k = 1/3$ see Breiman, 2001; R Core Team, 2020). Random Forest classifiers are a powerful method for causal agent attribution (Hermosilla et al., 2015; Kennedy et al., 2015; Oeser et al., 2017; Shimizu et al., 2017). Here, we applied them in a three-step approach: In the first step, we trained a base model including all predictors describing the spectral signal, topography and patch form (a total of 52 predictors), and selected 18 predictors with the highest predictive power via the *VSURF* procedure for variable selection described above (Genuer et al., 2015, 2010). In a second step, we added the newly developed landscape context predictor to the model. We tested different radii (i.e., 500 m, 2500 m, 5000 m, 10,000 m) to quantify the additional information that is provided by the spatial context of a patch, and to determine the landscape radius with the highest inferential power for determining causal agents of disturbance. In a third step, we selected the predictors of the final model by removing all variables that became redundant by adding the landscape context predictor, again using the *VSURF* procedure. We deliberately did not include disturbance year as predictor, as including this variable would have led to a potential bias in predictions stemming from an unequal temporal distribution of reference data. We trained the Random Forest classifier with all attributed disturbance patches of the reference sample ($n = 2620$).

2.4.4. Disturbance pattern analysis

We employed the final model to predict causal agents of disturbance (i.e., wind, bark beetles, harvest) for all disturbance patches identified in Austria between 1986 and 2016 ($n = 1,006,449$). Subsequently, we calculated annual disturbance rates (i.e., annual forest area disturbed / total forest area) for the three causal agents and investigated temporal rates and the prevalence of individual agents over time (with prevalence here describing the annual forest area disturbed per agent divided by the total forest area disturbed). Further, we analyzed spatial and temporal patterns as well as patch size distributions of the attributed maps and compared them among the three agents. All data analysis and visualization were conducted using R version 4.0.2. (R Core Team, 2020).

2.4.5. Causal agent model evaluation

We evaluated model performance on the basis of the Random Forest out of bag accuracy and on the basis of a spatial block cross-validation. While the former serves as estimation of model performance and is used for model selection, the latter presents an estimate of generalization power. Out of bag accuracy was calculated following the standard procedure implemented in the Random Forest package (Breiman, 2001). Spatial block cross-validation, which splits the data into spatial blocks before splitting into training and validation data, is helpful in avoiding overoptimistic map accuracies with large spatial datasets that might have high spatial correlation among training and validation data when randomly split (Meyer et al., 2019; Valavi et al., 2019). Here we used our 11 reference sites (i.e., nine forest enterprises and two national parks) as spatial blocks, as spatial correlation within reference sites is likely higher than between reference sites. By training the model on 10 reference sites and predicting causal agents for the remaining 11th site not used during model training, we obtained an estimate of the generalization power of the model when confronted with new data that is likely less correlated with the training data than using pure random splits (Meyer et al., 2019). We calculated average accuracy measures (overall accuracy, user's accuracy and producer's accuracy) and quantified uncertainty using bootstrapping.

In addition to formal model evaluation we further tested the potential of our model to reproduce national-scale trends in forest disturbance. We compared the prevalence of all three causal agents with

official logging records compiled by the Austrian Forest Service. We determined mean errors between the two data sources by calculating annual deviations and averaging over the study period (1986–2016). Data on salvage logging following wind and bark beetle disturbance were digitized from the website of the Federal Forest Research Institute (BFW, 2017). Data on total harvested timber volume were obtained from the Austrian Ministry of Forests (BMNT, 2008; Ebner, 2018). We compared prevalence of agents rather than absolute numbers due to differences in measurement units: official records report the timber volume disturbed, while we here quantified disturbed area.

3. Results

Landscape context was the most important predictor for determining causal disturbance agents in Austria. Using only predictors describing the spectral signal, topography and patch shape enabled us to determine the causal agent of disturbance with an overall accuracy of 43% (spatial block cross-validation) and 69% (out-of-bag) (SI 6 and SI 7). Including the landscape context significantly improved model performance (Fig. 4), resulting in an overall accuracy of 63% (spatial block cross-validation) and 75% (out-of-bag) (Table 4, SI 6, SI 7). Model performance improved with increasing radii up to 5000 m, but remained relative constant for larger radii. The landscape context was particularly important for identifying wind disturbance patches, but improved the classification of all three causal agents. The final model included eight predictors, with one predictor describing the topography of the patch (slope), three predictors from the spectral domain (pre-disturbance value in blue reflectance and NBR; change magnitude in NDVI), and all four landscape context predictors (same year, one year before, two years before, three years before) (Table 2, SI 8).

The spatial block cross-validation revealed user's accuracies between 30% and 68% and producer's accuracies between 15% and 84% per agent (Table 3). Bark beetle patches were most often confused with harvest patches, yet there was also a considerable number of patches that were falsely attributed to wind. In total, we observed 455 bark beetle patches but predicted only 223. The map thus underestimates the number of bark beetle patches in Austria and overestimates the number of harvest patches (with bark beetle patches being falsely labeled as harvest). Wind disturbances were mainly confused with harvest patches. We observed 760 wind patches but our model predicted only 660 patches. Harvest was the most accurately classified category, and confusions occurred with bark beetle and wind patches in equal parts. We predicted 1737 harvest patches but observed only 1405 in the reference data. Our attribution thus overestimates the number of regular harvests and underestimates the number of disturbance patches due to natural causes.

The comparison of the mapped prevalence per agent class across Austria (based on disturbed area) with official harvesting records (based on timber volume) yielded very good agreement, with mean errors of +0.40 percentage points for harvest, −2.34 percentage points for wind and +1.94 percentage points for bark beetle (Fig. 5). The temporal trajectories of wind and harvest disturbances were highly similar between both data sources. The well-known years with large wind disturbances (1990, 2003, 2007, 2008) are reflected in both trajectories with comparable magnitude, however differences of $\pm$ one year occurred in some disturbance years (e.g., 2003). The trajectories of bark beetle disturbance generally describe the same temporal pattern, however peak years (1993, 2005, 2009) are more distinct in the data of the Austrian Forest Service compared to Landsat-based estimates.

Regional and elevational hotspots of disturbance activity differed distinctly for wind, bark beetle and harvest disturbance (Fig. 6, SI 9, SI 10). Regional hotspots of wind disturbance were found on the Northern Front Range of the Alps (district Gmunden), in the south east of Austria (district Voitsberg) and in some valleys of the Central Alps (districts Tamsweg, Stainach and Zell am See) (SI 9). The highest prevalence of bark beetle disturbance was mapped in northern and south-eastern

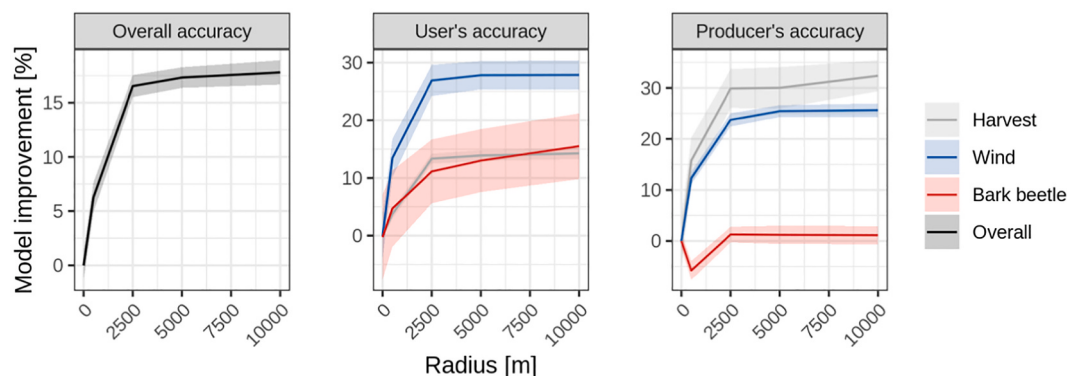


Fig. 4. Model improvement through adding predictors describing the landscape context (i.e., spatio-temporal autocorrelation of disturbances). Model improvement was evaluated based on overall accuracy (out-of-bag), user's accuracy and producer's accuracy. Panels show the relative model improvement over different radii used for calculating the landscape context (i.e. 500 m, 2500 m, 5000 m, 10,000 m). Note the individual scaling of the y-axes. A radius of zero corresponds to the base model without any metric quantifying the spatial context of a patch.

Table 3

Performance of the final model based on spatial block cross-validation. The confusion matrix shows number of patches per agent class (i.e., harvest, wind, bark beetle) in the reference database (columns) and the results of the model predictions (rows). Further, the table reports user's and producer's accuracy $\pm$ standard error, calculated per agent class as well as the overall accuracy.

	Harvest observed [n]	Wind observed [n]	Bark beetle observed [n]	User's accuracy [%]
Harvest predicted [n]	1175	298	264	67.7 (± 1.16)
Wind predicted [n]	121	416	123	63.0 (± 1.88)
Bark beetle predicted [n]	109	46	68	30.6 (± 3.21)
Producer's accuracy [%]	84.6 (± 1.01)	54.8 (± 1.78)	15.0 (± 1.73)	
Overall accuracy [%]				63.4 (± 0.97)

Austria. Elevational hotspots of wind disturbance were found between 756 and 1302 m a.s.l. (i.e., the interquartile range [IQR] of all mapped wind disturbance patches) with a median elevation of 1025 m. Median elevation of bark beetle patches was considerably lower (512 m, IQR 364–769 m), while harvest patches had the widest elevational distribution, with the IQR ranging from 622 to 1255 m (median = 922 m) (SI 10).

We identified considerable differences in the patch size distributions of the three causal agents analyzed (Table 4). Median patch sizes were similar among wind (0.45 ha), harvest (0.36 ha) and bark beetle (0.36 ha) disturbances, but maximum values varied considerably between agents (Table 4). Wind disturbances generally caused larger patches, compared to regular harvest. The largest disturbance patch in Austria between 1986 and 2016 was caused by wind, affecting a forest area of 354 ha. The largest bark beetle patch was 22 ha, and the largest patch identified as regular harvest was 38 ha. The average disturbance rotation period (i.e., the time needed to disturb an area that is equal to the total forest area) over all three agents was 206 years and was up to ten times higher for natural, compared to human causes. Average disturbance frequency ranged from 0.0005 patches ha year⁻¹ for bark beetles to 0.0054 patches ha year⁻¹ for harvest.

Wind and bark beetles strongly contributed to the observed increase in disturbance over the last thirty years in Austria (Fig. 7). We here note that we report map-based estimates of disturbance rate and agent prevalence, which cannot be validated rigorously (Palahí et al., 2021). The numbers reported in the following can thus only provide an

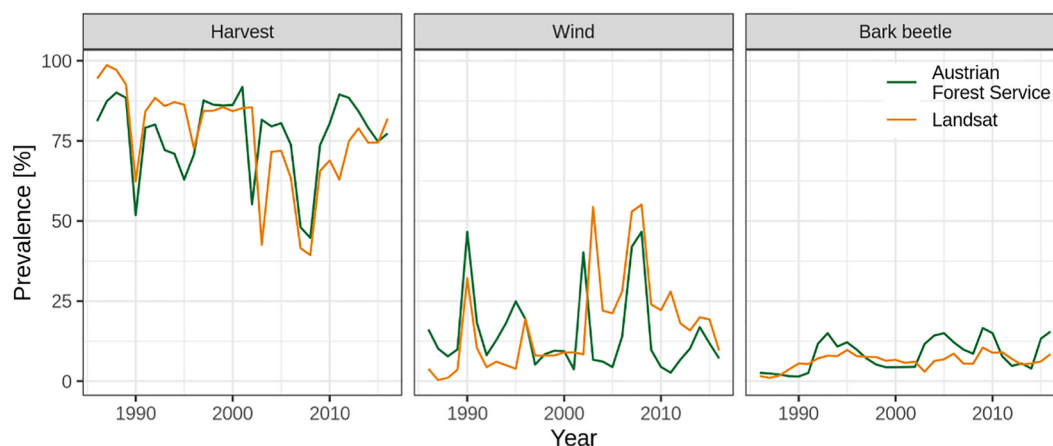


Fig. 5. Comparison of prevalence mapped from Landsat data (orange line) and official records from the Austrian Forest Service (green line) per agent. Note that the Austrian Forest Service reports extracted timber volume per agent class (i.e., harvest, wind, bark beetle), while we calculated the disturbed area per agent class based on Landsat data. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

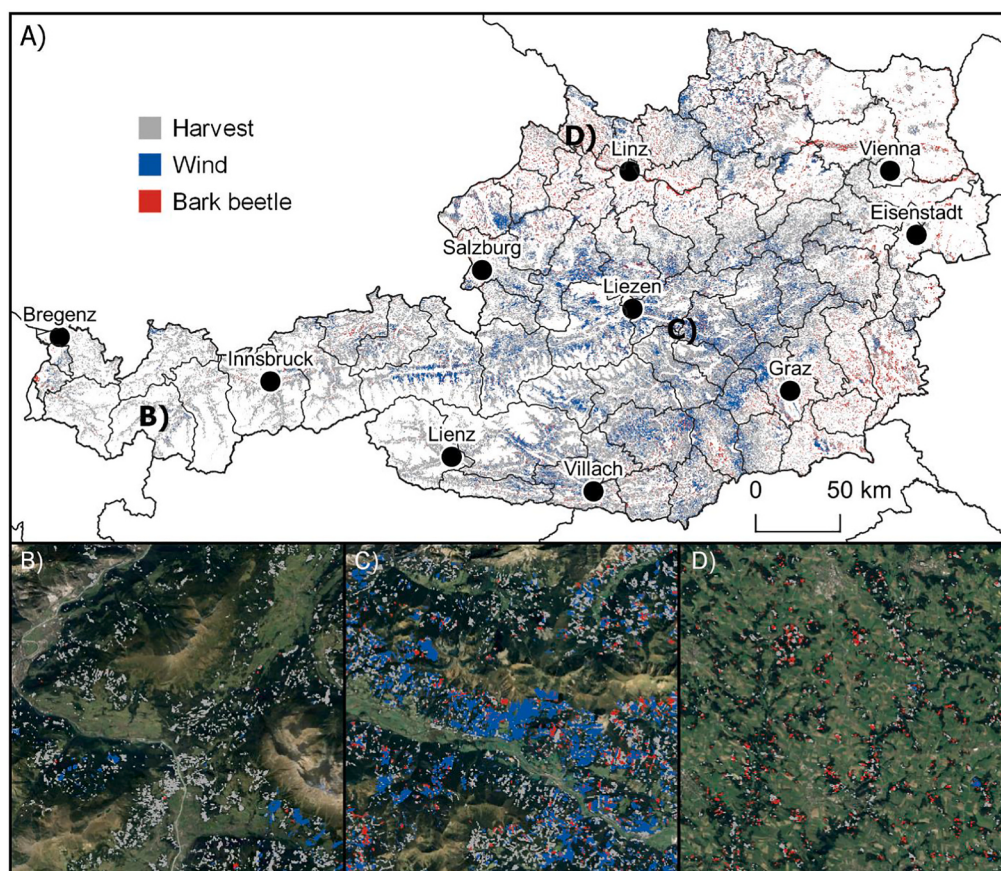


Fig. 6. Map of the causal agents of disturbance in Austria from 1986 to 2016, aggregated to a resolution of 200×200 m (A). Colors indicate the dominant agent per 200×200 m grid cell. Zoom-ins show landscapes, that are dominated by harvest (B), wind (C) and bark beetle (D) disturbances at the original resolution of the disturbance map (i.e., 30×30 m). The background of panels B–D is a high-resolution image provided by Google Maps.

Table 4

The Austrian forest disturbance regime 1986–2016. Disturbance rotation period is the average time it takes an agent to disturb an area equally to the total forest area. Q = quantile.

Agent	Patch size [ha]								Number of patches		Area		Rotation period	Frequency
	Min	Q5	Q25	Q50	Mean	Q75	Q95	Max	n	%	ha	%	years	n ha year ⁻¹
Harvest	0.09	0.18	0.27	0.36	0.64	0.72	1.8	38.9	772,111	77	491,605	71	293	0.0054
Wind	0.09	0.18	0.27	0.45	1.07	0.99	3.33	354.0	149,169	15	160,060	23	898	0.0010
Bark beetles	0.09	0.18	0.27	0.36	0.53	0.54	1.44	22.0	85,142	9	45,427	7	3165	0.0006
Overall	0.09	0.18	0.27	0.36	0.69	0.72	1.98	354.0	1,006,449		697,093		206	0.70

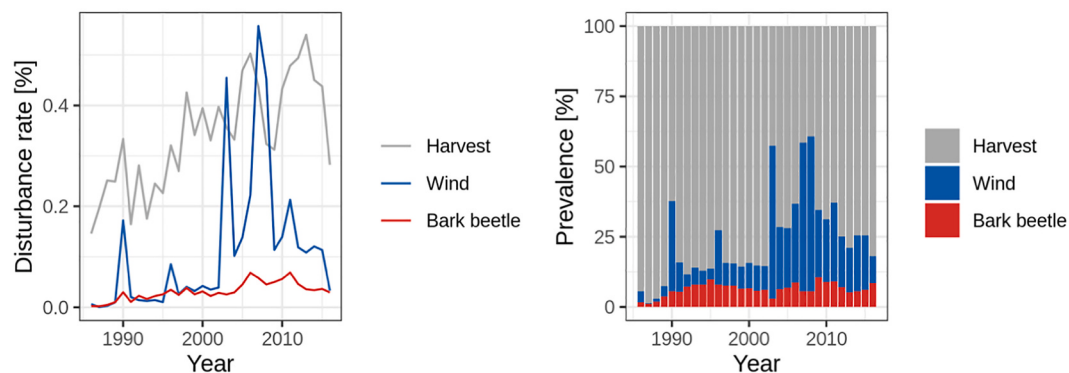


Fig. 7. Disturbance rate (i.e., disturbed area per year relative to the total forest area) and prevalence (i.e., % of disturbed forest area by agent) for harvest, wind and bark beetle disturbances in Austria from 1986 to 2016.

indication for interested ecologists and forest managers. Disturbance rates of wind and bark beetles increased by 408% and 99% between the first (1986–2000) and the second (2001–2016) half of the observation period. In contrast, regular harvests increased by only 43% over the same time period. Furthermore, not only absolute disturbance rates changed, but also the prevalence between the three causal agents of disturbance. In the first half of the observation period, on average 86% of the disturbed area were regular harvests. The prevalence of harvests decreased to 68% in the second half of the observation period, and that of wind and bark beetle disturbances increased from 14% to 32%. Increasing disturbance rates were primary driven by changes in disturbance frequency and only to a lesser extent by increases in patch size. Average disturbance frequency increased by 355% for wind, 77% for bark beetles, and 26% for harvest. Average patch size increased by 8% for wind, 14% for bark beetles, and 13% for harvest.

4. Discussion

4.1. Attributing causal agents of disturbance in Central Europe

The attribution of forest disturbances mapped from satellite data to causal agents is a central objective of current remote sensing research (McDowell et al., 2015). Here we determined the causal agents of ~1 million disturbance patches mapped in Austria between 1986 and 2016. We built upon previous works that have established a patch-based approach using Random Forest classifiers as the state-of-the-art for causal agent attribution of forest disturbances (Hermosilla et al., 2015; Kennedy et al., 2015; Oeser et al., 2017; Schroeder et al., 2017; Shimizu et al., 2017). We advanced the state-of-the-art by showing that the additional consideration of landscape context can considerably reduce error in the attribution of causal agents of forest disturbance.

A key innovation of our work lies in the establishment of a local reference database on agents of forest disturbances, utilizing the abundant local knowledge that is available in intensively managed regions such as in Central Europe. Involving stakeholders to address questions of environmental management has been established more than twenty years ago (Pretty, 1995). Specifically, research can benefit strongly from the interaction of scientist and resource managers (Reed, 2008). Recent studies emphasize that close science-management interactions are a powerful way forward for tackling complex problems (Asah and Blahna, 2020; Gaydos et al., 2019). Increasing forest disturbance is a problem that is highly relevant for forest managers in Austria (Seidl et al., 2016a), which is generally beneficial for the outcome of science-practice interactions (Bennett, 2017). This was also confirmed by a high willingness of forest enterprises to take part in our research. Out of the ten forest enterprises initially contacted, nine agreed to contribute. The amount of reference data that we collected could not have been obtained with classical field work alone. On average, we collected data on 194 patches in one day of interviews with managers, while a field crew of two persons collected, on average, data on 24 patches per day in the national parks surveyed. While being a very efficient approach for reference data collection, the interviews with managers also revealed a central conceptual challenge of causal agent attribution in the forests of Central Europe: for some patches, a single agent of disturbance cannot be determined, as multiple factors interacted in the creation of the patch. As mentioned above, forest managers often respond quickly to natural disturbances (with salvage and sanitation logging), and often fell trees when they are still in the green attack stage of bark beetle infestation (i.e., before the trees are actually killed by bark beetles). Furthermore, managers also fell adjacent trees that are suspected to be infested by bark beetles without conclusively diagnosing each tree's infection status. Also, bark beetle infestations and wind-throw often co-occur within a single patch. The true agent of disturbance is thus often a mix of individual agents that cannot be conclusively disentangled because of their causal interrelations. Here, we circumvented this conceptual problem by focusing on the agent that is responsible for the

largest proportion of a disturbed patch. However, for similar analyses at larger scales a “mixed” class might be more appropriate, explicitly highlighting the strong interactions between individual agents. Future work on causal agent attribution in Central Europe might also investigate the potential of pixel-based instead of patch-based approaches. Further, data sources with higher temporal and spatial resolution compared to the Landsat archive might help improving causal agent attribution, especially for instances where human and natural agents of disturbance interact strongly.

Including the landscape context of a disturbance patch as predictor substantially improved model performance compared to models based only on spectral signal, topography, and patch form. In particular, the discrimination between disturbances caused by wind and timber harvest improved through adding landscape context. While the spatial and temporal autocorrelation of wind and bark beetle disturbances are well documented in disturbance ecology (Everham and Brokaw, 1996; Turner et al., 1989; Turner and Gardner, 2015; Wermelinger, 2004), and landscape context predictors have been suggested for causal agent attribution previously (Kennedy et al., 2015), we here present the – to our knowledge – first formal test of their discriminating power. Our results indicate that in the intensively managed forests of Central Europe, landscape context is considerably more important for correctly predicting disturbance agents than any spectral or patch indicator. The high importance of landscape context in our study might, however, be specific to forests in Central Europe. First, disturbances in Austria are small (84% of the patches are below 1 ha), due to the applied silvicultural regimes and the prevailing management regulations. A high number of small patches limits the diversity of patch forms (i.e., given the fixed spatial grain of 30 m, there is a limited number of patch forms that can emerge for an average disturbance patch of 10 pixels). This might be the reason why none of the patch metrics were retained in the final model, despite the fact that patch metrics have been shown to be important predictors in other parts of the world (Kennedy et al., 2015; Schroeder et al., 2017; Shimizu et al., 2017). Another factor potentially contributing to a reduced importance of predictors describing the spectral signal and patch form is salvage logging. Post-disturbance salvage logging frequently simplifies patch forms and equalizes differences between natural disturbances and regular harvests, e.g. by removing standing and downed deadwood. We thus emphasize that in Central Europe, landscape context predictors are more important for causal agent attribution than the patch-based indicators used in previous studies (Kennedy et al., 2015; Schroeder et al., 2017; Shimizu et al., 2017). Whether these metrics are also useful in fire-driven disturbance regimes remains to be tested.

An evaluation of our results with spatial block cross-validation yielded an overall accuracy of 63% and (Table 3), whereas the out-of-bag accuracy was 75% (SI 6). These results underline the importance of spatial cross validation for machine learning applications in order to avoid overly optimistic estimates of model performance (Meyer et al., 2019). Comparing user's accuracies (OOB) of individual agent classes to those obtained in previous studies suggests that our results are comparable to those obtained in other regions of the world. We obtained user's accuracies of 75.0% for disturbances caused by harvest, while studies in other parts of the world report, e.g., 87.3% for Russia (Baumann et al., 2014), 98.8% for Minnesota (USA) (Baumann et al., 2014), 92% for Washington (USA) (Kennedy et al., 2015), between 63 and 87% (Schroeder et al., 2017) and 82.3% (Schleeweis et al., 2020) across the USA, 80.9% (Senf et al., 2015) and 91.8% (Hermosilla et al., 2015) for different regions in Canada, and 86.4% for Myanmar (Shimizu et al., 2017). Disturbances caused by wind were attributed with a user's accuracy of 78.7% here, while Baumann et al. (2014) report 71.9% for Russia and 63.0% for Minnesota (USA), and Schroeder et al. (2017) report 62% and 76% for two Landsat scenes in the USA. Bark beetle disturbances were attributed with a user's accuracy of 69.2% using our approach, compared to 66.7% (Schleeweis et al., 2020), 56% (Neigh et al., 2014a) and 38% (Neigh et al., 2014b) for insect disturbances in

the USA; and 70.8% in Canada (Senf et al., 2015). For Central Europe, only one study attributing harvest, wind and bark beetle disturbances existed to date: Oeser et al. (2017) report user's accuracies of 82.6% for harvest, 86.1% for bark beetle, 80.4% for windthrow and an overall accuracy of 83.0% for three National parks in Central Europe. They used intra-annual Landsat time series for attributing causal agents of disturbance from 1986 to 2016. However, their study focused on national parks (i.e., areas with little human influence), and they found elevation and disturbance year to be among the most important predictors. We deliberately excluded these two variables in our analyses, in order to prevent the model from learning the idiosyncrasies of the data (e.g., the occurrence of a large wind disturbance in a given year), and retain its ability for generalization beyond the reference data set. For example, there is a general pattern of increasing bark beetle occurrence with decreasing elevation, since bark beetles are more competitive in warmer climates (Jakoby et al., 2019). However, this relationship is not linear because in low elevations the share of suitable host trees (e.g., Norway spruce) decreases. Consequently, the true probability of bark beetle infestations first increases with decreasing elevation and subsequently decreases again after a threshold in host availability is crossed. A model that includes elevation likely misclassifies small clear-cuts in low elevation areas as bark beetle patches. The same is true for disturbance year as predictor, which can severely bias predictions if reference data is not equally distributed across years (i.e., the model learns that certain years are characterized by bark beetle disturbance and has trouble predicting bark beetle disturbance for years not included during model training). While the accuracy of our models was higher when elevation and disturbance year were included as predictors (data not shown), we excluded these variables at the cost of accuracy in order to ensure model generality.

Temporal trends in disturbance activity derived from Landsat data were remarkably consistent with official harvest records (Fig. 5). We thus conclude that our satellite-based analyses reflect the temporal patterns of wind, bark beetle and harvest disturbances in Austria well. Temporal dissimilarities between harvest records and Landsat-based trajectories can be attributed to uncertainties in the year attribution in the original map product, as well as to differences in the recording of dates (i.e., harvesting records = end of calendar year, Landsat = mid of vegetation period). Furthermore, harvesting records and Landsat-derived values differ because of different underlying indicators. While harvesting records report timber volume extracted, Landsat based maps report area disturbed.

4.2. Limitations

Although our results are based on a large and detailed reference data set, rigorous evaluations of our approach revealed limitations which should be considered when interpreting our results. First, correct model predictions depend on the reference data set representing the environmental conditions occurring in the domain of application. Disturbance regimes or environmental conditions that are not covered by our reference data set are thus prone to misclassification. A prominent example are ecosystems in flood plain forests along rivers (cf. Fig. 6, east of Vienna along the Danube river). These systems are often characterized by a high frequency of small clear-cuts in Central Europe, creating similar patterns as bark beetle disturbances. Yet bark beetle infestations do not occur in these areas, because they lack suitable conifer hosts. Second, our analysis focuses on the three most important agents causing stand-replacing disturbances in Central Europe – wind, bark beetles, and harvest (Thom et al., 2013) – and neglects all other disturbance agents. However, a number of additional processes cause forest disturbances in Austria, such as avalanches (Höller, 2009), debris flows (Scheidt et al., 2020), forest fires (Müller et al., 2013), and land use change (Nestroy, 2006). We recorded these events in our reference database, but their frequency was too low for them to be included in classification (fire $n = 1$, gravitational events $n = 114$, land use change $n = 74$, of the 2809

patches initially recorded in the reference data set). Third, we here utilized an existing disturbance map that does not contain information on sub-canopy processes and very low severity disturbances (e.g., single tree wind-throw, thinning from below). A considerable amount of disturbance might thus not be included in our analysis. Although the minimum mapping unit of the final disturbance map is 1 pixel (see Table 4), single pixel patches account for only 0.1% of all attributed patches ($n = 2017$) thus their influence on the accuracy of the final map is very limited. Fourth, although we believe that reference data collection with the help of forest managers is a promising approach to efficiently collect data on causal agents of forest disturbance in Central Europe, it is limited to areas where foresters spend long time periods of their professional career in the same district. It further depends on interviewers who sufficiently explain the process of reference data collection and subsequent analyses to participating forest managers. Forest managers should, for instance, be aware that a falsely attributed disturbance patch affects the prediction results more negative than a skipped patch (i.e., they should not guess the causal agent if they are not entirely sure, but rather skip such an uncertain patch).

5. Conclusions

We here present an important methodological advance of the causal attribution of forest disturbance agents. Our approach extends the previously applied method, developed for areas characterized by large disturbance patches, so that it is also applicable in areas characterized by small disturbances and intricate disturbance interactions. Here we demonstrate the utility of our approach for Austria, yet we are confident that it is transferable also to other countries of Central Europe, since the disturbance regimes prevailing in large parts of the continent are similar (Senf and Seidl, 2021). Our results are of central importance for forest policy and management. They show that changes in disturbance rates in Austria are mainly the result of increasing wind disturbances. Our results thus refute the notion that forest disturbance dynamics in Central Europe is primarily driven by management (Ceccherini et al., 2020; Curtis et al., 2018). We did, however, find increases in all three disturbance agents investigated here, indicating substantial changes in forest disturbance regimes. As global change continues to alter natural disturbance regimes, compensatory actions by management might be needed in future. We here demonstrate that disturbance change is more strongly driven by increases in disturbance frequency rather than size, which provides an important leverage point for adapting forest management. In conclusion our research provides an important step towards a comprehensive monitoring and management of forest disturbances in a changing world.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

J. Sebold and R. Seidl acknowledge funding from the Austrian Science Fund FWF START grant Y895-B25. The fieldwork and structured interviews for this research were funded by the Fund 120 Years University of Natural Resources and Life Sciences (BOKU), Vienna.

We thank the forest managers and forest enterprises for their help with collecting the reference data. We further thank Katharina Albrich, Laura Steinbach and Winslow D. Hansen for their help with field work in the two national parks.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.rse.2021.112502>.

org/10.1016/j.rse.2021.112502.

References

- Albrich, K., Rammer, W., Thom, D., Seidl, R., 2018. Trade-offs between temporal stability and level of forest ecosystem services provisioning under climate change. *Ecol. Appl.* 28, 1884–1896. <https://doi.org/10.1002/eap.1785>.
- Anderegg, W.R.L., Trugman, A.T., Badgley, G., Anderson, C.M., Bartuska, A., Ciais, P., Cullenward, D., Field, C.B., Freeman, J., Goetz, S.J., Hicke, J.A., Huntzinger, D., Jackson, R.B., Nickerson, J., Pacala, S., Randerson, J.T., 2020. Climate-driven risks to the climate mitigation potential of forests. *Science* 368. <https://doi.org/10.1126/science.aaz7005>.
- Asah, S.T., Blahna, D.J., 2020. Involving Stakeholders' knowledge in co-designing social valuations of biodiversity and ecosystem services: implications for decision-making. *Ecosystems* 23, 324–337. <https://doi.org/10.1007/s10021-019-00405-6>.
- Baumann, M., Ozdogan, M., Wolter, P.T., Krylov, A., Vladimirova, N., Radeloff, V.C., 2014. Landsat remote sensing of forest windfall disturbance. *Remote Sens. Environ.* 143, 171–179. <https://doi.org/10.1016/j.rse.2013.12.020>.
- Bender, E.A., Case, T.J., Gilpin, M.E., 1984. *Perturbation Experiments in Community Ecology : Theory and Practice* Author (s) : Edward A. Bender, Ted J. Case and Michael E. Gilpin Published by : Ecological Society of America perturbation experiments in community ecology : theory and practice. *Ecology* 65, 1–13.
- Bennett, E.M., 2017. Research Frontiers in ecosystem service science. *Ecosystems* 20, 31–37. <https://doi.org/10.1007/s10021-016-0049-0>.
- BFW, 2017. Borkenkäfer 2017: satte 3,5 Millionen Festmeter Schadholz in Österreich [WWW Document]. URL doi://bfw.ac.at/rz/bfwcms2.web?dok=9756.
- BFW, 2020. Österreichische Waldinventur [WWW Document]. URL doi://bfw.ac.at/rz/wi.home (accessed 10.8.20).
- BMFLUW, 2008. Nachhaltige Waldwirtschaft in Österreich - Österreichischer Waldbericht, p. 2008.
- BMNT, 2008. Nachhaltige Waldwirtschaft in Österreich - Österreichischer Waldbericht 2008. Vienna.
- Bonney, R., Cooper, C.B., Dickinson, J., Kelling, S., Phillips, T., Rosenberg, K.V., Shirk, J., 2009. Citizen Science : A Developing Tool for Expanding Science Knowledge and Scientific Literacy, 59, pp. 977–984. <https://doi.org/10.1525/bio.2009.59.11.9>.
- Breiman, L., 2001. Random forests. *Mach. Learn.* 45, 5–32. <https://doi.org/10.1007/978-3-662-46900-2>.
- Cadag, J.R.D., Gaillard, J.C., 2012. Integrating knowledge and actions in disaster risk reduction : the contribution of participatory mapping. *Area* 44, 100–109. <https://doi.org/10.1111/j.1475-4762.2011.01065.x>.
- Ceccherini, G., Duveiller, G., Grassi, G., Lemoine, G., Avitabile, V., Pilli, R., Cescatti, A., 2020. Abrupt increase in harvested forest area over Europe after 2015. *Nature* 583, 72–77. <https://doi.org/10.1038/s41586-020-2438-y>.
- Chambers, R., 2006. Participatory mapping and geographic information systems: whose map? Who is empowered and who disempowered? Who gains and who loses? *Electron. J. Inf. Syst. Dev. Ctries.* 25, 1–11.
- Copass, C., Antonova, N., Kennedy, R., 2018. Comparison of office and field techniques for validating landscape change classification in Pacific northwest National Parks. *Remote Sens.* 11, 3. <https://doi.org/10.3390/rs11010003>.
- Cope, M., Elwood, S., 2009. *Qualitative GIS: A Mixed Methods Approach*. Sage Publications, Thousand Oaks, CA.
- Curtis, P.G., Slay, C.M., Harris, N.L., Tyukavina, A., Hansen, M.C., 2018. Classifying drivers of global forest loss. *Science* (80-.) 361, 1108–1111. <https://doi.org/10.1126/science.aau3445>.
- Dickinson, J.L., Zuckerman, B., Bonter, D.N., 2010. Citizen Science as an Ecological Research Tool : Challenges and Benefits. <https://doi.org/10.1146/annurev-ecolsys-102209-144636>.
- Dobor, L., Hlásny, T., Rammer, W., Barka, I., Trombik, J., Pavlenda, P., Šebn, V., Štěpánek, P., Seidl, R., 2018. Post-disturbance recovery of forest carbon in a temperate forest landscape under climate change. *Agric. For. Meteorol.* 263, 308–322. <https://doi.org/10.1016/j.agrformet.2018.08.028>.
- Ebner, G., 2018. Einschlag sank leicht, deutlich mehr Schadholz Plus 18% beim Schadholz in Österreich [WWW Document]. URL %0AEinschlag sank leicht, deutlich mehr Schadholz%0APlus 18%25 beim Schadholz in Österreich%0A (accessed 9.18.20).
- Everham, E.M., Brokaw, N.V.L., 1996. Forest damage and recovery from catastrophic wind. *Bot. Rev.* 62, 113–185. <https://doi.org/10.1007/BF02857920>.
- Flood, N., 2013. Seasonal composite landsat TM/ETM+ images using the medoid (a multi-dimensional median). *Remote Sens.* 5, 6481–6500. <https://doi.org/10.3390/rs5126481>.
- Forzieri, G., Pecchi, M., Girardello, M., Mauri, A., Klaus, M., Nikolov, C., Rütschi, M., Gardiner, B., Tomastik, J., Small, D., Nistor, C., Jonikavicius, D., Spinoni, J., Feyen, L., Giannetti, F., Comino, R., Wolynski, A., Pirotti, F., Maistrelli, F., Savulescu, I., Wurrpillot-Lucas, S., Karlsson, S., Zieba-Kulawik, K., Strejcek-Jazwinska, P., Mokros, M., Franz, S., Krejci, L., Haidu, I., Nilsson, M., Wezyk, P., Catani, F., Chen, Y.Y., Luyssaert, S., Chirici, G., Cescatti, A., Beck, P.S.A., 2020. A spatially explicit database of wind disturbances in European forests over the period 2000–2018. *Earth Syst. Sci. Data* 12, 257–276. <https://doi.org/10.5194/essd-12-257-2020>.
- Gaydos, D.A., Petrasova, A., Cobb, R.C., Meentemeyer, R.K., 2019. Forecasting and control of emerging infectious forest disease through participatory modelling. *Philos. Trans. R. Soc. B Biol. Sci.* 374 <https://doi.org/10.1098/rstb.2018.0283>.
- Genuer, R., Poggi, J., Tuleau-malot, C., 2010. Variable selection using random forests. *Pattern Recogn. Lett.* 31, 2225–2236. <https://doi.org/10.1016/j.patrec.2010.03.014>.
- Genuer, R., Poggi, J., Tuleau-malot, C., 2015. VSURF : an R package for variable selection using random forests. *R J.* 7 (2), 19–33.
- Gorelick, N., Hancher, M., Dixon, M., Ilyushchenko, S., Thau, D., Moore, R., 2017a. Google earth engine: planetary-scale geospatial analysis for everyone. *Remote Sens. Environ.* 202, 18–27. <https://doi.org/10.1016/j.rse.2017.06.031>.
- Gorelick, N., Hancher, M., Dixon, M., Ilyushchenko, S., Thau, D., Moore, R., 2017b. Google earth engine: planetary-scale geospatial analysis for everyone. *Remote Sens. Environ.* 202, 18–27. <https://doi.org/10.1016/j.rse.2017.06.031>.
- Griffiths, P., Kuemmerle, T., Baumann, M., Radeloff, V.C., Abrudan, I.V., Lieskovsky, J., Munteanu, C., Ostapowicz, K., Hostert, P., 2014. Forest disturbances, forest recovery, and changes in forest types across the carpathian ecoregion from 1985 to 2010 based on landsat image composites. *Remote Sens. Environ.* 151, 72–88. <https://doi.org/10.1016/j.rse.2013.04.022>.
- Hais, M., Jonášová, M., Langhammer, J., Kučera, T., 2009. Comparison of two types of forest disturbance using multitemporal Landsat TM/ETM+ imagery and field vegetation data. *Remote Sens. Environ.* 113, 835–845. <https://doi.org/10.1016/j.rse.2008.12.012>.
- Hansen, M.C., Potapov, P.V., Moore, R., Hancher, M., Turubanova, S.A., Tyukavina, A., Thau, D., Stehman, S.V., Goetz, S.J., Loveland, T.R., Kommareddy, A., Egorov, A., Chini, L., Justice, C.O., Townshend, J.R.G., 2013. High-resolution global maps of 21st-century forest cover change. *Science* (80-.) 342, 850–853. <https://doi.org/10.1126/science.1244693>.
- Hermosilla, T., Wulder, M.A., White, J.C., Coops, N.C., Hobart, G.W., 2015. Remote Sensing of Environment Regional detection, characterization, and attribution of annual forest change from 1984 to 2012 using Landsat-derived time-series metrics, 170, pp. 121–132.
- Hesselbarth, M.H.K., Scialini, M., With, K.A., Wiegand, K., Nowosad, J., 2019. Landscape metrics: an open-source R tool to calculate landscape metrics. *Ecography* (Cop.) 42, 1648–1657. <https://doi.org/10.1111/ecog.04617>.
- Hilmers, T., Friess, N., Bässler, C., Heurich, M., Brandl, R., Pretzsch, H., Seidl, R., Müller, J., 2018. Biodiversity along temperate forest succession. *J. Appl. Ecol.* 55, 2756–2766. <https://doi.org/10.1111/1365-2664.13238>.
- Höller, P., 2009. Avalanche cycles in Austria: an analysis of the major events in the last 50 years. *Nat. Hazards* 48, 399–424. <https://doi.org/10.1007/s11069-008-9271-1>.
- Hughes, T.P., Carpenter, S., Rockström, J., Scheffer, M., Walker, B., 2013. Multiscale regime shifts and planetary boundaries. *Trends Ecol. Evol.* 28, 389–395. <https://doi.org/10.1016/j.tree.2013.05.019>.
- Jakoby, O., Lischke, H., Wermelinger, B., 2019. Climate change alters elevational phenology patterns of the European spruce bark beetle (*Ips typographus*). *Glob. Chang. Biol.* <https://doi.org/10.1111/gcb.14766>.
- Kautz, M., Dworschak, K., Gruppe, A., Schopf, R., 2011. Quantifying spatio-temporal dispersion of bark beetle infestations in epidemic and non-epidemic conditions. *For. Ecol. Manag.* 262, 598–608. <https://doi.org/10.1016/j.foreco.2011.04.023>.
- Kennedy, R.E., Yang, Z., Cohen, W.B., 2010. Detecting trends in forest disturbance and recovery using yearly Landsat time series: 1. LandTrendr - Temporal segmentation algorithms. *Remote Sens. Environ.* 114, 2897–2910. <https://doi.org/10.1016/j.rse.2010.07.008>.
- Kennedy, R.E., Yang, Z., Braaten, J., Copass, C., Antonova, N., Jordan, C., Nelson, P., 2015. Attribution of disturbance change agent from Landsat time-series in support of habitat monitoring in the Puget Sound region, USA. *Remote Sens. Environ.* 166, 271–285. <https://doi.org/10.1016/j.rse.2015.05.005>.
- Kennedy, R.E., Yang, Z., Gorelick, N., Braaten, J., Cavalcante, L., Cohen, W.B., Healey, S., 2018. Implementation of the LandTrendr algorithm on Google earth engine. *Remote Sens.* 10, 1–10. <https://doi.org/10.3390/rs10050691>.
- Klein, T., Hartmann, H., 2018. Climate change drives tree mortality. *Science* (80-.) 362. <https://doi.org/10.1126/science.aav6508>, 758.1–758.
- Kortmann, M., Heurich, M., Latif, H., Röser, S., Seidl, R., Müller, J., Thorn, S., 2018. Forest structure following natural disturbances and early succession provides habitat for two avian flagship species, capercaillie (*Tetrao urogallus*) and hazel grouse (*Tetrastes bonasia*). *Biol. Conserv.* 226, 81–91. <https://doi.org/10.1016/j.biocon.2018.07.014>.
- Leverkus, A.B., Lindenmayer, D.B., Thorn, S., Gustafsson, L., 2018. Salvage logging in the world's forests: interactions between natural disturbance and logging need recognition. *Glob. Ecol. Biogeogr.* 27, 1140–1154. <https://doi.org/10.1111/geb.12772>.
- Marini, L., Lindelöw, Å., Jönsson, A.M., Wulff, S., Schroeder, L.M., 2013. Population dynamics of the spruce bark beetle: a long-term study. *Oikos* 122, 1768–1776. <https://doi.org/10.1111/j.1600-0706.2013.00431.x>.
- Masek, J.G., Goward, S.N., Kennedy, R.E., Cohen, W.B., Moisen, G.G., Schleeweis, K., Huang, C., 2013. United States Forest disturbance trends observed using Landsat time series. *Ecosystems* 16, 1087–1104. <https://doi.org/10.1007/s10021-013-9669-9>.
- McDowell, N.G., Coops, N.C., Beck, P.S.A., Chambers, J.Q., Gangadagam, C., Hicke, J.A., Huang, C., Ying, Kennedy, R., Krofcheck, D.J., Litvak, M., Meddens, A.J.H., Muss, J., Negrón-Juarez, R., Peng, C., Schwantes, A.M., Swenson, J.J., Vernon, L.J., Williams, A.P., Xu, C., Zhao, M., Running, S.W., Allen, C.D., 2015. Global satellite monitoring of climate-induced vegetation disturbances. *Trends Plant Sci.* 20, 114–123. <https://doi.org/10.1016/j.plants.2014.10.008>.
- McDowell, N.G., Allen, C.D., Anderson-Teixeira, K., Aukema, B.H., Bond-Lamberty, B., Chini, L., Clark, J.S., Dietze, M., Grossiord, C., Hanbury-Brown, A., Hurr, G.C., Jackson, R.B., Johnson, D.J., Kueppers, L., Lichstein, J.W., Ogle, K., Poulter, B., Pugh, T.A.M., Seidl, R., Turner, M.G., Uriarte, M., Walker, A.P., Xu, C., 2020. Pervasive shifts in forest dynamics in a changing world. *Science* 368. <https://doi.org/10.1126/science.aaz9463>.
- Meyer, H., Reudenbach, C., Wöllauer, S., Nauss, T., 2019. Importance of spatial predictor variable selection in machine learning applications – moving from data reproduction

- to spatial prediction. *Ecol. Model.* 411 <https://doi.org/10.1016/j.ecolmodel.2019.108815>.
- Müller, M.M., Vacik, H., Diendorfer, G., Arpaci, A., Formayer, H., Gossow, H., 2013. Analysis of lightning-induced forest fires in Austria. *Theor. Appl. Climatol.* 111, 183–193. <https://doi.org/10.1007/s00704-012-0653-7>.
- Neigh, C.S.R., Bolton, D.K., Diabate, M., Williams, J.J., Carvalhais, N., 2014a. An automated approach to map the history of forest disturbance from insect mortality and harvest with landsat time-series data. *Remote Sens.* 6, 2782–2808. <https://doi.org/10.3390/rs6042782>.
- Neigh, C.S.R., Bolton, D.K., Williams, J.J., Diabate, M., 2014b. Evaluating an automated approach for monitoring forest disturbances in the Pacific northwest from logging, fire and insect outbreaks with landsat time series data. *Forests* 5, 3169–3198. <https://doi.org/10.3390/f5123169>.
- Nestroy, O., 2006. Soil sealing in Austria and its consequences. *Ecophysiol. Hydrobiol.* 6, 171–173. [https://doi.org/10.1016/S1642-3593\(06\)70139-2](https://doi.org/10.1016/S1642-3593(06)70139-2).
- Oeser, J., Pflugmacher, D., Senf, C., Heurich, M., Hostert, P., 2017. Using intra-annual Landsat time series for attributing forest disturbance agents in Central Europe. *Forests* 8. <https://doi.org/10.3390/f8070251>.
- Palahí, M., Valbuena, R., Senf, C., Acil, N., Pugh, T.A.M., Sadler, J., Seidl, R., Potapov, P., Gardiner, B., Hetemäki, L., Chirici, G., Francini, S., Hlásny, T., Lerink, B.J.W., Olsson, H., Olabarria, J.R.G., Ascoli, D., Asikainen, A., Bauhus, J., Berndes, G., Donis, J., Fridman, J., Hanewinkel, M., Jactel, H., Lindner, M., Marchetti, M., Marušák, R., Sheil, D., Tomé, M., Trasobares, A., Verkerk, P.J., Korhonen, M., Nabuurs, G.J., 2021. Concerns about reported harvests in European forests. *Nature* 592, E15–E17. <https://doi.org/10.1038/s41586-021-03292-x> in press.
- Passtor, F., Matulla, C., Rammer, W., Lexer, M.J., 2014. Drivers of the bark beetle disturbance regime in alpine forests in Austria. *For. Ecol. Manag.* 318, 349–358. <https://doi.org/10.1016/j.foreco.2014.01.044>.
- Pickett, S.T.A., White, P.S., 1985. The Ecology of Natural Disturbance and Patch Dynamics. Academic Press. <https://doi.org/10.1016/C2009-0-02952-3>.
- Pretty, J.N., 1995. Participatory learning for sustainable agriculture. *World Dev.* 23, 1247–1263. [https://doi.org/10.1016/0305-750X\(95\)00046-F](https://doi.org/10.1016/0305-750X(95)00046-F).
- Pugh, T.A.M., Arneith, A., Kautz, M., Poulter, B., Smith, B., 2019. Important role of forest disturbances in the global biomass turnover and carbon sinks. *Nat. Geosci.* 12, 730–735. <https://doi.org/10.1038/s41561-019-0427-2>.
- R Core Team, 2020. R: A language and environment for statistical computing.
- Reed, M.S., 2008. Stakeholder participation for environmental management: a literature review. *Biol. Conserv.* 141, 2417–2431. <https://doi.org/10.1016/j.biocon.2008.07.014>.
- Riley, S., 1999. Index that quantifies topographic heterogeneity. *Int. J. Therm. Sci.* 5, 23–27.
- Roy, D.P., Kovalsky, V., Zhang, H.K., Vermote, E.F., Yan, L., Kumar, S.S., Egorov, A., 2016. Characterization of Landsat-7 to Landsat-8 reflective wavelength and normalized difference vegetation index continuity. *Remote Sens. Environ.* 185, 57–70. <https://doi.org/10.1016/j.rse.2015.12.024>.
- Scheidt, C., Heiser, M., Kamper, S., Thaler, T., Klebinder, K., Nagl, F., Lechner, V., Markart, G., Rammer, W., Seidl, R., 2020. Science of the Total environment the influence of climate change and canopy disturbances on landslide susceptibility in headwater catchments. *Sci. Total Environ.* 742, 140588. <https://doi.org/10.1016/j.scitotenv.2020.140588>.
- Schleeweis, K.G., Moisen, G.G., Schroeder, T.A., Toney, C., Freeman, E.A., Goward, S.N., Huang, C., Dungan, J.L., 2020. US national maps attributing forest change: 1986–2010. *Forests* 11, 1–20. <https://doi.org/10.3390/F11060653>.
- Schroeder, T.A., Wulder, M.A., Healey, S.P., Moisen, G.G., 2011. Mapping wildfire and clearcut harvest disturbances in boreal forests with Landsat time series data. *Remote Sens. Environ.* 115, 1421–1433. <https://doi.org/10.1016/j.rse.2011.01.022>.
- Schroeder, T.A., Schleeweis, K.G., Moisen, G.G., Toney, C., Cohen, W.B., Freeman, E.A., Yang, Z., Huang, C., 2017. Testing a Landsat-based approach for mapping disturbance causality in U.S. forests. *Remote Sens. Environ.* 195, 230–243. <https://doi.org/10.1016/j.rse.2017.03.033>.
- Schuler, L.J., Bugmann, H., Petter, G., Snell, R.S., 2019. How multiple and interacting disturbances shape tree diversity in European mountain landscapes. *Landscape Ecol.* 34, 1279–1294. <https://doi.org/10.1007/s10980-019-00838-3>.
- Schurman, J.S., Trotsiuk, V., Bače, R., Čada, V., Fraver, S., Janda, P., Kulakowski, D., Labusova, J., Mikoláš, M., Nagel, T.A., Seidl, R., Synek, M., Svobodová, K., Chaskovskyy, O., Teodosiu, M., Svoboda, M., 2018. Large-scale disturbance legacies and the climate sensitivity of primary *Picea abies* forests. *Glob. Chang. Biol.* 24, 2169–2181. <https://doi.org/10.1111/gcb.14041>.
- Sebal, J., Senf, C., Heiser, M., Scheidl, C., Pflugmacher, D., Seidl, R., 2019. The effects of forest cover and disturbance on torrential hazards: large-scale evidence from the eastern Alps. *Environ. Res. Lett.* <https://doi.org/10.1088/1748-9326/ab4937>.
- Seidl, R., Rammer, W., Jäger, D., Lexer, M.J., 2008. Impact of bark beetle (*Ips typographus* L.) disturbance on timber production and carbon sequestration in different management strategies under climate change. *For. Ecol. Manag.* 256, 209–220. <https://doi.org/10.1016/j.foreco.2008.04.002>.
- Seidl, R., Schelhaas, M.J., Rammer, W., Verkerk, P.J., 2014. Increasing forest disturbances in Europe and their impact on carbon storage. *Nat. Clim. Chang.* 4, 806–810. <https://doi.org/10.1038/nclimate2318>.
- Seidl, R., Aggestam, F., Rammer, W., Blennow, K., Wolfslehner, B., 2016a. The sensitivity of current and future forest managers to climate-induced changes in ecological processes. *Ambio* 45, 430–441. <https://doi.org/10.1007/s13280-015-0737-6>.
- Seidl, R., Müller, J., Hothorn, T., Bässler, C., Heurich, M., Kautz, M., 2016b. Small beetle, large-scale drivers: how regional and landscape factors affect outbreaks of the European spruce bark beetle. *J. Appl. Ecol.* 53, 530–540. <https://doi.org/10.1111/1365-2664.12540>.
- Seidl, R., Thom, D., Kautz, M., Martin-Benito, D., Peltoniemi, M., Vacchiano, G., Wild, J., Ascoli, D., Petr, M., Honkaniemi, J., Lexer, M.J., Trotsiuk, V., Mairota, P., Svoboda, M., Fabrika, M., Nagel, T.A., Rey, C.P.O., 2017. Forest disturbances under climate change. *Nat. Clim. Chang.* 7, 395–402. <https://doi.org/10.1038/nclimate3303>.
- Seidl, R., Honkaniemi, J., Aakala, T., Aleinikov, A., Angelstam, P., Bouchard, M., Boulanger, Y., Burton, P.J., De Grandpré, L., Gauthier, S., Hansen, W.D., Jepsen, J. U., Jögi, K., Kneeshaw, D.D., Kuuluvainen, T., Lisitsyna, O., Makoto, K., Mori, A. S., Pureswaran, D.S., Shorohova, E., Shubnitsina, E., Taylor, A.R., Vladimirova, N., Vode, F., Senf, C., 2020. Globally consistent climate sensitivity of natural disturbances across boreal and temperate forest ecosystems. *Ecography (Cop.)*. 1–12. <https://doi.org/10.1111/ecog.04995>.
- Senf, C., Sebal, J., Seidl, R., 2021. Increasing canopy mortality affects the future demographic structure of Europe's forests. *One Earth* 4, 1–7. <https://doi.org/10.1016/j.oneear.2021.04.008>.
- Senf, C., Seidl, R., 2018. Natural disturbances are spatially diverse but temporally synchronized across temperate forest landscapes in Europe. *Glob. Chang. Biol.* 24, 1201–1211. <https://doi.org/10.1111/gcb.13897>.
- Senf, C., Seidl, R., 2021. Mapping the forest disturbance regimes of Europe. *Nat. Sustain.* 4, 63–70. <https://doi.org/10.1038/s41893-020-00609-y>.
- Senf, C., Pflugmacher, D., Wulder, M.A., Hostert, P., 2015. Characterizing spectral-temporal patterns of defoliator and bark beetle disturbances using Landsat time series. *Remote Sens. Environ.* 170, 166–177. <https://doi.org/10.1016/j.rse.2015.09.019>.
- Senf, C., Pflugmacher, D., Hostert, P., Seidl, R., 2017. Using Landsat time series for characterizing forest disturbance dynamics in the coupled human and natural systems of Central Europe. *ISPRS J. Photogramm. Remote Sens.* 130, 453–463. <https://doi.org/10.1016/j.isprsjprs.2017.07.004>.
- Senf, C., Pflugmacher, D., Zhiqiang, Y., Sebal, J., Knorn, J., Neumann, M., Hostert, P., Seidl, R., 2018. Canopy mortality has doubled in Europe's temperate forests over the last three decades. *Nat. Commun.* 9, 4978. <https://doi.org/10.1038/s41467-018-07539-6>.
- Shimizu, K., Ahmed, O.S., Ponce-Hernandez, R., Ota, T., Win, Z.C., Mizoue, N., Yoshida, S., 2017. Attribution of disturbance agents to forest change using a Landsat time series in tropical seasonal forests in the Bago Mountains, Myanmar. *Forests* 8, 1–16. <https://doi.org/10.3390/f8060218>.
- Sommerfeld, A., Senf, C., Buma, B., D'Amato, A.W., Després, T., Díaz-Hormazábal, I., Fraver, S., Frelich, L.E., Gutiérrez, Á.G., Hart, S.J., Harvey, B.J., He, H.S., Hlásny, T., Holz, A., Kitzberger, T., Kulakowski, D., Lindenmayer, D., Mori, A.S., Müller, J., Paritsis, J., Perry, G.L.W., Stephens, S.L., Svoboda, M., Turner, M.G., Veblen, T.T., Seidl, R., 2018. Patterns and drivers of recent disturbances across the temperate forest biome. *Nat. Commun.* 9, 4355. <https://doi.org/10.1038/s41467-018-06788-9>.
- Stadelmann, G., Bugmann, H., Wermelinger, B., Bigler, C., 2014. Spatial interactions between storm damage and subsequent infestations by the European spruce bark beetle. *For. Ecol. Manag.* 318, 167–174. <https://doi.org/10.1016/j.foreco.2014.01.022>.
- Thom, D., Seidl, R., 2016. Natural disturbance impacts on ecosystem services and biodiversity in temperate and boreal forests. *Biol. Rev. Camb. Philos. Soc.* 91, 760–781. <https://doi.org/10.1111/brv.12193>.
- Thom, D., Seidl, R., Steyrer, G., Krehan, H., Formayer, H., 2013. Slow and fast drivers of the natural disturbance regime in central European forest ecosystems. *For. Ecol. Manag.* 307, 293–302. <https://doi.org/10.1016/j.foreco.2013.07.017>.
- Thom, D., Rammer, W., Dirnböck, T., Müller, J., Kobler, J., Katzensteiner, K., Helm, N., Seidl, R., 2017. The impacts of climate change and disturbance on spatio-temporal trajectories of biodiversity in a temperate forest landscape. *J. Appl. Ecol.* 54, 28–38. <https://doi.org/10.1111/1365-2664.12644>.
- Thom, D., Rammer, W., Garstenauer, R., Seidl, R., 2018. Disturbance legacies have a stronger effect on future carbon exchange than climate in a temperate forest landscape. *Biogeosci. Discuss.* 1–44. <https://doi.org/10.5194/bg-2018-145>.
- Thorn, S., Bässler, C., Svoboda, M., Müller, J., 2017. Effects of natural disturbances and salvage logging on biodiversity – lessons from the Bohemian Forest. *For. Ecol. Manag.* 388, 113–119. <https://doi.org/10.1016/j.foreco.2016.06.006>.
- Thorn, S., Chao, A., Georgiev, K.B., Müller, J., Bässler, C., Campbell, J.L., Castro, J., Chen, Y.-H., Choi, C.-Y., Cobb, T.P., Donato, D.C., Durska, E., Macdonald, E., Feldhaar, H., Fontaine, J.B., Fornwalt, P.J., Hernández, R.M.H., Hutto, R.L., Koivula, M., Lee, E.-J., Lindenmayer, D., Mikusiński, G., Obrist, M.K., Perlík, M., Rost, J., Waldron, K., Wermelinger, B., Weiß, I., Žmihorski, M., Leverkus, A.B., 2020. Estimating retention benchmarks for salvage logging to protect biodiversity. *Nat. Commun.* 1–8. <https://doi.org/10.1038/s41467-020-18612-4> in press.
- Turner, M.G., Gardner, R.H., 2015. Landscape ecology in theory and practice. In: *Landscape Ecology in Theory and Practice*. Springer New York, New York, NY, p. 482. <https://doi.org/10.1007/978-1-4939-2794-4>.
- Turner, M.G., Gardner, R.H., Dale, V.H., O'Neill, R.V., 1989. Predicting the spread of disturbance across heterogeneous landscapes. *Oikos* 55, 121. <https://doi.org/10.2307/3565881>.
- Valavi, R., Elith, J., Lahoz-Monfort, J.J., Guillerá-Arroita, G., 2019. blockCV: an R package for generating spatially or environmentally separated folds for k-fold cross-validation of species distribution models. *Methods Ecol. Evol.* 10, 225–232. <https://doi.org/10.1111/2041-210X.13107>.

- Wermelinger, B., 2004. Ecology and management of the spruce bark beetle *Ips typographus* - a review of recent research. *For. Ecol. Manag.* 202, 67–82. <https://doi.org/10.1016/j.foreco.2004.07.018>.
- White, J.C., Wulder, M.A., Hermosilla, T., Coops, N.C., Hobart, G.W., 2017. A nationwide annual characterization of 25 years of forest disturbance and recovery for Canada using Landsat time series. *Remote Sens. Environ.* 194, 303–321. <https://doi.org/10.1016/j.rse.2017.03.035>.
- Zhu, Z., 2017. Change detection using landsat time series: a review of frequencies, preprocessing, algorithms, and applications. *ISPRS J. Photogramm. Remote Sens.* 130, 370–384. <https://doi.org/10.1016/j.isprsjprs.2017.06.013>.

Appendix B: The effects of forest cover and disturbance on torrential hazards: large-scale evidence from the Eastern Alps

Published 2019 in *Environmental Research Letters*

Impact factor 2019: 6.090

LETTER • OPEN ACCESS

The effects of forest cover and disturbance on torrential hazards: large-scale evidence from the Eastern Alps

To cite this article: Julius Sebald *et al* 2019 *Environ. Res. Lett.* **14** 114032

View the [article online](#) for updates and enhancements.

Environmental Research Letters



LETTER

OPEN ACCESS

RECEIVED
11 April 2019

REVISED
2 September 2019

ACCEPTED FOR PUBLICATION
30 September 2019

PUBLISHED
8 November 2019

Original content from this work may be used under the terms of the [Creative Commons Attribution 3.0 licence](#).

Any further distribution of this work must maintain attribution to the author(s) and the title of the work, journal citation and DOI.



The effects of forest cover and disturbance on torrential hazards: large-scale evidence from the Eastern Alps

Julius Sebold^{1,4}, Cornelius Senf¹, Micha Heiser² , Christian Scheidl² , Dirk Pflugmacher³ and Rupert Seidl¹

¹ Institute of Silviculture, Department of Forest and Soil Sciences, University of Natural Resources and Life Sciences (BOKU), Vienna, Peter-Jordan-Str. 82, A-1190 Vienna, Austria

² Institute of Mountain Risk Engineering, Department of Civil Engineering and Natural Hazards, University of Natural Resources and Life Sciences (BOKU), Vienna, Peter-Jordan-Str. 82, A-1190 Vienna, Austria

³ Geography Department, Humboldt-Universität zu Berlin, Unter den Linden 6, D-10099 Berlin, Germany

⁴ Author to whom correspondence should be addressed.

E-mail: julius.sebold@boku.ac.at

Keywords: forest, disturbance, natural hazards, torrential hazards, debris flow, flood

Supplementary material for this article is available [online](#)

Abstract

Global human population growth, limited space for settlements and a booming tourism industry have led to a strong increase of human infrastructure in mountain regions. As this infrastructure is highly exposed to natural hazards, a main role of mountain forests is to regulate the environment and reduce hazard probability. However, canopy disturbances are increasing in many parts of the world, potentially threatening the protection function of forests. Yet, large-scale quantitative evidence on the influence of forest cover and disturbance on natural hazards remains scarce to date. Here we quantified the effects of forest cover and disturbance on the probability and frequency of torrential hazards for 10 885 watersheds in the Eastern Alps. Torrential hazard occurrences were derived from a comprehensive database documenting 3768 individual debris flow and flood events between 1986 and 2018. Forest disturbances were mapped from Landsat satellite time series analysis. We found evidence that forests reduce the probability of natural hazards, with a 25 percentage point increase in forest cover decreasing the probability of torrential hazards by $8.7\% \pm 1.2\%$. Canopy disturbances generally increased the probability of torrential hazard events, with the regular occurrence of large disturbance events being the most detrimental disturbance regime for natural hazards. Disturbances had a bigger effect on debris flows than on flood events, and press disturbances were more detrimental than pulse disturbances. We here present the first large scale quantification of forest cover and disturbance effects on torrential hazards. Our findings highlight that forests constitute important green infrastructure in mountain landscapes, efficiently reducing the probability of natural hazards, but that increasing forest disturbances can weaken the protective function of forests.

Introduction

Global human population growth in combination with an increasing demand for recreational activities have led to a strong increase of human infrastructure in some mountain regions around the globe (e.g. the European Alps, the Northern Front Range of the Rocky Mountains) (Casteller *et al* 2018). These settlements and infrastructure are highly exposed to natural hazards such as rockfall, avalanches, and torrential hazards (i.e. debris flow and flooding). As a result,

global losses from these natural hazards increased by almost 70% within the last 30 years (MunichRe 2019). In the Eastern Alps, torrential hazards caused damages of 877 million € (~1 billion US dollars) between 1972 and 2004, and 49 people lost their lives as a result of such events (Oberndorfer *et al* 2007). This underlines the strong need to protect humans and their infrastructure from torrential hazards in mountain regions.

An important means to address the risk from natural hazards are technical measures, such as snow barriers, rockfall nets, dams, and retention areas. Austria,

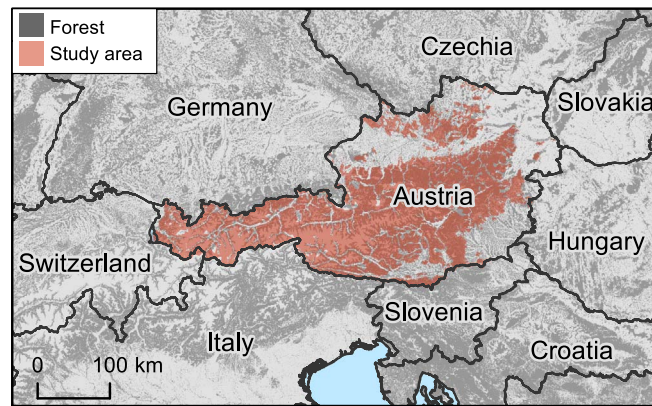


Figure 1. Map of the study area. The red areas mark the study area, whereas the grey parts indicate forest cover.

for example, currently directs more than 85% of the resources used to combat natural hazards into the construction and maintenance of such technical measures (BMNT 2018). However, it has long been established that forests are efficient in providing protection against natural hazards (Swanson *et al* 1998, Brang *et al* 2001). They contribute to slope stability in steep terrain as their rooting systems reinforces and stabilizes the soil (Amann *et al* 2009). Additionally, forests buffer surface runoff during peak precipitation events through canopy water interception and improved soil infiltration, and are thus able to reduce soil erosion in torrential watersheds (Sakals *et al* 2006).

In contrast to technical measures, forests are dynamic systems that change over time. This means that also the services they provide to society are not static but vary over time (Wohlgemuth *et al* 2017, Albrich *et al* 2018). Natural disturbances (i.e. large pulses of tree mortality from natural causes such as wind-throw events, wildfires, or bark beetle outbreaks) are integral drivers of mountain forest dynamics (Kulakowski *et al* 2017). Disturbances open up the forest canopy and decrease leaf area, substantially reducing the protective function of forests (Thom and Seidl 2016). Specifically, disturbances reduce the protective effects of forests by increasing precipitation through-fall and surface water runoff, as well as by decreasing the live root density in the soil. Also forest management interventions such as timber harvesting open up the forest canopy. However, as they are applied deliberately to regenerate forests, they are frequently seen as an important means to maintain the long-term protective function of forests against natural hazards (Brang *et al* 2006, Streit *et al* 2009). Recent quantitative studies indicated, however, that unmanaged forests provide a higher level of protection against natural hazards than managed forests (Irauschek *et al* 2017, Mina *et al* 2017, Seidl *et al* 2019). It thus remains unclear how forest disturbances—both natural and human—affect the occurrence probability and frequency of torrential hazards.

The currently available evidence on the effects of forest cover and disturbance on torrential hazard risk largely stems from local case studies (Brardinoni *et al* 2003, Imaizumi *et al* 2008, Nyman *et al* 2015), and large-scale investigations on the efficiency of forest protection against natural hazards are largely missing (but see Bradshaw *et al* 2007, Yin *et al* 2018). This knowledge gap is problematic, as a push towards a bio-based economy increases the pressure on forest ecosystems, e.g. increasing harvest levels across Europe's forests (Levers *et al* 2014). Furthermore, natural disturbances are intensifying across Europe (Seidl *et al* 2014, Senf *et al* 2018) as a result of past land use and anthropogenic climate change. The ongoing large-scale changes in forest disturbances call for an assessment of their impacts on the protective effect of forests, in order to provide robust recommendations to forest managers and political makers.

A major limitation for large-scale research on the effects of forest disturbances on torrential hazards is the lack of consistent large-scale data sets on both disturbances and torrential hazard events. However, recent efforts to systematically catalogue torrential hazard events (Heiser *et al* 2019) and identify forest disturbances using remote sensing data (Senf *et al* 2017) offer new avenues for quantitative analyses. We here build upon these recent developments by quantifying the effects of forest cover and canopy disturbances on the probability of torrential hazards in the Eastern Alps, jointly analyzing 31 years of disturbance data and 3768 documented torrential hazard events for 10 885 watersheds. Specifically, we address three research questions:

- I. Does forest cover reduce the probability and frequency of torrential hazard events?
- II. How do forest disturbances influence the probability and frequency of torrential hazard events?
- III. If forest disturbances influence the occurrence probability and frequency of torrential hazards, how does their effect differ with disturbance type?

Data and methods

Study area

We focused our analysis on the Eastern Alps in Austria (figure 1). The geology of the central parts of the mountain range is dominated by crystalline bedrock (i.e. granite and gneiss), whereas the northern and the southern front ranges are characterized by calcareous bedrock. Mean annual precipitation varies greatly with elevation and location, and ranges from 600 mm on the dry and warm eastern slopes of the Alps to >2500 mm in high elevation areas of the northern front range. Mean annual temperature ranges from 11 °C in low-lying areas in the east to below −5 °C in areas above the timber line in the center of the range (ZAMG 2019). Over the entire study area, the mean annual temperature between 1986 and 2018 was 7.3 °C, with an average annual precipitation of 1098 mm (ZAMG 2019). In total we analyzed 10 885 watersheds covering an area of 4.8 million hectares, and spanning an elevational gradient from 114 to 3725 m a.s.l. The mean watershed area is 437 ha (minimum of 4 ha and maximum of 19 843 ha) and the mean elevation is 996 m a.s.l.

The mean forest cover of the investigated watersheds is 63%. The natural vegetation composition changes along an elevational gradient. In elevations <600 m a.s.l. forests are dominated by broadleaved species (primarily European beech [*Fagus sylvatica* L.] and oak species [*Quercus* spp.]). In mid elevations between 600 and 1200 m a.s.l. mixed broadleaved and coniferous forests (dominated by European beech, Norway spruce [*Picea abies* (L.) Karst.] and silver fir [*Abies alba* Mill.]) form the natural vegetation. Forests in elevations above 1200 m a.s.l. are naturally conifer-dominated (Norway spruce, European larch [*Larix decidua* Mill.], and Swiss stone pine [*Pinus cembra* L.]). The tree-line is generally situated between 1800 and 2200 m a.s.l. and is often characterized by a *krummholz* belt of mountain pine [*Pinus mugo* Turra]. Forest structure and species composition have been strongly modified by forest management as most parts of the study area have experienced intensive land use over the past 300 years (Bebi *et al* 2017).

Disturbance data

We created disturbance maps at a spatial grain of 30 m and at annual resolution for the period from 1986 to 2016 based on all available Collection 1 Level 1 surface reflectance images from the USGS Landsat archive. We employed state-of-the-art disturbance detection algorithms (Kennedy *et al* 2010, Cohen *et al* 2018) implemented in the Google Earth Engine cloud computing platform (Gorelick *et al* 2017, Kennedy *et al* 2018). The algorithm first builds annual best-observation composites from all available Landsat images. Subsequently, it segments each annual time

series into linear segments of either stable, declining or increasing vegetation conditions based on the individual spectral bands and a series of spectral indices. This segmentation is used to identify forest canopy disturbances (see Kennedy *et al* 2010 for details) at the level of an individual pixel. A random forest model (Breiman 2001) is subsequently applied to classify each pixel in any given year into disturbed or stable conditions, filtering for the false positives frequently occurring with automatic disturbance detection algorithms (Cohen *et al* 2017). We calibrated and validated the random forest models using 1828 pixel-based reference data collected in a previous study (Senf *et al* 2018). Annual disturbance probabilities were aggregated into a map indicating the year of the first disturbance. The overall map accuracy was 90.5% (<0.1% SE) with balanced errors of omission (19.6%, SE 0.8%) and commission (19.3%, SE 0.8%).

Torrential hazard data

We define hazards according to IPCC (2012), describing physical events that have caused damages to human infrastructure or livelihood. Torrential hazards are hazards from ravines, creeks, rivers, and streams in small, steep headwater catchments. Information about torrential hazard events was extracted from the Austrian torrential event catalogue (Hübl *et al* 2008). This database contains torrential events that have caused damage to humans or human infrastructure in small steep headwater catchments. In addition, it provides shapefiles describing the watershed outlines and the torrential event locations. From 1986 to 2018, 3768 torrential hazard events were recorded in 2018 watersheds, whereof 2646 were flood events and 1122 were debris flow events. As reference condition for our analysis we selected all watersheds which did not experience any torrential events between 1980 and 2018 (i.e. 8867 watersheds). We here extended the time period in order to omit watersheds that experienced a torrential event just before 1986. Flood processes in steep headwater catchments are characterized by variable sediment transport rates with a volumetric concentration of solid particles in water of up to 20% (ONR-24800 2014). Coarser particles are transported as bedload, moving much slower than the water stream. In contrast, sediment concentrations of debris flow events can exceed 40% (ONR-24800 2014), and particles and water travel at the same velocity. While differing in their constitutive features both debris flow and flood events are triggered by heavy rainfall events and are capable to relocate and deposit large amounts of material from the slopes to the valley bottoms. This frequently results in damaged roads and destroyed houses.

Table 1. Predictors for modeling the probability of torrential hazards. For the values and range of all predictors see supplement SI 4.

Domain	Predictor	Definition	Expected effect on torrential hazard probability	Source
Geography	Area	Area of focal watershed in km ²	+	Pflugmacher <i>et al</i> 2019
	Elevation	Mean elevation of watershed in m a.s.l.	+	
	Infrastructure	Area share covered by urban infrastructure in focal watershed in %.	+	
	Ecoregion	The ecoregion in which the majority of the focal watershed is situated		
Geomorphology	Melton ratio	$\frac{\text{Elevation}_{\text{max}} - \text{Elevation}_{\text{min}}}{\sqrt{\text{Area}}}$	+	Melton 1957
	Elevation ratio	$\frac{\text{Elevation}_{\text{max}} - \text{Elevation}_{\text{mean}}}{\text{Elevation}_{\text{max}} - \text{Elevation}_{\text{min}}}$	+	Wood and Snell 1960
	Elongation	$\frac{\text{Diameter of a circle with area of watershed}}{\sqrt{\text{length}_{\text{max}} \text{ of watershed}}}$	–	Schumm 1956
	Circularity	$\frac{\text{Area}}{\text{Area of a circle with circumference of watershed}}$	–	Miller 1953
Forest	Forest cover	Forest cover of watershed in %	–	Pflugmacher <i>et al</i> 2019
	Patch density	Number of forest patches per km ² i.e. forest distribution in the watershed ranging from contiguous to patchy	+	Pflugmacher <i>et al</i> 2019
Disturbance	Extent	Forest canopy cover disturbed between 1986 and 2016 in %	+	
	Type	$\text{Gini}_{\text{coefficient}}(\text{yearly disturbance extent})$	–	
	Extent x Type	Interaction between extent and type (see supplement SI 3)	+	

Geographical and geomorphological watershed attributes

We derived three geographical attributes for each watershed from remote sensing products in order to adjust for differences in extent, elevation and level of human infrastructure exposed to natural hazards (table 1, section *Geographical*). We expected larger watersheds and watersheds with a high level of human infrastructure to have a higher probability of being affected by torrential hazards. The level of exposed human infrastructure was approximated as the relative proportion of urban areas within each watershed, based on a 2015 land cover map with a spatial resolution of 30 m, created from Landsat satellite data (Pflugmacher *et al* 2019). As precipitation increases with elevation in our study area and torrential hazards are frequently triggered by periods of heavy rainfall, we included elevation to account for differences in exposure between watersheds. Furthermore, to account for climatic and geological differences among watersheds we also controlled for the ecoregion (according to Kilian *et al* 1994) in our analyses (see supplement SI 1 available online at stacks.iop.org/ERL/14/114032/mmedia).

We described the geomorphological predisposition of a watershed to torrential hazards based on indicators which have been identified as influential in previous studies (table 1, section *Geomorphology*). Heiser *et al* (2015) analyzed 11 fluvial geomorphometric parameters with regard to their influence on torrential

processes. Based on their findings we selected the Melton ratio (Melton 1957) as well as the elevation relief ratio (Wood and Snell 1960) as geomorphological predictors of torrential processes. In addition, we also included circularity (Schumm 1956) and the elongation ratio (Miller 1953) in our analysis to account for the specific form of watersheds.

Forest- and disturbance-related watershed attributes

To evaluate the role of forests and canopy disturbances on the probability of torrential hazards we used four indicators, i.e. forest cover, forest patch density, disturbance extent and disturbance type (see table 1 section *Forest*). Forest cover was calculated as the relative proportion of forested area within a watershed in 2015 based on a 30 × 30 m land cover map (Pflugmacher *et al* 2019). As forest cover changes over time we also tested how land-use change influences our results (see supplement SI 2). Forest patch density was derived by dividing the number of distinct forest patches (using an eight-cell-neighborhood to identify patches) by the total watershed area. The indicator thus describes the distribution of the forest area within the watershed, ranging from contiguous forest cover to highly patchy forest cover.

Canopy disturbances occur as a result of timber logging (clearcutting as well as thinning) or natural forest disturbances (i.e. primarily windthrow and insect infestation) in our study area. Since previous

studies showed that the attribution of satellite-based disturbance patches to different causes of canopy disturbance remains challenging (Hicke *et al* 2012, Kasischke *et al* 2013, Oeser *et al* 2017, Senf *et al* 2017), we here jointly analyzed canopy disturbances from both human and natural causes. Specifically, we calculated two indices describing the disturbance regime of a watershed based on the annual disturbance maps described above (Section *Disturbance data*), i.e. disturbance extent and disturbance type (see supplement SI 3). Disturbance extent describes the relative forest area of a watershed affected by canopy disturbances over the 31-year study period. Disturbance type describes the temporal distribution of disturbances, with *pulse disturbances* happening in a short period of time and *press disturbances* being distributed regularly over the study period (Bender *et al* 1984). To derive a continuous indicator between the two poles of pulse and press disturbance we calculated the Gini coefficient of the annual forest area affected by canopy disturbances. A Gini coefficient of one indicates a pulse disturbance regime signifying that the disturbance of a watershed occurred in one year. A Gini index of zero indicates a press disturbance regime signifying that equal areas were disturbed every year between 1986 and 2016. High Gini values mean maximum inequality in the annually disturbed area and low values mean minimum inequality in the annual area disturbed. In addition to the ecological relevance of distinguishing between pulse and press disturbances, disturbance type also serves as a proxy for the dominant disturbance agent in our study region. While human-induced canopy disturbances (i.e. clearcutting and thinning) are generally small but occur regularly (i.e. *press* disturbance), natural disturbances are potentially large but only happen rarely (i.e. *pulse* disturbance). We *a priori* checked for correlation between forest cover and disturbance extent/type. We found only a weak correlation of Pearson's $r = 0.18$ for disturbance extent and Pearson's $r = -0.11$ for disturbance type. For an overview of the range of variability within the data see supplement SI 4.

Statistical analysis

All analyses were conducted at the watershed scale. We developed separate models for the occurrence and frequency of debris flow and flooding. For modelling the occurrence, we assumed a Bernoulli distribution, where the occurrence probability p_i in watershed i is modeled by a linear combination of all predictor variables $\mathbf{X}_i$ (see table 1) using a logistic link function:

$$\begin{aligned} \text{Occurrence}_i &\sim \text{Bernoulli}(p_i) \\ p_i &= \text{logit}^{-1}(\beta \mathbf{X}_i). \end{aligned} \quad (1)$$

In equation (1), the vector β contains the direction and strength of each predictors (see table 1) effect on the probability of occurrence.

To model the frequency of torrential hazard events we assumed a negative binomial distribution,

predicting the count of events per watershed over the study period. The mean μ_i is modeled by a linear combination of all predictor variables $\mathbf{X}_i$ using a log link function to assure positive response values:

$$\begin{aligned} \text{Count}_i &\sim \text{Negativebinomial}(\mu_i, \phi) \\ \mu_i &= \log^{-1}(\beta \mathbf{X}_i). \end{aligned} \quad (2)$$

In equation (2) the parameter ϕ is a dispersion parameter accounting for over-dispersion and is estimated from the data.

We used Bayes' rule to calculate posterior distributions of all model parameters (i.e. the intercept and effect sizes contained in β as well as the dispersion parameter ϕ) from the model likelihoods and prior parameter distributions assigned to each parameter. After z-transforming the data, we used $N(0, 0.5)$ priors for β and an $\text{Exp}(1)$ prior for ϕ . Those priors can be seen as weakly informative, regularizing priors that prevent the model from overfitting the data. Joint posterior distributions were sampled using Monte-Carlo-Markov-Chain (MCMC) methods implemented in the Software Stan (Carpenter *et al* 2017) via the *rstanarm* package (Stan Development Team 2016). We used four chains à 4000 iterations, with the first 2000 iterations dropped as warm-up samples. We checked the convergence of the chains via the $\hat{R}$ statistic (Gelman *et al* 2014a). The $\hat{R}$ statistic compares the variability within and between chains and approaches one if all four chains converge to a similar solution. We further evaluated whether the model fitted the data properly by performing posterior-predictive checks (Gelman *et al* 2014a), that is drawing randomly from the model and comparing the draws to the observed data. If the model is well specified, there should be no substantial deviation between model draws and observed data (see supplement SI 5 and SI 6).

We fitted and compared different predictor combinations to test the importance of different predictor domains (see table 1). First, we fitted a null model containing only an intercept, assuming constant torrential hazard probabilities across all watersheds. Subsequently, we successively included predictors of the domains *geography*, *geomorphology*, *forest* and *disturbances*, resulting in a total of five models with increasing model complexity. We compared all five models by estimating the approximate leave-one-out expected log predictive density (LOO-ELPD; Vehtari *et al* 2017). The LOO-ELPD is a relative measure of model performance—similar to the Watanabe–Akaike information criterion—but preferable in most settings (Gelman *et al* 2014b). In essence, it estimates the predictive accuracy of the model when confronted with unknown data. Thus, a positive difference in ELPD between two competing models implies a better predictive performance of the second model. However, as the ELPD itself is uncertain, we assume a difference in ELPD to be only meaningful whenever it is two standard deviations larger than zero.

We finally summarized and compared the joint posterior distributions from the full models of both occurrence probability and frequency to gain insights into the direction and strength of each covariate. We further drew posterior predictive distributions for fixed values of disturbance extent and type (holding the watershed predictors constant), in order to further investigate the effects of different disturbance regimes on the occurrence probability and frequency of torrential hazard events.

The data that support the findings of this study are openly available at Sebold (2019):

<https://doi.org/10.6084/m9.figshare.9758891.v1>

Results

In line with our expectations, the *geographical* watershed characteristics were important for controlling for differences in watersheds across our study area (large difference in ELPD compared to the null model; table 2). Larger watersheds had a higher probability of one or more torrential events occurring. Watersheds in higher elevations had a higher occurrence probability and frequency of debris flow events, but a lower occurrence probability and frequency of flood events. The level of human infrastructure in a watershed had no influence on the occurrence probability and frequency of debris flows, but slightly decreased the occurrence probability and frequency of flood events (figure 2).

The *Geomorphological* characteristics were important for predicting occurrence probability and frequency of torrential events, substantially increasing predictive performance (table 2). Melton ratio, circularity and elevation ratio were positively related with occurrence probability and frequency of both hazards. Elongation was negatively correlated with flood events, but had a slightly positive correlation with debris flow events (figure 2).

Forest-related predictors also had an important effect on the occurrence and frequency of torrential events (table 2). Forest cover was the predictor with the strongest negative effect on occurrence probability and frequency of both hazards (figure 2). Compared to the average forest cover in the study area (i.e. 63%), an increase by one standard deviation in forest cover (i.e. to 88%) decreased torrential hazard probability by $8.7\% \pm 1.2\%$. A higher patch density, representing a distributed occurrence of forests over the watershed, also reduced the occurrence probability and frequency of torrential hazards. Compared to the average patch density (i.e. 6.5 forest patches per km^2) an increase by one standard deviation (i.e. to 12.5 forest patches per km^2) decreased debris flow probability by $-8.2\% \pm 1.8\%$ and flood probability by $-5.7\% \pm 1.2\%$ (figure 2).

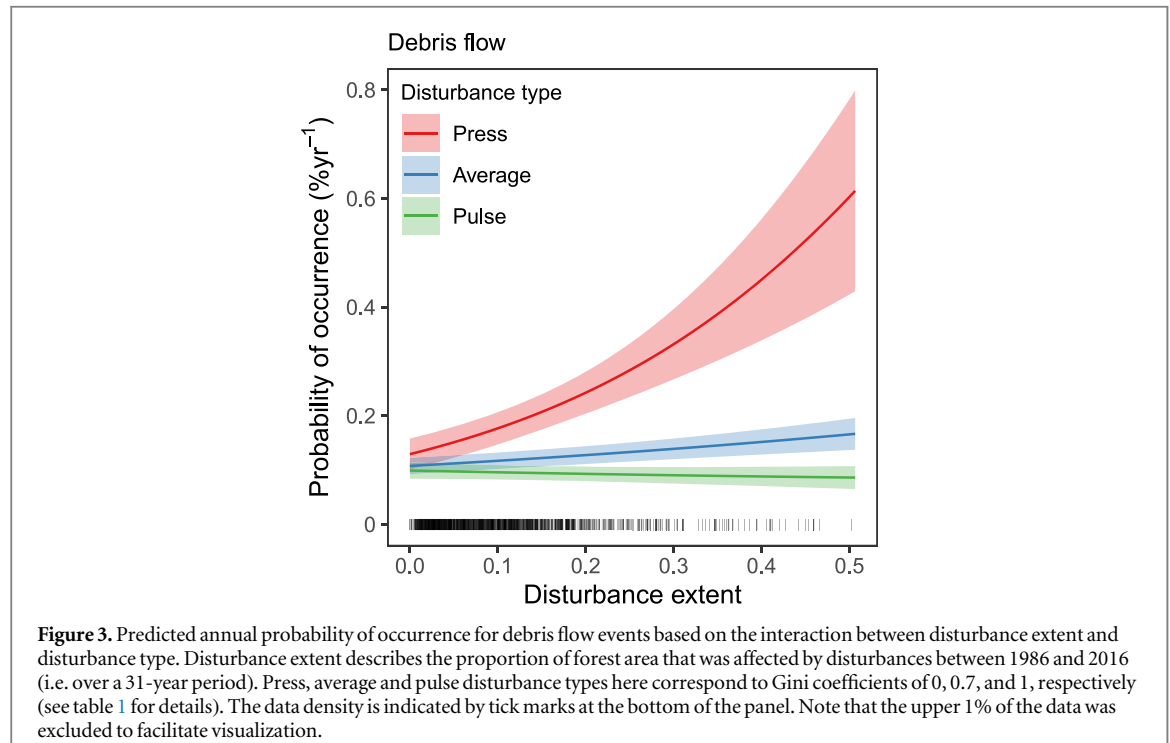
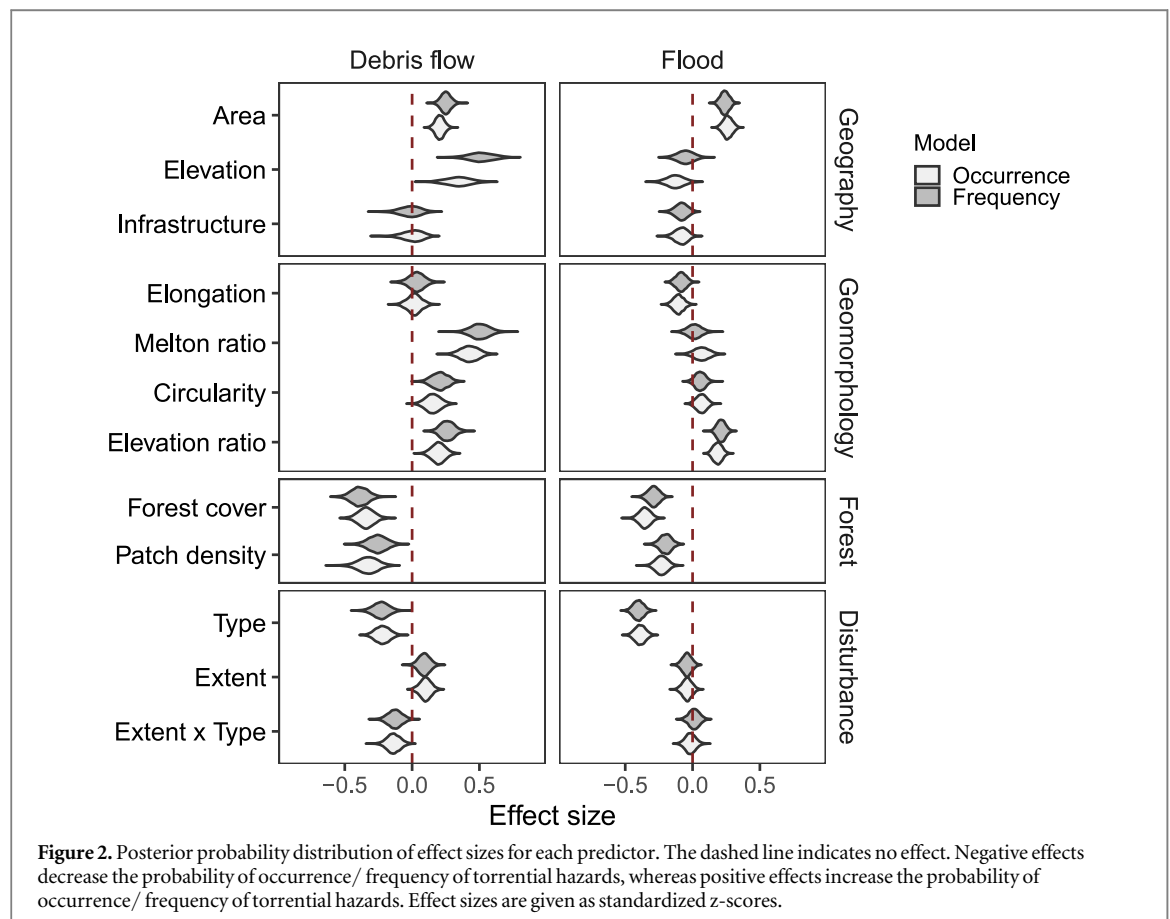
Finally, also *disturbances* significantly influenced the occurrence and frequency of torrential events (table 2). Large disturbance extents increased the probability of debris flow events but had no significant effect on flood events. Furthermore, press type disturbances (i.e. disturbances occurring regularly across the study period) increased the probability of both debris flow and flood events (figure 2). For debris flow, the effect of disturbance extent was further modulated by disturbance type (figure 3). Here, the highest probability of occurrence was observed in watersheds with regular, large forest canopy disturbances. Given a press disturbance regime (Gini = 0), the annual probability of a debris flow event increased from 0.18% to 0.60% (+248%) when moving from 10% of the forest cover disturbed to 50% of the forest cover disturbed within the 31-year study period. In contrast, the probability did only moderately increase (+42%) for the same increase in disturbance extent under the average disturbance type, and no change was found for pulse disturbance regimes (Gini = 1, figure 3). A similar signal could be observed for hazard frequency, where the annual probability of two or more debris flow events increased from 0.03% to 0.15% (+466%) when moving from 10% of the forest cover disturbed to 50% of the forest cover disturbed in 31 years under a press disturbance regime (figure 4a). In contrast, there was only weak evidence for an interaction between disturbance extent and disturbance type for flood events (figure 2). Probability of occurrence and frequency of flood events were primarily influenced by disturbance type, increasing with press-type disturbances. For floods the annual probability of one event occurring within the 31-year study period increased from 0.22% to 0.40% (+83%), and the annual probability of two or more events from 0.03% to 0.21% (+530%) when moving from a pulse disturbance regime to a press disturbance regime (figure 4b). Including an interaction between disturbance type/extent and forest cover did not improve model performance compared to a model without this interaction (ELPD difference $\pm$ standard error for the debris flow model was 1.62 ± 2.64 and -0.75 ± 1.37 for the flood model).

Discussion

We here for the first time quantified the effect of forest cover and disturbance on natural hazards across a large spatial domain, using a novel combination of remote sensing data and a national scale database on natural hazard events. Our findings highlight the importance of forests for mitigating torrential hazards for humans and their infrastructure. Across a wide social and ecological gradient, we found that the occurrence probability and frequency of torrential hazards was reduced with higher shares of forest cover in a watershed. This result is in line with the process-based understanding of mechanisms influencing the occurrence of torrential hazards,

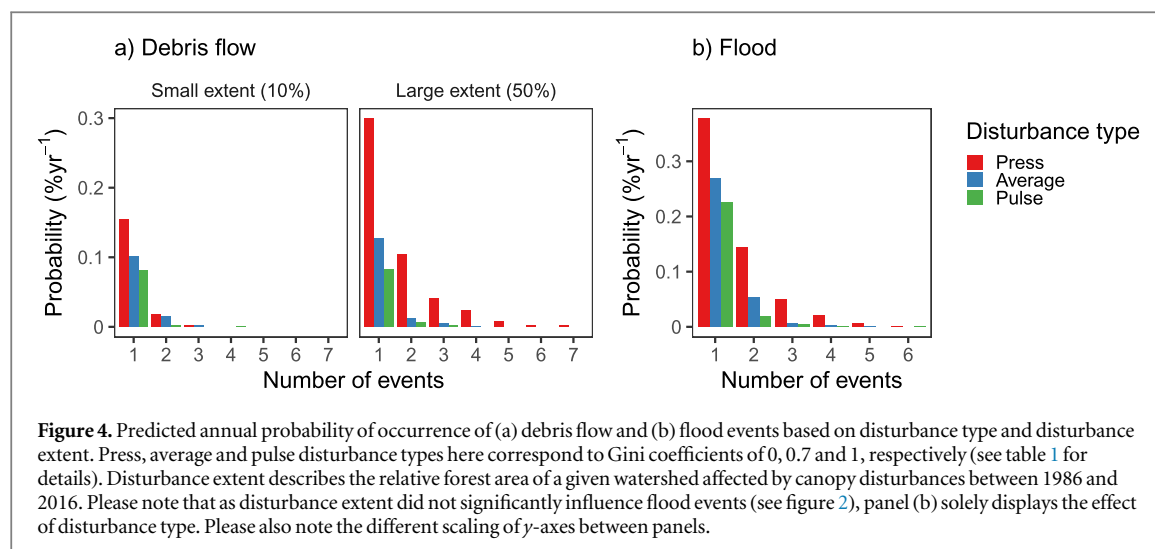
Table 2. Improvement of predictive power with increasing model complexity. The table shows the model improvement compared to the previous level of model complexity (difference in ELPD $\pm$ one standard deviation; see section statistical analysis). Predictors were included in groups following the domains outlined in table 1. The first model, containing only predictors from the domain Geography (see table 1), is compared to a Null-model containing only an intercept (i.e. constant torrential hazard probabilities across all watersheds). An ELPD difference of more than two standard deviations is considered as a meaningful improvement (see Vehtari *et al* 2017 for details on interpreting the ELPD).

Response Predictor domains	Difference in ELPD ($\pm$ SD)			
	Geography	Geography + Geomorphology	Geography + Geomorphology + Forest	Geography + Geomorphology + Forest + Disturbances
Debris flow				
Occurrence	+322 $\pm$ 25	+19 $\pm$ 7	+18 $\pm$ 6	+18 $\pm$ 6
Frequency	+361 $\pm$ 27	+28 $\pm$ 9	+15 $\pm$ 6	+15 $\pm$ 6
Flood				
Occurrence	+282 $\pm$ 27	+53 $\pm$ 11	+27 $\pm$ 8	+48 $\pm$ 10
Frequency	+351 $\pm$ 29	+59 $\pm$ 12	+18 $\pm$ 7	+53 $\pm$ 12



derived from local case studies (Imaizumi *et al* 2008, Moos *et al* 2016, Altieri *et al* 2018). Torrential events occur through hydrological transport of soil and debris from slopes, and their deposition in valley bottoms which are frequently settled by humans in the Alps. The amount of soil and debris that is deposited is

determined by the availability of loose material on the slopes as well as the transportation rate of streams. Forests reduce the availability of material for transport as their root system stabilizes the soil and thus retains material on slopes (Sakals *et al* 2006). Furthermore, forests decrease stream transportation rates as their



canopy intercepts precipitation. In addition, trees transpire water and thus free up pore space in the soil. In combination with improved soil water infiltration surface runoff is reduced (Noguchi *et al* 2001) and runoff peaks are dampened by forests, reducing sediment transportation rates.

While forests generally reduce the probability of natural hazards, this protective function can be weakened by increasing canopy disturbances. Our results provide clear evidence for a significant influence of forest canopy disturbances on the probability of torrential hazards, which is in line with findings from local studies (Roberts and Church 1986, Jakob 2000, Imaizumi *et al* 2008, Silins *et al* 2009, Buma and Johnson 2015). Disturbances reduce canopy cover and—with a time lag of a few years to decades—also rooting density in the soil, thus leading to elevated transportation rates and decreased soil stability. Disturbances also increase the amount of loose soil material available for transport in torrential events, e.g. via root plates of uprooted trees or erosion from logging activity. However, based on our analyses the extent of the detrimental effect of forest disturbances varies with disturbance regime. We found that regular canopy disturbances were more detrimental to the protection against torrential hazards than singular disturbance events. This can be explained by the fact that the risks from canopy disturbances are greatest in the years immediately after a disturbance event (Wohlgemuth *et al* 2017), and that both canopy disturbances and the heavy rainfall events triggering torrential hazards are rare. At low disturbance frequency the likelihood of a heavy rainfall event occurring immediately after a disturbance is also low. In contrast, if canopy disturbances happen regularly in a watershed, any heavy rainfall event will affect partly disturbed areas. Regular canopy disturbances thus increase the probability of torrential hazards, particularly if they affect a large portion of the watershed (figure 3, 4). This is of special relevance since there is growing evidence that both the occurrence of heavy precipitation events (IPCC 2012) and the frequency and extent of

disturbances (Seidl *et al* 2017, Senf *et al* 2018) is increasing as a result of climate change.

Although our results are based on an exceptionally large empirical dataset (10 885 watersheds in which 3768 torrential events were recorded over a period of 31 years) and we combine these data with novel, comprehensive maps of canopy disturbance, it is important to consider the limitations of our materials and analyses. First, the disturbance maps created for this study are not able to capture sub-canopy disturbances (such as thinnings from below) or disturbances happening at the sub-pixel scale (i.e. <30 m horizontal grain). They thus give a conservative estimate of disturbance extent in our study area. Furthermore, an attribution of disturbances to different disturbance agents (e.g. insect infestation, wind breakage, logging etc) was not possible with our data and remains a major methodological challenge for remote sensing in Central Europe (Senf *et al* 2017). We circumvented this limitation by developing a novel indicator of disturbance type (see supplement SI 3) based on ecologically important disturbance characteristics (press-pulse disturbance, Bender *et al* 1984). Such a categorization has recently been found to hold high inferential potential e.g. in the assessment of disturbance effects on a wide range of ecosystem services (Cantarello *et al* 2017). Second, a limitation of the natural hazard events database used here is that only events which have caused actual damage to humans and/or human infrastructure are recorded. Although even small damages are recorded (e.g. a minor amount of debris being deposited on a road by a creek), our data (i) likely underestimate the total amount of torrential events that occurred, and (ii) might be skewed towards watersheds with significant levels of human infrastructure. We controlled for the latter by including a proxy of human infrastructure in our analysis. However, watersheds with a high level of human infrastructure frequently also have a higher level of technical hazards mitigation measures, such as dams and overflow basins. As such measures reduce the damage caused by torrential hazards (Holub and Hübl 2008), they might introduce a bias in our analysis.

This effect could explain the slightly negative correlation of our infrastructure variable with occurrence probability and frequency of flood events (figure 2). Third, we note that factors not considered here might influence the probability and frequency of torrential hazards. Those include, e.g. the frequency of high intensity rainfall event, which was not considered explicitly in our analysis. Further, the probability and frequency of torrential hazard events might also be affected by differences in the hydrological system, and in particular by differences in technical measures of flood control (i.e. dams).

The large-scale evidence for a strong link between forest cover, canopy disturbance and torrential hazards provided here is of crucial importance for forest management. For instance, guidelines for the management of protective forests in the Alps propose frequent, small-scale logging interventions to increase structural diversity and continuously regenerate the forest (Motta and Haudemand 2000, Frehner *et al* 2005, Brang *et al* 2006). However, our results suggest that forest management in torrential watersheds should aim for as little interventions as possible to keep the probability of torrential hazards low. This insight is in line with recent simulation-based studies across the Alps, finding that non-intervention management is best able to provide regulating ecosystem services and protect against natural hazards (Irauschek *et al* 2017, Langner *et al* 2017, Mina *et al* 2017, Seidl *et al* 2019). A major concern of managers in this regard remains the thread of large-scale natural disturbances (Wohlgemuth *et al* 2017). However, the return intervals of such events are an order of magnitude lower than those of regular management interventions in the Eastern Alps (100–300 years and 10–30 years, respectively, Thom *et al* 2013). And while natural disturbances from wind and bark beetles can have strong detrimental effects on the local protection function against natural hazards (Badoux *et al* 2006, Brang *et al* 2006), our large-scale analysis revealed that their overall impact remains limited due to their low frequency. Natural disturbances could, however, become more influential in the future, as they are widely expected to increase in frequency and magnitude (Seidl *et al* 2017, 2014). In conclusion our study provides important empirical evidence for the efficiency of forests as green infrastructure protecting against torrential hazards and highlights the complex effects of canopy disturbances on forests and the services they provide to society.

Acknowledgments

R Seidl and J Sebald acknowledge funding from Austrian Science Fund FWF START grant Y895-B25. C Senf acknowledges funding from the Austrian Science Fund (FWF) Lise-Meitner Program (Nr. M2652). C Scheidl, M Heiser and R Seidl acknowledge funding from the Austrian Climate Research Program (PROTECTED, KR16AC0K13167). The authors are

grateful to the Agency for Spatial Information of the Forest Technical Service for Avalanche and Torrent control of Austria, for providing the torrential data. We are grateful to two anonymous reviewers for helpful comments on an earlier version of the manuscript.

ORCID iDs

Micha Heiser  <https://orcid.org/0000-0002-8675-0579>

Christian Scheidl  <https://orcid.org/0000-0002-5625-6238>

References

- Albrich K, Rammer W, Thom D and Seidl R 2018 Trade-offs between temporal stability and level of forest ecosystem services provisioning under climate change *Ecol. Appl.* **28** 1884–96
- Altieri V, De Franco S, Lombardi F, Marziliano P A, Giuliano M and Porto P 2018 The role of silvicultural systems and forest types in preventing soil erosion processes in mountain forests: a methodological approach using cesium-137 measurements *J. Soils Sediments* **18** 3378–87
- Amann M, Böll A, Rickli C, Speck T and Holdenrieder O 2009 Significance of tree root decomposition for shallow landslides *Forest Snow Landsc. Res.* **82** 79–94
- Badoux A, Jeisy M, Kienholz H, Lüscher P, Weingartner R, Witzig J and Hegg C 2006 Influence of storm damage on the runoff generation in two sub-catchments of the sperbelgraben, swiss emmental *Eur. J. Forest Res.* **125** 27–41
- Bebi P, Seidl R, Motta R, Fuhr M, Firm D, Krumm F, Conedera M, Ginzler C, Wohlgemuth T and Kulakowski D 2017 Changes of forest cover and disturbance regimes in the mountain forests of the Alps *For. Ecol. Manage.* **388** 43–56
- Bender E A, Case T J and Gilpin M E 1984 Perturbation experiments in community ecology: theory and practice author (s): Edward A Bender, Ted J Case and Michael E Gilpin Published by: ecological Society of America perturbation experiments IN community ecology: theory and practice *Ecology* **65** 1–13
- BMNT 2018 Schutz vor Naturgefahren-Gesamtmitel 2017
- Bradshaw C J A, Sodhi N S, Peh K S H and Brook B W 2007 Global evidence that deforestation amplifies flood risk and severity in the developing world *Glob. Change Biol.* **13** 2379–95
- Brang P, Schönenberger W, Frehner M, Schwitter R, Thormann J-J and Wasser B 2006 Management of protection forests in the European Alps: an overview *Forest Snow Landsc. Res.* **80** 23–44
- Brang P, Schönenberger W, Ott E and Gardner B 2001 Forests as protection from natural hazards *The Forests Handbook: Applying Forest Science for Sustainable Management* ed J Evans vol 2 (Oxford, UK: Blackwell Science Ltd) (<https://doi.org/10.1002/9780470757079.ch3>)
- Brardinoni F, Hassan M A and Slaymaker H O 2003 Complex mass wasting response of drainage basins to forest management in coastal British Columbia *Geomorphology* **49** 109–24
- Breiman L 2001 Random forests *Mach. Learn.* **45** 5–32
- Buma B and Johnson A C 2015 The role of windstorm exposure and yellow cedar decline on landslide susceptibility in southeast Alaskan temperate rainforests *Geomorphology* **228** 504–11
- Cantarello E, Newton A C, Martin P A, Evans P M, Gosal A and Lucash M S 2017 Quantifying resilience of multiple ecosystem services and biodiversity in a temperate forest landscape *Ecol. Evol.* **7** 9661–75
- Carpenter B, Gelman A, Hoffman M D, Lee D, Goodrich B, Betancourt M, Brubaker M, Guo J, Li P and Riddell A 2017 Stan: a probabilistic programming language *J. Stat. Softw.* **76** 1–32

- Casteller A, Häfelfinger T, Cortés Donoso E, Podvin K, Kulakowski D and Bebi P 2018 Assessing the interaction between mountain forests and snow avalanches at Nevados de Chillán, Chile and its implications for ecosystem-based disaster risk reduction *Nat. Hazards Earth Syst. Sci.* **18** 1173–86
- Cohen W B *et al* 2017 How similar are forest disturbance maps derived from different Landsat time series algorithms? *Forests* **8** 1–19
- Cohen W B, Yang Z, Healey S P, Kennedy R E and Gorelick N 2018 A LandTrendr multispectral ensemble for forest disturbance detection *Remote Sens. Environ.* **205** 131–40
- Frehner M, Schwittr R and Wasser B 2005 *Nachhaltigkeit und Erfolgskontrolle im Schutzwald. Wegleitung für Pflegemaßnahmen in Wäldern mit Schutzfunktion* [Sustainability and controlling in protection forests. Guidelines for tending forests with protective function] Federal Office for the Environment, Forests and Landscape, Bern
- Gelman A, Carlin J B, Stern H S, Dunson D B, Vehtari A and Rubin D B 2014a *Bayesian Data Analysis* (London: Chapman and Hall)
- Gelman A, Hwang J and Vehtari A 2014b Understanding predictive information criteria for Bayesian models *Stat. Comput.* **24** 997–1016
- Gorelick N, Hancher M, Dixon M, Ilyushchenko S, Thau D and Moore R 2017 Google Earth engine: planetary-scale geospatial analysis for everyone *Remote Sens. Environ.* **202** 18–27
- Heiser M, Hübl J and Scheidl C 2019 Completeness analyses of the Austrian torrential event catalogue *Landslides* (accepted) pp 1–12
- Heiser M, Scheidl C, Eisl J, Spangl B and Hübl J 2015 Process type identification in torrential catchments in the eastern Alps *Geomorphology* **232** 239–47
- Hicke J A *et al* 2012 Effects of biotic disturbances on forest carbon cycling in the United States and Canada *Glob. Chang. Biol.* **18** 7–34
- Holub M and Hübl J 2008 Local protection against mountain hazards—state of the art and future needs *Nat. Hazards Earth Syst. Sci.* **8** 81–99
- Hübl J, Totschnig R, Sitter F, Schneider A, Krawtschuk A, Dusi G, Fischer N, Swoboda P and Neckel N 2008 *Historische Ereignisse—Band 3: Aufarbeitung historischer Ereignisse (Verlagerungsarten Wasser und Schnee) in Österreich* Report 111 Institute of Mountain Risk Engineering, University of Life Sciences and Natural Resources, Vienna
- Imaizumi F, Sidle R C and Kamei R 2008 Effects of forest harvesting on the occurrence of landslides and debris flows in steep terrain of central Japan *Earth Surf. Process Landforms* **33** 827–40
- IPCC 2012 *Managing the Risks of Extreme Events and Disasters to Advance Climate Change Adaptation. A Special Report of Working Groups I and II of the Intergovernmental Panel on Climate Change* ed C B Field *et al* (Cambridge, UK: Cambridge University Press) p 582
- Irauschek F, Rammer W and Lexer M J 2017 Evaluating multifunctionality and adaptive capacity of mountain forest management alternatives under climate change in the Eastern Alps *Eur. J. Forest Res.* **136** 1051–69
- Jakob M 2000 The impacts of logging on landslide activity at Clayoquot Sound, British Columbia *Catena* **38** 279–300
- Kasischke E S, Amiro B D, Barger N N, French N H F, Goetz S J, Grosse G, Harmon M E, Hicke J A, Liu S and Masek J G 2013 Impacts of disturbance on the terrestrial carbon budget of North America *J. Geophys. Res. Biogeosci.* **118** 303–16
- Kennedy R E, Yang Z and Cohen W B 2010 Detecting trends in forest disturbance and recovery using yearly Landsat time series: I. LandTrendr—Temporal segmentation algorithms *Remote Sens. Environ.* **114** 2897–910
- Kennedy R E, Yang Z, Gorelick N, Braaten J, Cavalcante L, Cohen W B and Healey S 2018 Implementation of the LandTrendr algorithm on Google Earth Engine *Remote Sens.* **10** 1–10
- Kilian W, Müller F and Starlinger F 1994 Die forstlichen Wuchsgebiete Österreichs. Eine Naturraumgliederung nach waldökologischen Gesichtspunkten. FBVA-Berichte, Schriftenr. der Forstl. Bundesversuchsanstalt Wien, Vienna, Austria, 82, 60
- Kulakowski D *et al* 2017 A walk on the wild side: disturbance dynamics and the conservation and management of European mountain forest ecosystems *Forest Ecol. Manage.* **388** 120–31
- Langner A, Irauschek F, Perez S, Pardos M, Zlatanov T, Öhman K, Nordström E-M and Lexer M J 2017 Value-based ecosystem service trade-offs in multi-objective management in European mountain forests *Ecosyst. Serv.* **26** 245–57
- Levers C, Verkerk P J, Müller D, Verburg P H, Butsic V, Leitão P J, Lindner M and Kuemmerle T 2014 Drivers of forest harvesting intensity patterns in Europe *Forest Ecol. Manage.* **315** 160–72
- Melton M A 1957 An analysis of the relations among elements of climate, surface properties, and geomorphology *Technical Report 11* NR 389–042 Off. Nav Res Dept Geol Columbia Univ, NY
- Miller V 1953 A quantitative geomorphic study of drainage basin characteristics in the Clinch mountain area Project no. 389-042. *Technical Report no. 3* Virginia and Tennessee 1–30
- Mina M, Bugmann H, Cordonnier T, Irauschek F, Klopčič M, Pardos M and Cailleret M 2017 Future ecosystem services from European mountain forests under climate change *J. Appl. Ecol.* **54** 389–401
- Moos C, Bebi P, Graf F, Mattli J, Rickli C and Schwarz M 2016 How does forest structure affect root reinforcement and susceptibility to shallow landslides? *Earth Surf. Process. Landforms* **41** 951–60
- Motta R and Haudemand J-C 2000 Protective forests and silvicultural stability *Mt. Res. Dev.* **20** 180–7
- MunichRe 2019 NatCatSERVICE (<https://natcatservice.munichre.com/>)
- Noguchi S, Tsuboyama Y, Sidle R C and Hosoda I 2001 Subsurface runoff characteristics from a forest hillslope soil profile including macropores, Hitachi Ohta, Japan *Hydrol. Process.* **15** 2131–49
- Nyman P, Smith H G, Sherwin C B, Langhans C, Lane P N J and Sheridan G J 2015 Predicting sediment delivery from debris flows after wildfire *Geomorphology* **250** 173–86
- Oberndorfer S, Fuchs S, Rickenmann D and Andreu P 2007 BFW-BERICHT Vulnerabilitätsanalyse und monetäre Schadensbewertung von Wildbachereignissen in Österreich Vulnerability Analysis and Monetary Loss Assessment of Torrent Events in Austria, BFW, Wien
- Oeser J, Pflugmacher D, Senf C, Heurich M and Hostert P 2017 Using intra-annual Landsat time series for attributing forest disturbance agents in Central Europe *Forests* **8** 251
- ONR-24800 2014 *Normensammlung Schutz vor Naturgefahren + Umwelt* (Vienna: Austrian Standards+Publ)
- Pflugmacher D, Rabe A, Peters M and Hostert P 2019 Mapping pan-European land cover using Landsat spectral-temporal metrics and the European LUCAS survey *Remote Sens. Environ.* **221** 583–95
- Roberts R G and Church M 1986 The sediment budget in severely disturbed watersheds, Queen Charlotte ranges, British Columbia *Can. J. Forest Res.* **16** 1092–105
- Sakals M E, Innes J L, Wilford D J, Sidle R C and Grant G E 2006 The role of forests in reducing hydrogeomorphic hazards *Forest Snow Landsc. Res.* **80** 11–22
- Schumm S 1956 Evolution of drainage systems and slopes in badlands at Perth Amboy, New Jersey *Geol. Soc. Am. Bull.* **67** 597–646
- Sebald J 2019 dis-haz database (Figshare) (<https://doi.org/10.6084/m9.figshare.9758891.v1>)
- Seidl R, Albrich K, Erb K, Formayer H, Leidinger D, Leitinger G, Tappeiner U, Tasser E and Rammer W 2019 What drives the future supply of regulating ecosystem services in a mountain forest landscape? *Forest Ecol. Manage.—Revis.* **445** 37–47

- Seidl R, Schelhaas M J, Rammer W and Verkerk P J 2014 Increasing forest disturbances in Europe and their impact on carbon storage *Nat. Clim. Change* **4** 806–10
- Seidl R *et al* 2017 Forest disturbances under climate change *Nat. Clim. Change* **7** 395–402
- Senf C, Pflugmacher D, Hostert P and Seidl R 2017 Using Landsat time series for characterizing forest disturbance dynamics in the coupled human and natural systems of Central Europe *ISPRS J. Photogramm. Remote Sens.* **130** 453–63
- Senf C, Pflugmacher D, Zhiqiang Y, Sebal J, Knorn J, Neumann M, Hostert P and Seidl R 2018 Canopy mortality has doubled in Europe's temperate forests over the last three decades *Nat. Commun.* **9** 4978
- Silins U, Stone M, Emelko M B and Bladon K D 2009 Sediment production following severe wildfire and post-fire salvage logging in the Rocky Mountain headwaters of the Oldman River Basin, Alberta *Catena* **79** 189–97
- Stan Development Team 2016 'rstanarm': Bayesian applied regression modelling via Stan R package version 2.13.1.
- Streit K, Wunder J and Brang P 2009 Slit-shaped gaps are a successful silvicultural technique to promote *Picea abies* regeneration in mountain forests of the Swiss Alps *Forest Ecol. Manage.* **257** 1902–9
- Swanson F J, Johnson S L, Gregory S V and Acker S A 1998 Flood disturbance in a forested mountain landscape *Bioscience* **48** 681–9
- Thom D and Seidl R 2016 Natural disturbance impacts on ecosystem services and biodiversity in temperate and boreal forests *Biol. Rev. Camb. Philos. Soc.* **91** 760–81
- Thom D, Seidl R, Steyrer G, Krehan H and Formayer H 2013 Slow and fast drivers of the natural disturbance regime in central European forest ecosystems *Forest Ecol. Manage.* **307** 293–302
- Vehtari A, Gelman A and Gabry J 2017 Practical Bayesian model evaluation using leave-one-out cross-validation and WAIC *Stat. Comput.* **27** 1413–32
- Wohlgemuth T, Schwitter R, Bebi P, Sutter F and Brang P 2017 Post-windthrow management in protection forests of the Swiss Alps *Eur. J. For. Res.* **136** 1029–40
- Wood W F and Snell J B 1960 A quantitative system for classifying landforms *Tech. Rep.* EP-124 US Army Natick Lab. Massachusetts
- Yin J, Gentine P, Zhou S, Sullivan S C, Wang R, Zhang Y and Guo S 2018 Large increase in global storm runoff extremes driven by climate and anthropogenic changes *Nat. Commun.* **9** 4389
- ZAMG 2019 Klima aktuell Klimamonitoring (<https://www.zamg.ac.at/cms/de/klima/klima-aktuell/klimamonitoring/?param=t&period=period-ymd-2019-10-07&ref=3>)

Appendix C: Mixing tree species at different spatial scales: the effects of alpha, beta and gamma diversity on disturbance impacts under climate change

Published 2021 in *Journal of Applied Ecology*

Impact factor 2019: 6.135

RESEARCH ARTICLE

Mixing tree species at different spatial scales: The effect of alpha, beta and gamma diversity on disturbance impacts under climate change

Julius Sebald^{1,2}  | Timothy Thrippleton^{3,4}  | Werner Rammer²  |
Harald Bugmann³ | Rupert Seidl^{1,2,5} 

¹Department of Forest- and Soil Sciences,
Institute of Silviculture, University of
Natural Resources and Life Sciences (BOKU)
Vienna, Vienna, Austria

²Ecosystem Dynamics and Forest
Management Group, School of Life Sciences,
Technical University of Munich, Freising,
Germany

³Department of Environmental Systems
Science, Forest Ecology, Swiss Federal
Institute of Technology (ETH Zurich), Zürich,
Switzerland

⁴Forest Resources and Management,
Sustainable Forestry, Swiss Federal
Research Institute WSL, Birmensdorf,
Switzerland

⁵Berchtesgaden National Park,
Berchtesgaden, Germany

Correspondence

Julius Sebald
Email: julius.sebald@tum.de

Funding information

Austrian Science Fund, Grant/Award
Number: Y895-B25; European Forest
Institute

Handling Editor: Jos Barlow

Abstract

1. Single species forest systems often suffer from low resistance and resilience to perturbations. Consequently, fostering tree species diversity is discussed as an important management approach to address the impacts of changing climate and disturbance regimes. Yet, the effect of the spatial grain of tree species mixtures remains unknown.
2. We asked whether increasing tree species diversity between stands (beta diversity) has the same effect as increasing tree species diversity within stands (alpha diversity) at similar overall levels of richness (gamma diversity). We conducted a multi-model simulation experiment under climate change, applying two forest landscape models (iLand and LandClim) across two contrasting landscapes of Central Europe. We analysed the effect of different levels and configurations of diversity on the disturbance impact and the temporal stability of biomass stocks and forest structure.
3. In general, increasing levels of diversity decreased disturbance impacts. Positive diversity effects increased with increasing severity of climate change. Beta diversity buffered disturbance impacts on landscape-level biomass stocks more strongly than alpha diversity. The effects of the spatial configuration on forest structure were more variable. Diversity effects on temporal stability were less pronounced compared to disturbance impacts, and mixture within and between stands had comparable effects on temporal stability.
4. Diversity effects were context-dependent, with patterns varying between landscapes and indicators. Furthermore, we found a strong species identity effect, with increasing diversity being particularly beneficial in conifer-dominated systems of the European Alps. The two models agreed on the effects of different levels and configurations of tree species diversity, underlining the robustness of our findings.
5. *Synthesis and application.* Enhancing tree species diversity can buffer forest ecosystems against increasing levels of perturbation. Mixing tree species between stands is at least as effective as mixing tree species within stands. Given the managerial advantages of between-stand mixtures (e.g. reduced need to control

This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

© 2021 The Authors. *Journal of Applied Ecology* published by John Wiley & Sons Ltd on behalf of British Ecological Society

competition to maintain diversity, higher timber quality, lower logistic effort), we conclude that forest management should consider enhancing diversity at multiple spatial scales.

KEYWORDS

beta diversity, biodiversity, climate change, disturbances, forest, forest management, resilience, species diversity

1 | INTRODUCTION

Global change increases the pressure on forest ecosystems through changed environmental conditions, which, in turn, alter ecological processes substantially (Trumbore et al., 2015). One of the most climate-sensitive processes in forest ecosystems is disturbance (Seidl et al., 2020; Sommerfeld et al., 2018). As a consequence, forests that have developed under historic disturbance regimes may change drastically in the future due to the emergence of novel disturbance regimes (Turner, 2010). In addition, the societal demand for ecosystem services changes at an accelerating pace, challenging ecosystem managers to adapt forests so that they are able to deliver broad portfolios of ecosystem services. Given the high uncertainty in future environmental conditions and societal demands, fostering tree species diversity has been recommended as a particularly suitable management approach (Griess et al., 2012; Knoke et al., 2008; Neuner et al., 2015). Diverse forests facilitate the provisioning of a wide range of ecosystem services (Gamfeldt & Roger, 2017) and increase the resistance and resilience to changing disturbance regimes (Silva Pedro et al., 2015). Consequently, increasing tree species diversity is frequently proposed as an important forest management strategy to ensure ecosystem service provisioning and forest multi-functionality (Messier et al., 2015; van der Plas et al., 2018).

Theory suggests that a high diversity of species varying in their ecological responses leads to stable systems in a changing environment (Mori et al., 2013; Peterson et al., 1998). If the performance of one tree species declines or even fails under a certain set of conditions, other species with different traits better adapted to the emerging environmental drivers will ensure ecosystem functioning. In the face of increasing disturbances, for instance, diverse ecosystems are more likely to include species that are resistant to a specific disturbance agent (insurance hypothesis; Yachi & Loreau, 1999). Furthermore, trait diversity among different tree species determines their ability to respond to changing climate and disturbance regimes. Diverse traits increase the probability of a positive response to disturbances, thereby enhancing the speed of recovery and thus rendering the ecosystem more resilient (Mori et al., 2013).

Building on these theoretical considerations, a number of quantitative studies have shown that tree species diversity increases the resistance of forest ecosystems to disturbances (see the reviews of Jactel et al., 2017; Knoke et al., 2008). In addition, there is mounting evidence that diverse forests are often more resistant to climatic

extremes such as drought (Grossiord, 2019; Lebourgeois et al., 2013; Metz et al., 2016; Pretzsch et al., 2013). Furthermore, also the resilience to disturbances increases in diverse forests (Honkaniemi et al., 2020; Silva Pedro et al., 2015).

While there is growing evidence for the benefits of diverse forests in a changing world, the effects of the spatial grain of mixing tree species have not yet been investigated systematically. Most analyses to date focus on tree species diversity within forest stands, that is, the smallest entity of forest management (in Europe typically 0.5–10 ha in size). While the effects of within-stand diversity (alpha diversity) have been explored previously (e.g. del Río et al., 2017; Guyot et al., 2016; Huang et al., 2018; Rothe & Binkley, 2001), tree species diversity between stands (beta diversity) has received relatively little attention. Beta diversity has been identified as an important element of ecosystem functioning (Mori et al., 2018; Schuler et al., 2017) and is a key element for the provisioning of multiple ecosystem goods and services at the landscape scale (Van Der Plas et al., 2016). Furthermore, landscape configuration is increasingly recognized as an important element of ecosystem resilience (Honkaniemi et al., 2020; Lamy et al., 2016). Also, evidence is mounting that focusing forest management solely on alpha diversity might not be sufficient for conserving biodiversity (Schall et al., 2018; Schuler et al., 2019). In broader terms, the effect of the spatial grain of tree species mixtures remains an unresolved issue in applied ecology (Ammer, 2019).

In the context of ecosystem management, increasing diversity between stands rather than within stands can have operational advantages: First, high levels of species diversity might be easier to achieve between stands compared to within stands, since inter-specific competition often leads to the dominance of one species over the others in mixed stands (Larocque et al., 2013). Maintaining high levels of tree species diversity within forest stands thus often requires considerable regulatory actions by management (e.g. via tending and thinning), which is labour-intensive and costly (Larocque et al., 2013). Second, timber production in mixed stands can be complicated by yielding many different assortments and a low amount of timber per assortment, which is a drawback for timber logistics and sales. Lastly, high-quality stemwood is often difficult to achieve in stands of high alpha diversity (Höwler et al., 2019; Zingg & Ramp, 1997) while straight and self-pruned stems of low taper often emerge naturally under intraspecific competition (Kint et al., 2010).

One reason for the scarcity of studies on diversity beyond the stand scale is the inherent difficulty of systematic investigations at

larger spatial scales. Field experiments that manipulate diversity at different spatial scales in forests are often not feasible due to resource limitations resulting from the extended observation times required by such experiments. Furthermore, studying diversity effects requires replicated experiments that control for the influence of confounding factors, yet such experiments are well-nigh impossible due to the inability to replicate real landscapes (Keane et al., 2015; Phillips, 2007). Simulation models are an important tool of scientific inquiry in this context, as they can extend the spatial scope of field experiments to the landscape scale and efficiently implement replicated large-scale experiments over extended time periods under otherwise fully controlled conditions (He, 2008; Scheller & Mladenoff, 2007). Furthermore, computer simulation allows us to investigate the effects of no-analogue future environmental conditions, for example, in terms of novel climate and disturbance regimes (Bugmann, 2014). Simulation-based studies are, however, inherently limited by the uncertainties with regard to our quantitative understanding of ecological processes (Huber et al., 2020). An important way to address these uncertainties is to apply multiple different models under identical forcing, as multi-model studies give an indication of the process uncertainty in models and increase the robustness of the model-derived inference (Bugmann et al., 2019; Petter et al., 2020; Valle et al., 2009).

Therefore, we conducted a simulation experiment applying two well-established forest landscape models (i.e. iLand and LandClim) in two contrasting forest landscapes of Central Europe, aiming to study the effects of tree species diversity at different spatial scales across a wide environmental gradient. Specifically, we investigated whether the effects of tree species diversity vary with the spatial grain at which species are mixed. We focused on the response of above-ground forest biomass and the abundance of large trees (i.e. the number of trees >30 cm dbh/ha), two indicators tightly linked to ecosystem service supply in the two study regions. We evaluated how diversity modulates the impact of different climate and disturbance scenarios on these indicators. We also investigated the temporal stability in these indicators, as this aspect of ecosystem service provisioning is gaining importance in practical forest management (Albrich et al., 2018). Our overarching research questions were as follows:

1. Does tree species diversity at the landscape scale (gamma diversity) reduce disturbance impacts and increase the temporal stability of biomass stocks and the abundance of large trees under climate change in Central Europe? Based on theoretical considerations (Yachi & Loreau, 1999, insurance hypothesis) and previous research (del Río et al., 2017; Jactel et al., 2017), we expected a significant positive effect (i.e. lower impacts, higher stability) of tree species diversity.
2. What is the effect of the spatial configuration of tree species diversity, that is, is there a difference in disturbance impact and temporal stability if tree species are mixed within stands (alpha diversity) or between stands (beta diversity)? Here we tested the Null hypothesis that for a given level of tree species diversity

the spatial configuration of the species on the landscape does not matter. Alternatively, if local processes are the main driver of positive diversity effects, we would expect alpha diversity to yield higher positive effects than beta diversity at a given level of gamma diversity.

2 | MATERIALS AND METHODS

2.1 | Study landscapes

To investigate the effects of tree species diversity across a wide ecological gradient, we studied two contrasting forest landscapes in Central Europe (Figure 1). The Rosalia landscape (1,231 ha, 47.70 N, 16.30 E) is located at the easternmost edge of the Alps in Austria at the border of the Pannonic plains of central Eastern Europe. The landforms are dominated by pre-alpine ridges running in north-south direction with generally low topographic complexity and an elevation range from 374 to 728 m a.s.l. Historic mean annual temperature (1981–2010) decreases with elevation from 9.4 to 8.0°C, while mean annual precipitation increases with elevation from 717 to 916 mm. The potential natural vegetation is dominated by European beech (*Fagus sylvatica* L.) with silver fir (*Abies alba* Mill.) as admixed species (Kilian et al., 1994). The Dischma landscape (924 ha, 46.78 N, 9.87 E) is located in Eastern Switzerland and represents a mountain landscape of the Central Alps with harsh climate conditions and high topographic complexity. Elevation ranges from 1,545 to 2,738 m a.s.l. Historic mean annual temperature decreases from 4.4°C at low elevations to −0.6°C at the natural treeline (located at approximately 2,300 m a.s.l. under historic climate, see Gehrig-Fasel et al., 2007), with annual precipitation ranging from 1,074 to 1,297 mm. The potential natural vegetation consists of subalpine forests (up to approximately 1,900 m a.s.l.) dominated by Norway spruce (*Picea abies* (L.) Karst.), subalpine forests with Norway spruce and European larch (*Larix decidua* L.), and Swiss stone pine (*Pinus cembra* L.) forests at treeline (Schumacher et al., 2004). Both landscapes are dominated by crystalline bedrock covered by cambisols of varying soil depth and nutrient content. Both landscapes are approximately three orders of magnitude larger than the average disturbance patch size (1.09 ha, Senf & Seidl, 2021), and are thus large enough to be considered quasi-equilibrium landscapes in the context of disturbance analysis (see Urban et al., 1987).

2.2 | Simulation models

We simultaneously employed two process-based forest landscape models in our study, iLand and LandClim, to increase the robustness of our results.

iLand (Seidl et al., 2012) was developed to study the dynamic interactions between forest development, climate and disturbance, and has been successfully applied to address a wide range of ecological and management-oriented questions (e.g. Albrich et al., 2018;

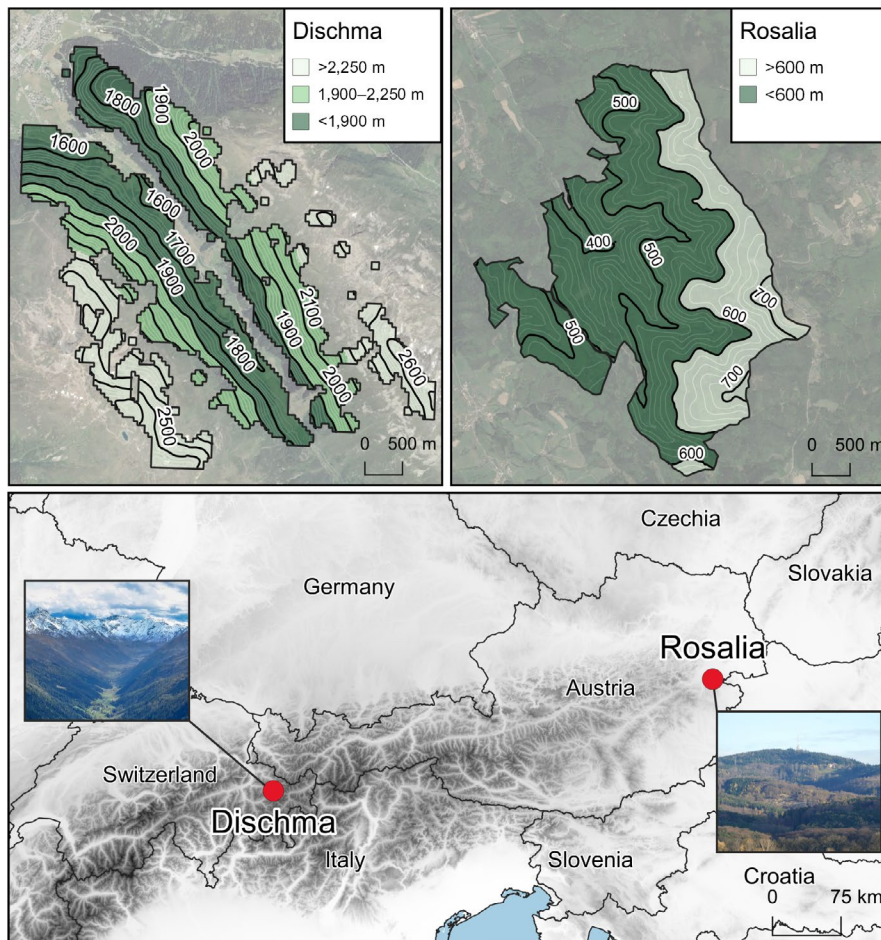


FIGURE 1 Map showing the location of the two study landscapes *Dischma* (CH) and *Rosalia* (AT), and their respective elevation belts

Seidl et al., 2019; Thom et al., 2017). iLand is a multi-scale model; it simulates growth, competition and mortality at the level of individual trees, primary production at the stand scale, and processes like seed dispersal and disturbances at the landscape scale. iLand is driven by daily climate data and forest structure is updated annually (i.e. demographic processes and disturbances are simulated with an annual time step).

LandClim (Schumacher et al., 2004, 2006) is a stochastic process-based forest landscape model that operates at the grain of tree cohorts, simulated at a spatial resolution of 25×25 m. LandClim has been successfully applied in numerous studies in Europe and other parts of the world, demonstrating the utility of the model to study landscape dynamics under a wide range of environmental conditions (e.g. Elkin et al., 2013; Temperli et al., 2013; Thrippleton et al., 2016). LandClim is driven by monthly climate data and forest structure is updated annually (even though tree regeneration and disturbances are simulated with a decadal time step).

For a detailed comparison of LandClim and iLand including a description of the models using the ODD protocol (Grimm et al., 2006), we refer to Petter et al. (2020). The models have been tested and evaluated in the two landscapes in previous studies (Honkaniemi et al., 2020; Petter et al., 2020). To ensure that the models are able to capture the expected tree species dynamics for both landscapes (a crucial ability in the context of the current study), we ran

additional model tests comparing the simulated potential natural vegetation from both models to expected values (see Appendix SI1 and Section 2.1 below). These tests showed good agreement of simulated successional patterns with expectations, indicating that both models are well able to reproduce the competitive relationships between tree species across the wide ecological gradients covered by the two study landscapes.

2.3 | Experimental design

We performed a factorial experiment of varying levels ($n = 4$) and spatial configurations ($n = 2$) of tree species diversity with the two models for both landscapes under different climate ($n = 3$) and disturbance ($n = 3$) scenarios. The underlying premises of our experimental design were (a) to simulate the exact same scenarios with both models (which required the harmonization of some elements of the design, for example, with regard to the different time steps of iLand and LandClim, see also Petter et al., 2020) and (b) to focus on the diversity effects of interest here while controlling for other potential drivers of forest dynamics (e.g. legacy effects from past disturbances and land use; Kulakowski et al., 2017). Specifically, we initialized four levels of tree species diversity (gamma diversity) in two spatial configurations (alpha and beta diversity), see Figure 2a.

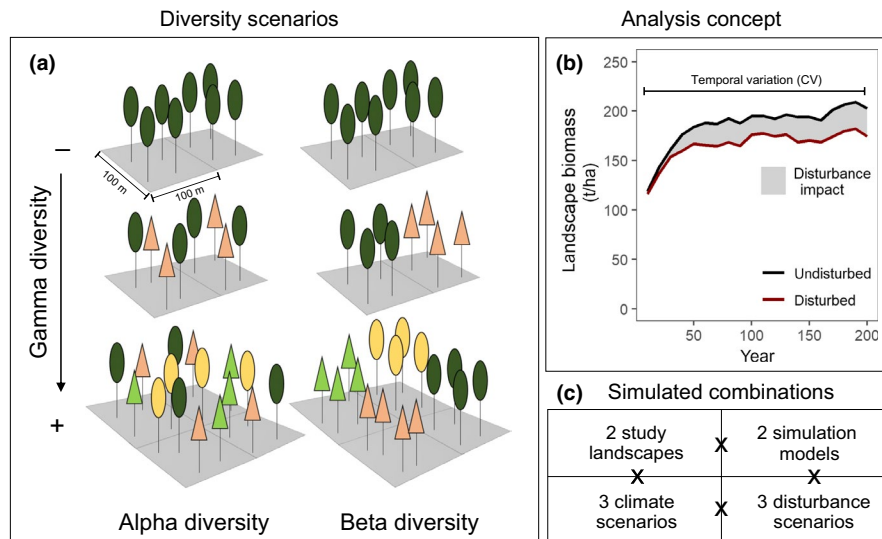


FIGURE 2 Conceptual visualization of the study design. We initialized varying levels of tree species diversity (gamma diversity) in two spatial configurations at a grain of 100×100 m (a). Subsequently, we exposed these initial states to a series of disturbances and derived disturbance impacts by comparing landscape values for biomass stock and forest structure to an undisturbed reference simulation. In addition, we quantified temporal variation in biomass stocks and forest structure by calculating the coefficient of variation over the 200-year simulation period (20 time steps, b). All analyses were conducted in two contrasting landscapes with two simulation models, studying vegetation development under three alternative climate and disturbance scenarios (c)

The grain for the spatial configurations was 100×100 m (henceforth referred to as a stand). For beta diversity, species were varied between stands (with only one species occupying a stand), while for alpha diversity species were mixed within a stand. Based on these initial conditions of landscape composition and configuration, we simulated 200 years of forest development under a common management regime. Furthermore, we exposed the simulated forest to three prescribed sequences of disturbance under three climate scenarios (Figure 2c). Disturbance impacts were derived by comparing landscape-scale response variables to simulations without disturbance (i.e. the reference runs). The individual elements of the study design are described in detail below; Figure 2 provides a graphical overview of our approach.

2.4 | Initialization

We initialized simulations with different levels of gamma diversity in tree species: *no* diversity (initializing only the most productive species over the entire landscape), *low* diversity (initializing only species that obtain dominance in natural forest development) and *high* diversity (initializing dominant and co-dominant species). The level of dominance of each species in natural forest development was determined by simulating forest succession from bare ground over 2,000 years in both landscapes and with both models under historic climate (see Appendix S11). To account for changing species dominance with elevation, both landscapes were divided into elevation belts: for the Dischma landscape, we considered three elevation belts (1,545–1,899 m; 1,900–2,249 m; 2,250–2,738 m), while for the Rosalia landscape two elevational belts (374–599 m; 600–728 m)

were distinguished (Figure 1). We defined dominant (co-dominant) species as those reaching a proportion of at least 35% (3%) of total biomass in a particular elevation belt at any point in time during succession (see Appendices S11 and S12). This ensured that both early and late seral species were included in the design. As we expected climate change to alter the species pool of both landscapes and shift the competitive balance between species, we added a fourth gamma diversity scenario, referred to as the *high+* scenario. For this scenario, we ran succession simulations also under climate change (see details below) and again determined all species that reached a level of at least 3% of total biomass. The initialization of the *high+* scenario was identical to the *high* diversity scenario, but in the course of the simulation the species pool was extended by the additional species that reached at least co-dominance in the succession runs under climate change. The *high+* scenario thus had the highest gamma diversity of all simulated diversity scenarios (see Appendix S12).

All levels of gamma diversity were initialized in two spatial configurations: alpha diversity and beta diversity. For the alpha diversity configuration, all tree species from the species pool were mixed within stands. For the beta diversity configuration, each of the 100×100 m stands consisted of only one species, with species varying between stands (see Figure 2). In total, we simulated seven combinations of gamma diversity and spatial configuration in each landscape (3 levels of gamma diversity $\times$ 2 spatial configurations + 1 no diversity scenario).

The initial age of each stand was sampled with replacement from a uniform distribution ranging from 0 to 100 years in the Rosalia landscape and from 0 to 150 years in the Dischma landscape. These values represent realistic rotation periods under current management in the two landscapes. The resulting forest structure corresponds to a 'normal forest' (Assmann, 1961), in which all stand ages

are represented equally across the landscape. The effects of different age class distributions were tested in a sensitivity analysis, and the results were found to be robust to changes in age class distribution (Appendices SI9 and SI10). Stand structure (i.e. stem density in 5 cm dbh classes, tree height and height–diameter-ratio) for specific initialization ages was derived from model runs with iLand (i.e. the structurally more detailed of the two models) for all species in all stands of both landscapes.

2.5 | Forest management

Forest management was implemented in both models based on a common set of rules, describing a rotation forestry system (e.g. Bianchi et al., 2020). Simulated management interventions were thinnings (removing 20% of basal area of a stand), clear-cutting and planting. We assumed a rotation period R of 100 years in Rosalia and 150 years in Dischma, based on the different growing conditions in both study landscapes. Thinnings were scheduled at $R \times 0.35$ (i.e. stand age 35 in Rosalia and stand age 53 in Dischma) and $R \times 0.55$ (i.e. stand age 55 in Rosalia and stand age 83 in Dischma). After the final cut at the end of the rotation period, each stand was replanted with the species composition prescribed by the respective diversity scenario. During a rotation period, species composition varied due to the simulated growth dynamics of the models.

2.6 | Climate

We simulated each diversity scenario for 200 years under three climate scenarios, representing a constant historic climate as well as two contrasting climate change scenarios. The latter represent moderate climate change (RCP4.5, see IPCC, 2014) with a peak of CO₂ emissions around 2040, and a Business-As-Usual scenario with increasing greenhouse gas emissions throughout the 21st century (RCP8.5, see IPCC, 2014). Historic climate conditions were sampled with replacement from past climate data (1981–2010) to obtain a stationary 200-year climate record. Climate change scenarios followed the trajectory of the respective RCP scenario for the first

100 years of the simulation period (representing climate development throughout the 21st century). For the second 100-year period, we assumed a hypothetical stabilization of climate, and randomly sampled years from the period 2070 to 2099, an approach that is often taken in long-term simulations of climate change impacts (e.g. Elkin et al., 2013). For details on the climate scenarios, see Table 1.

2.7 | Disturbances

Disturbances were simulated in a two-step approach, granting a consistent forcing between the two models while dynamically considering disturbance responses in the context of the simulated forest state. In a first step, we created sequences of disturbance events by sampling the size (patch area), location and timing of disturbances. In a second step, disturbance severity (i.e. which trees died within a disturbance perimeter) was determined dynamically within the simulation models.

Each simulation run was driven by a different sequence of disturbance events. Year of disturbance was sampled with replacement from a uniform distribution ranging from 1 to 200 (i.e. the first and last year of the simulation period, respectively). Disturbance size was sampled from an empirically derived disturbance size distribution representative for Central Europe (Senf et al., 2017, see Appendix SI3). The location of each disturbance patch was selected randomly on the landscape, and the spatial grain of disturbance was 1 ha, thus matching the resolution of the simulated stands (see Section 2.4 above). We simulated three disturbance scenarios: historic disturbance, future disturbance and no disturbance. The three scenarios differed in disturbance frequency, as determined by the disturbance rotation period (i.e. the average time it takes for the cumulative area of disturbance to reach the size of the study landscape), which was set to 400 years in the *historic* disturbance scenario (Čada et al., 2016; Thom et al., 2013), and to 200 years in the *future* disturbance scenario (Schumacher & Bugmann, 2006). This implies that in the future disturbance scenario twice as many disturbance events occurred compared to the historic disturbance scenario, which is within the range of expectations for Central European forest ecosystems (Schumacher &

TABLE 1 Mean annual precipitation, temperature and CO₂ concentration for both study landscapes (Dischma, Rosalia) and the three climate scenarios investigated (historic, RCP4.5, RCP8.5)

Study landscape	Rosalia			Dischma		
	Historic (1981–2010)	RCP4.5 (2070–2099)	RCP8.5 (2070–2099)	Historic (1981–2010)	RCP4.5 (2070–2099)	RCP8.5 (2070–2099)
GCM-RCM combination	—	EC-EARTH and KNMI-RACMO22E	EC-EARTH and KNMI-RACMO22E	—	HadGEM2-ES	HadGEM2-ES
Mean annual temperature [°C]	8.51	10.40 (+1.89)	12.13 (+3.62)	1.69	5.36 (+3.67)	8.02 (+6.33)
Mean annual precipitation [mm]	810	883 (+73)	835 (+25)	1,179	1,130 (–49)	1,012 (–167)
CO ₂ concentration [ppm]	369	537	927	369	537	927

Bugmann, 2006; Thom et al., 2013). The effect of different disturbance rotation periods was investigated in a sensitivity analysis, which showed that main patterns were robust to changes in disturbance rotations (Appendix SI8). Each scenario was replicated 20 times to account for the stochastic variability in the timing, location and size of disturbances. For each replication, we generated a unique sequence of disturbance events that was used in both models. This approach ensured that both iLand and LandClim simulated the same disturbance patches in the same year and location. Our simulations thus solely focus on disturbance responses rather than on future projections of disturbance activity.

Disturbance severity (i.e. the number of trees killed within a disturbance perimeter) was contingent on the simulated vegetation state in the different diversity scenarios considered. Specifically, we employed the empirically derived disturbance impact model of Schmidt et al. (2010), which quantifies the susceptibility of Central European forests to storm events (i.e. the most important agent of natural disturbance in Europe's forests; Schelhaas et al., 2003; Seidl et al., 2014). The model (see Appendix SI4) predicts probability of tree mortality dependent on tree species and tree height. Simulated disturbance impacts thus reflect emergent differences in susceptibility (as determined by the development of vegetation structure and composition) in the different scenarios. The effect of different disturbance impact models is shown in Appendix SI12.

In total, 5,040 simulation runs with a duration of 200 years were conducted (2 models $\times$ 2 landscapes $\times$ [3 levels of gamma diversity $\times$ 2 spatial configurations + 1 $\times$ no diversity] $\times$ 3 climate scenarios $\times$ 3 disturbance scenarios $\times$ 20 replicates).

2.8 | Analyses

We quantified the effects of tree species diversity under different climate and disturbance regimes on two response variables for both disturbance impact and temporal variation. The two response variables were above-ground biomass (t/ha) and the average number of trees >30 cm dbh/ha. Biomass was selected because it is a widely used variable for quantifying disturbance effects in ecosystems, integrating over disturbance impact and recovery (Temperli et al., 2013). Furthermore, forest biomass stocks are closely related to important ecosystem services such as timber production and carbon storage (Mina et al., 2017). The number of large trees is an indicator of forest structure. It was selected because the presence of large trees is a characteristic feature of current forest ecosystems in Central Europe (Albrich et al., 2020), yet future projections suggest a shift towards smaller trees (McDowell et al., 2020). Furthermore, large trees are also important in the context of the provisioning of regulating services that are of particular relevance in mountain ecosystems (Frehner et al., 2005). Disturbance impact was quantified as relative (biomass) or absolute (forest structure) difference to the corresponding no disturbance run (i.e. the run with the same climate, spatial configuration and gamma diversity level, without disturbances; see Figure 2 and Equations 1 and 2). Temporal variation was

quantified by calculating the coefficient of variation of the response variables (i.e. biomass t/ha and trees >30 cm dbh/ha) over the 200-year simulation period in 20 time steps.

$$\text{biomass impact (\%)} = \left(1 - \frac{\text{biomass}_{\text{disturbed}}[\text{t/ha}]}{\text{biomass}_{\text{undisturbed}}[\text{t/ha}]} \right) \times 100, \quad (1)$$

$$\begin{aligned} \text{structural impact (trees > 30 cm dbh/ha)} = \\ \text{tree}_{\text{disturbed}}[\text{n/ha}] - \text{trees}_{\text{undisturbed}}[\text{n/ha}]. \end{aligned} \quad (2)$$

To test for differences in species dominance between the two spatial configurations of tree diversity, we also calculated the realized gamma diversity of the landscape at the end of the simulation period (i.e. simulation year 200). Realized gamma diversity was expressed as the exponent of the Shannon Entropy over the biomass of all species (i.e. effective number of species; see Jost, 2006), with a theoretical maximum equal to the size of the species pool if all species are represented equally on the landscape. All data analysis and visualization were accomplished with R version 4.0.2 (R Core Team, 2020).

3 | RESULTS

3.1 | Realized gamma diversity

As expected, the realized gamma diversity emerging from the simulations was lower than the theoretical maximum in most diversity scenarios and spatial configurations (Figure 3). In the scenario *high+*, realized gamma diversity at the end of the 200-year simulation period reached on average 84% (Figure 3a,c) and 92% (Figure 3b,d) of the theoretical maximum in Dischma (under RCP8.5) and Rosalia (under historic climate), respectively. The qualitative differences between the four diversity scenarios were well reflected in the realized gamma diversity. The effective number of species ranged from 1 in the no diversity scenarios to 8.9 in the *high+* scenarios of the high-elevation Dischma landscape under climate change (scenario RCP8.5). Climate change strongly increased realized gamma diversity in Dischma (Figure 3a,c), but slightly decreased realized gamma diversity in Rosalia (Figure 3b,d). We found no notable differences in realized gamma diversity between the two spatial configurations (alpha and beta) and the three disturbances scenarios (no disturbance, historic disturbance and future disturbance). Both models were able to maintain high levels of species diversity over the full 200-year simulation period and agreed well on the patterns of realized diversity.

3.2 | Effects of tree species diversity on disturbance impacts

Increasing tree species diversity at the landscape scale (gamma diversity) generally reduced disturbance impact for both indicators investigated (biomass, structure; Figure 4). A notable exception to this pattern was the Rosalia landscape, where lowest disturbance impacts

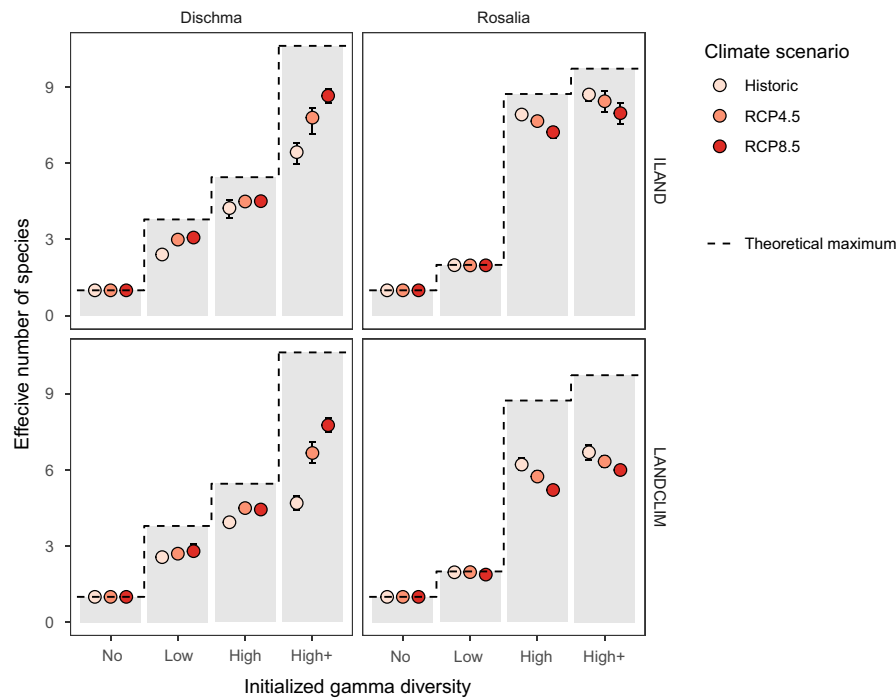


FIGURE 3 Realized gamma diversity (i.e. effective number of species at the landscape level) in the different diversity scenarios after 200 years of simulation. Results are shown for the two study landscapes (columns) and the two models (rows) under the three climate scenarios (colours) investigated. Data points show mean values over the three disturbance scenarios (no disturbance, historic disturbance and future disturbance), two spatial arrangements and 20 replicates. Error bars show the range of the data. The effective number of species was calculated as the exponent of Shannon Entropy based on biomass shares, which reaches a theoretical maximum at an equal representation of all species from the species pool on the landscape (indicated by the dashed line and shaded bars)

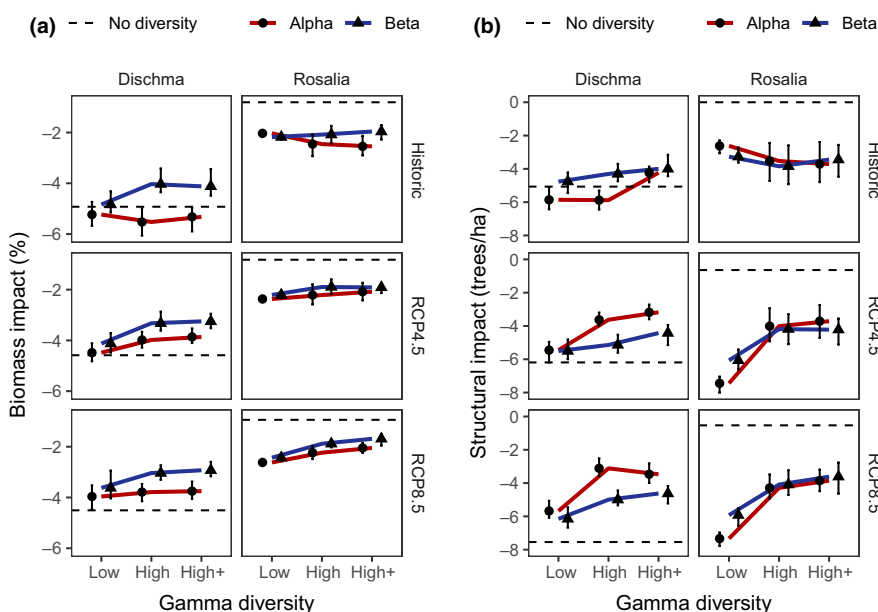


FIGURE 4 Disturbance impacts on biomass (a) and forest structure (b) for two spatial configurations of tree species diversity (alpha and beta) along a gradient of gamma diversity. Effects are displayed separately for the two study landscapes (Dischma and Rosalia) and three climate scenarios (historic, RCP4.5, RCP8.5). The data points are mean values over two disturbance frequencies (400- and 200-year disturbance rotation), two models (iLand, LandClim), 20 time steps and 20 replicates. The error bars show the range of the data. Individual results for the two simulation models can be found in the Supporting Information (Appendix S16)

were simulated for the no diversity scenario (representing pure beech forests over the entire landscape) compared to the scenarios of higher species diversity (Figure 4). Disturbance impacts were generally more pronounced in the conifer-dominated Dischma landscape compared to the broadleaved-dominated Rosalia landscape. Overall, climate change amplified the positive effect of increasing diversity in both landscapes

(Figure 4). Furthermore, we found that the effect of spatial configuration was context-dependent, with patterns varying between landscapes and indicators. Biomass impacts were generally lower when species were mixed between stands (beta scenario). Conversely, disturbance impacts on forest structure were lower in the alpha scenario in Dischma, and did not differ between configuration scenarios in Rosalia (Figure 4).

3.3 | Effects of tree species diversity on temporal variation

The temporal variation in biomass stocks and forest structure generally increased with increasing intensity of climate change in both landscapes (Figure 5). The role of tree species diversity on temporal variation was strongly context-dependent: For biomass stocks, the *low* and *no* diversity scenario were most stable under historic climate

while under future climate scenarios of higher tree species diversity were more stable. Forest structure was generally more variable in simulations under the *low* diversity scenario compared to scenarios with higher gamma diversity. Overall, however, differences between gamma diversity scenarios were small relative to the variation within each scenario. Furthermore, we did not detect differences in the simulated temporal variation between the two spatial configurations (i.e. alpha and beta diversity; see Appendix SI5).

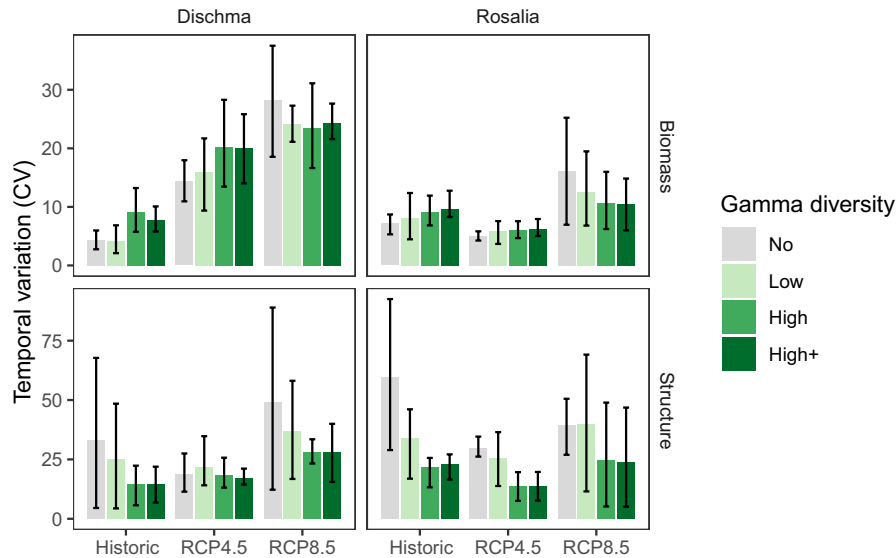


FIGURE 5 Temporal variation, expressed as the coefficient of variation over time in biomass stocks (top) and forest structure (bottom) under three different climate scenarios and four levels of gamma diversity. The bars show mean values, with the whiskers indicating the range over two models (iLand and LandClim), two spatial configurations (alpha and beta), three disturbance scenarios (no disturbance, 400-year disturbance rotation and 200-year disturbance rotation) and 20 replicates. Temporal variation was calculated over the 200-year simulation period in 10-year time steps. We did not detect differences in the simulated temporal variation between the two spatial configurations (i.e. alpha and beta diversity), which is why they are pooled together here (see Appendix SI5). Individual results for the two simulation models are found in the Supplementary Information (Appendix SI7)

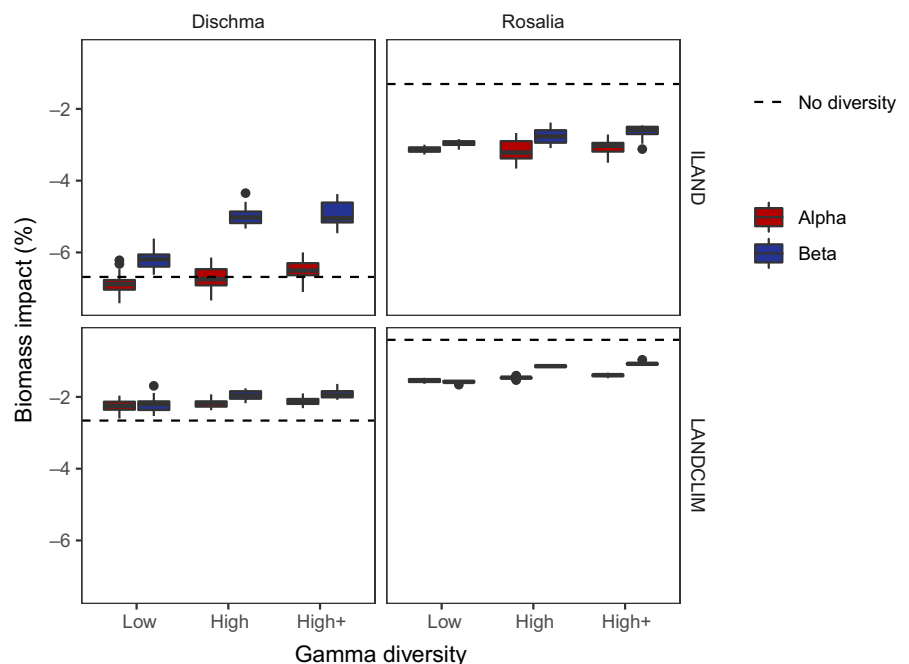


FIGURE 6 Differences in disturbance impact between the two models (iLand and LandClim) and the two spatial configurations (alpha and beta). Biomass impact is the relative difference in average biomass stocks compared to simulations without disturbance (see Figure 2). Values are averaged over two disturbance scenarios (200- and 400-year rotation period), three climate scenarios (historic, RCP4.5 and RCP8.5) and 20 replicates. Note the different scaling of the y-axes. See Supporting Information Table Appendices SI6 and SI7 for a comparison between models regarding the simulated temporal variation and the disturbance impact on forest structure

3.4 | Model effects

iLand and LandClim were mostly consistent in their projections of the effects of gamma diversity and spatial configuration (alpha and beta scenarios, Figure 6). They agreed on biomass impacts generally decreasing with increasing gamma diversity. Furthermore, both models were consistent in simulating lower disturbance impacts on biomass stocks under beta mixtures compared to alpha mixtures.

We did, however, also detect differences between the two models (Appendices SI6 and SI7). iLand generally simulated a denser forest structure (trees >30 cm dbh/ha) and thus higher biomass stocks. Consequently, also disturbance impacts were more pronounced in iLand compared to LandClim for both indicators investigated. Furthermore, model differences were generally greater for forest structure than biomass stocks: While disturbances decreased the number of trees >30 cm dbh/ha in iLand, their numbers even increased slightly under some scenarios in LandClim (Appendix SI6). Temporal variation of biomass stocks and forest structure increased with climate change and decreased with species diversity, consistently across both models. However, buffering effects of species diversity were more pronounced in LandClim compared to iLand.

4 | DISCUSSION

4.1 | Increasing tree species diversity at different spatial scales

We found evidence that higher levels of tree species diversity can reduce disturbance impacts on biomass stocks and forest structure in two contrasting forest landscapes of Central Europe, representing broadleaved-dominated lowland ecosystems and conifer-dominated mountain ecosystems. Our results thus generally confirm our first hypothesis of positive biodiversity effects on forest ecosystems under changing climate and disturbance regimes, and are in line with previous research (Griess et al., 2012; Jactel et al., 2017; Knoke et al., 2008; Silva Pedro et al., 2015). However, we went one step beyond previous studies by testing whether the spatial grain of mixing modulates diversity effects (see also Griess & Knoke, 2013 for an economic investigation). Our results indicate that positive diversity effects arise irrespective of whether species are mixed within or between stands, in line with our null hypothesis regarding the influence of spatial configuration. However, our analyses also highlight that diversity effects are strongly context-specific, and differ with study landscape and response variable. With regard to the impacts of disturbances on biomass stock, for instance, we found that species mixtures between stands (beta scenario) are more resistant than simulations in which species are mixed within a stand (alpha scenario), especially in the conifer-dominated Dischma landscape. This finding is consistent with a previous analysis investigating the effects of landscape configuration and composition on the resilience of Norway spruce (Honkaniemi et al., 2020).

An important insight from our analysis is the strong effect of species identity on diversity effects, that is, the effect being strongly contingent on the presence of certain species and their particular traits (see also Blaško et al., 2020; De Wandeler et al., 2018; Hantsch et al., 2013; Schwarz et al., 2015). In our simulations, the effects of diversity differed considerably depending on the species being present in the local species pool. In Dischma, for instance, the species serving as baseline in the 'no diversity' scenario is Norway spruce, which is more susceptible to disturbance compared to other species of the species pool (Schmidt et al., 2010). Thus, enhancing species diversity with, for example, European larch and Silver birch resulted in a considerable reduction of disturbance impacts on the landscape (Figure 4). In contrast, the tree species simulated in the 'no diversity' scenario in Rosalia is European beech, which is more resistant to disturbance than most of the naturally co-occurring species (Schmidt et al., 2010). Here, adding species such as Silver fir and Norway spruce to the mix increased disturbance impacts. Our results therefore underline that species identity is a key element in determining the interactions between forest composition and the disturbance regime of a given landscape. Specifically, we found that species identity effects can reverse the patterns expected under the insurance hypothesis (Yachi & Loreau, 1999).

In addition to identity effects and the resulting differences between landscapes, we also found differences in the response to the spatial configuration between the two indicators studied. For biomass stocks, increasing beta diversity had consistently stronger positive effects than increasing alpha diversity while the effect of increasing gamma diversity was moderately positive. For forest structure (i.e. trees >30 cm in dbh/ha), the effect of increasing gamma diversity was more pronounced, yet effects of spatial configuration differed between the two landscapes. In Dischma, the prevalence of large trees was less affected by disturbances in within-stand mixtures of species (alpha scenario) under climate change while in Rosalia both the alpha and beta scenario performed similarly under all climate scenarios. This suggests that especially under the high-elevation conditions of Dischma, increasing resource availability for tree growth linked to climate change (e.g. resulting from longer growing seasons, cf. Delbart et al., 2008; Menzel et al., 2006) can be utilized better when tree species are mixed within a stand (complementary resource use, Larocque et al., 2013; Morin et al., 2018). Overall, the differences between indicators highlight that diversity effects are strongly contingent on the functions and services under consideration, suggesting that there is no universally best mixture, and that the social-ecological context is a matter of central importance.

Temporal variation of biomass stocks and forest structure generally increased with increasing intensity of climate change. We found that single species systems of the currently most productive species (i.e. Norway Spruce in Dischma and European beech in Rosalia) had highly stable biomass stocks under historic climate conditions. Under severe climate change, however, these were the most volatile systems, suggesting that forest dynamics could become significantly more variable in the future (McDowell et al., 2020; Seidl et al., 2017;

Sommerfeld et al., 2018). However, temporal variation of biomass stocks and forest structure also increased in response to climate change in scenarios of higher tree species diversity, suggesting that increasing tree species alone will not be enough to buffer Central European forests from the impacts of climate change.

4.2 | Methodological considerations

We conducted a simulation experiment investigating the effects of alpha, beta and gamma diversity on disturbance impacts and temporal variation of biomass stocks and forest structure. Using models, we were able to study spatiotemporal scales that are beyond the realm of experimental research. A novelty of our analysis is that it is based not on one but on two well-established forest landscape models (Keane et al., 2015). Multi-model inference is frequently used in other fields of science (Eyring et al., 2007; Tebaldi & Knutti, 2007), and is increasingly applied in ecology (McDowell et al., 2013; Renwick et al., 2018; Reyer et al., 2017). However, in ecological studies, multi-model analyses have to date largely focused on methodological questions (e.g. Bugmann et al., 2019; Ichii et al., 2010) while questions of applied ecology are commonly addressed only with a single model. We emphasize that using multiple models also in the context of applied questions considerably increases the robustness of the management implications deduced from such studies (see below). The consistency in the general patterns and effects between iLand and LandClim suggests that our results are robust, and that model-specific uncertainties are not impeding the general conclusions of our study.

We nonetheless identified differences between the two models, particularly with regard to disturbance impacts on both biomass stocks and forest structure, which were generally stronger in iLand than in LandClim. These differences can mostly be attributed to different spatial (iLand: individual tree, LandClim: tree cohort) and temporal (iLand: year, LandClim: decade) resolutions of the two models, resulting in different simulations of disturbance impacts. Specifically, for the predominantly moderate disturbance severities simulated here, in LandClim forest attributes recover faster than in iLand, as tree regeneration is assumed to completely recolonize a disturbed patch within the first 10-year time step after disturbance if seed trees are nearby (Schumacher et al., 2004). In contrast, regeneration processes in iLand are simulated at finer temporal and spatial grain, which results in slower regeneration trajectories and larger biomass impacts of disturbances. Overall, however, the results were remarkably consistent between the two models, especially when taking into account the strong differences in model architecture (Petter et al., 2020).

While we emphasize that multi-model inference is an important way to quantify model uncertainties (Keane et al., 2015), such an approach has shortcomings as well. Multi-model inference necessarily requires that driver data are harmonized between the models, which can result in simplified simulation designs. An example in the current study is the implementation of natural disturbance. While both models include dynamic modules of natural disturbances,

their differences in process representation were deemed too large to warrant a meaningful comparison. In other words, if forced with their respective dynamic disturbance modules, the inference on our main research questions (how diversity modulates the effects of disturbances on forest biomass and structure) would have likely been masked strongly or even rendered impossible by the differing disturbance trajectories in the models. This element was controlled by the simplified and standardized implementation of wind disturbances in the current application. As a consequence, however, our analysis disregards other, potentially important aspects of the disturbance regime such as other disturbance agents (e.g. biotic disturbances, Kautz et al., 2018), disturbance interactions (Temperli et al., 2013) and edge effects (Mezei et al., 2014). As our approach excludes processes of spatial spread (e.g. of bark beetle populations, Kautz et al., 2011), our finding on the positive effects of fostering beta diversity are likely conservative, as landscape configuration can strongly reduce the spread of biotic disturbance agents (Honkaniemi et al., 2020). Future work could further investigate effects of tree species diversity and configuration using fully dynamic disturbance simulations and considering multiple disturbance agents.

Another important limitation of our study lies in its fixed grain (100 × 100 m) and categorical representation of alpha and beta diversity. While we were able to show that beta diversity can reduce disturbance impacts, we cannot determine at which spatial grain beta diversity effects are optimized. We a priori chose a grain of 1 ha, corresponding roughly to the average stand size and median disturbance patch size in Central Europe (Senf et al., 2017). Future work could analyse the effects of beta diversity over varying stand sizes, to, for example, determine the maximum stand size for which a landscape still benefits from increased beta diversity. Furthermore, to increase contrasts, we assumed minimal alpha diversity in our beta diversity scenario. In reality, alpha and beta diversity do, however, exist on a continuum, and future analyses could quantify potential trade-offs along this continuum explicitly.

4.3 | Implications for forest management

Our results have important implications for forest ecosystem management. We showed that mixing tree species between stands (i.e. fostering beta diversity) can be as effective or even more effective in buffering disturbance impacts under climate change than mixing tree species within a stand (i.e. focusing on alpha diversity). This finding opens up opportunities for forest managers to extend the spatial scope of fostering tree species diversity from the stand to the landscape scale, potentially capitalizing on the many other advantages of beta diversity for ecosystem service provisioning (Blattert et al., 2018; Schall et al., 2018; van der Plas et al., 2018). Our results are thus in line with growing evidence on the importance of beta diversity in ecosystem management (Blattert et al., 2018; Mori et al., 2018; Schall et al., 2018). Moving the focus from mixtures within stands to mixtures between stands could also have many operational advantages for forest

management, as it may reduce the efforts needed to regulate competition between species, improve stem quality and simplify harvesting logistics.

However, our results also document that diversity effects vary with context and indicator, underlining that fostering beta diversity is no silver-bullet solution. Enhancing tree species diversity may not be enough to meet the multiple threats of global change on forests (McDowell et al., 2020), and may need to be accompanied by additional measures such as increasing resistance through improved thinning and reduced rotation periods (Zimová et al., 2020) or increasing resilience through advance regeneration (Johnstone et al., 2016) and enhanced structural diversity (Millar et al., 2007). Nonetheless, fostering tree species diversity across spatial scales is a powerful means to buffer the impacts of changing climate and disturbance regimes, and should thus be considered as a powerful tool in the adaptation toolbox of forest ecosystem managers.

ACKNOWLEDGEMENTS

This research is an outcome of the FORMASAM (Forest Management Scenarios for Adaptation and Mitigation) project funded by the European Forest Institute (EFI). J.S., W.R. and R.S. acknowledge funding from Austrian Science Fund FWF START grant Y895-B25). The authors thank the whole FORMASAM group for inspiring discussions and critical feedback during the four workshops in Wageningen, Grenoble, Zvolen and Potsdam. We furthermore thank three anonymous Reviewers for their constructive comments on an earlier version of the manuscript.

AUTHORS' CONTRIBUTIONS

J.S., R.S. and H.B. designed the study; J.S., W.R. and T.T. ran simulations with iLand and LandClim; J.S. analysed the data; J.S. wrote the initial draft of the manuscript. All Authors contributed critically to the initial drafts and the revised version, and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data and code are available via the Zenodo Digital Repository <https://doi.org/10.5281/zenodo.4739037> (Sebald et al., 2021).

ORCID

Julius Sebald  <https://orcid.org/0000-0002-0246-4760>

Timothy Thrippleton  <https://orcid.org/0000-0002-1017-7083>

Werner Rammer  <https://orcid.org/0000-0001-6871-6759>

Rupert Seidl  <https://orcid.org/0000-0002-3338-3402>

REFERENCES

- Albrich, K., Rammer, W., & Seidl, R. (2020). Climate change causes critical transitions and irreversible alterations of mountain forests. *Global Change Biology*, 26(7), 4013–4027. <https://doi.org/10.1111/gcb.15118>
- Albrich, K., Rammer, W., Thom, D., & Seidl, R. (2018). Trade-offs between temporal stability and level of forest ecosystem services provisioning under climate change. *Ecological Applications*, 28(7), 1884–1896. <https://doi.org/10.1002/eap.1785>
- Ammer, C. (2019). Diversity and forest productivity in a changing climate. *New Phytologist*, 221(1), 50–66. <https://doi.org/10.1111/nph.15263>
- Assmann, E. (1961). *Waldertragskunde*. BLV Verlagsgesellschaft.
- Bianchi, S., Huuskonen, S., Siipilehto, J., & Hynynen, J. (2020). Differences in tree growth of Norway spruce under rotation forestry and continuous cover forestry. *Forest Ecology and Management*, 458(December 2019), 117689. <https://doi.org/10.1016/j.foreco.2019.117689>
- Blaško, R., Forsmark, B., Gundale, M. J., Lundmark, T., & Nordin, A. (2020). Impacts of tree species identity and species mixing on ecosystem carbon and nitrogen stocks in a boreal forest. *Forest Ecology and Management*, 458(September 2019). <https://doi.org/10.1016/j.foreco.2019.117783>
- Blatter, C., Lemm, R., Thees, O., Hansen, J., Lexer, M. J., & Hanewinkel, M. (2018). Segregated versus integrated biodiversity conservation: Value-based ecosystem service assessment under varying forest management strategies in a Swiss case study. *Ecological Indicators*, 95(May), 751–764. <https://doi.org/10.1016/j.ecolind.2018.08.016>
- Bugmann, H. (2014). Forests in a greenhouse atmosphere: Predicting the unpredictable. In D. A. Coomes (Ed.), *Forests and global change* (pp. 359–380). Cambridge University Press.
- Bugmann, H., Seidl, R., Hartig, F., Bohn, F., Brůna, J., Cailleret, M., François, L., Heinke, J., Henrot, A.-J., Hickler, T., Hülsmann, L., Huth, A., Jacquemin, I., Kollas, C., Lasch-Born, P., Lexer, M. J., Merganič, J., Merganičová, K., Mette, T., ... Rey, C. P. O. (2019). Tree mortality submodels drive simulated long-term forest dynamics: Assessing 15 models from the stand to global scale. *Ecosphere*, 10(2). <https://doi.org/10.1002/ecs2.2616>
- Čada, V., Morrissey, R. C., Michalová, Z., Bače, R., Janda, P., & Svoboda, M. (2016). Frequent severe natural disturbances and non-equilibrium landscape dynamics shaped the mountain spruce forest in central Europe. *Forest Ecology and Management*, 363, 169–178. <https://doi.org/10.1016/j.foreco.2015.12.023>
- De Wandeler, H., Bruehlheide, H., Dawud, S. M., Dănilă, G., Domisch, T., Finér, L., Muys, B. (2018). Tree identity rather than tree diversity drives earthworm communities in European forests. *Pedobiologia*, 67(August 2017), 16–25. <https://doi.org/10.1016/j.pedobi.2018.01.003>
- del Río, M., Pretzsch, H., Ruiz-Peinado, R., Ampoorter, E., Annighöfer, P., Barbeito, I., Bielak, K., Brazaitis, G., Coll, L., Drössler, L., Fabrika, M., Forrester, D. I., Heym, M., Hurt, V., Kurylyak, V., Löf, M., Lombardi, F., Madrickiene, E., Matović, B., ... Bravo-Oviedo, A. (2017). Species interactions increase the temporal stability of community productivity in *Pinus sylvestris*-*Fagus sylvatica* mixtures across Europe. *Journal of Ecology*, 105(4), 1032–1043. <https://doi.org/10.1111/1365-2745.12727>
- Delbart, N., Picard, G., Le toan, T., Kergoat, L., Quegan, S., Woodward, I., Dye, D., & Fedotova, V. (2008). Spring phenology in boreal Eurasia over a nearly century time scale. *Global Change Biology*, 14(3), 603–614. <https://doi.org/10.1111/j.1365-2486.2007.01505.x>
- Elkin, C., Gutiérrez, A. G., Leuzinger, S., Manusch, C., Temperli, C., Rasche, L., & Bugmann, H. (2013). A 2°C warmer world is not safe for ecosystem services in the European Alps. *Global Change Biology*, 19(6), 1827–1840. <https://doi.org/10.1111/gcb.12156>
- Eyring, V., Waugh, D. W., Bodeker, G. E., Cordero, E., Akiyoshi, H., Austin, J., Beagley, S. R., Boville, B. A., Braesicke, P., Brühl, C., Butchart, N., Chipperfield, M. P., Dameris, M., Deckert, R., Deushi, M., Frith, S. M., Garcia, R. R., Gettelman, A., Giorgetta, M. A., ... Yoshiki, M. (2007). Multimodel projections of stratospheric ozone in the 21st century. *Journal of Geophysical Research Atmospheres*, 112(16). <https://doi.org/10.1029/2006JD008332>
- Frehner, M., Schwitter, R., & Wasser, B. (2005). *Nachhaltigkeit und Erfolgskontrolle im Schutzwald. Wegleitung für Pflegemaßnahmen in Wäldern mit Schutzfunktion [Sustainability and controlling in protection forests. Guidelines for tending forests with protective function]*.

- Gamfeldt, L., & Roger, F. (2017). Revisiting the biodiversity-ecosystem multifunctionality relationship. *Nature Ecology and Evolution*, 1(7), 1–7. <https://doi.org/10.1038/s41559-017-0168>
- Gehrig-Fasel, J., Guisan, A., & Zimmermann, N. E. (2007). Tree line shifts in the Swiss Alps: Climate change or land abandonment? *Journal of Vegetation Science*, 18(4), 571–582. <https://doi.org/10.1111/j.1654-1103.2007.tb02571.x>
- Griess, V. C., Acevedo, R., Härtl, F., Staupendahl, K., & Knoke, T. (2012). Does mixing tree species enhance stand resistance against natural hazards? A case study for spruce. *Forest Ecology and Management*, 267, 284–296. <https://doi.org/10.1016/j.foreco.2011.11.035>
- Griess, V. C., & Knoke, T. (2013). Bioeconomic modeling of mixed Norway spruce-European beech stands: Economic consequences of considering ecological effects. *European Journal of Forest Research*, 132(3), 511–522. <https://doi.org/10.1007/s10342-013-0692-3>
- Grimm, V., Berger, U., Bastiansen, F., Eliassen, S., Ginot, V., Giske, J., Goss-Custard, J., Grand, T., Heinz, S. K., Huse, G., Huth, A., Jepsen, J. U., Jørgensen, C., Mooij, W. M., Müller, B., Pe'er, G., Piou, C., Railsback, S. F., Robbins, A. M., ... DeAngelis, D. L. (2006). A standard protocol for describing individual-based and agent-based models. *Ecological Modelling*, 8, 115–126. <https://doi.org/10.1016/j.ecolmodel.2006.04.023>
- Grossiord, C. (2019). Having the right neighbors: How tree species diversity modulates drought impacts on forests. *New Phytologist*, 228(1), 42–49. <https://doi.org/10.1111/nph.15667>
- Guyot, V., Castagneyrol, B., Vialatte, A., Deconchat, M., & Jactel, H. (2016). Tree diversity reduces pest damage in mature forests across Europe. *Biology Letters*, 12(4). <https://doi.org/10.1098/rsbl.2015.1037>
- Hantsch, L., Braun, U., Scherer-Lorenzen, M., & Bruehlheide, H. (2013). Species richness and species identity effects on occurrence of foliar fungal pathogens in a tree diversity experiment. *Ecosphere*, 4(7), 1–12. <https://doi.org/10.1890/ES13-00103.1>
- He, H. S. (2008). Forest landscape models: Definitions, characterization, and classification. *Forest Ecology and Management*, 254(3), 484–498. <https://doi.org/10.1016/j.foreco.2007.08.022>
- Honkaniemi, J., Rammer, W., & Seidl, R. (2020). Norway spruce at the trailing edge: The effect of landscape configuration and composition on climate resilience. *Landscape Ecology*, 35(3), 591–606. <https://doi.org/10.1007/s10980-019-00964-y>
- Höwler, K., Vor, T., Seidel, D., Annighöfer, P., & Ammer, C. (2019). Analyzing effects of intra- and interspecific competition on timber quality attributes of *Fagus sylvatica* L.—From quality assessments on standing trees to sawn boards. *European Journal of Forest Research*, 138(2), 327–343. <https://doi.org/10.1007/s10342-019-01173-7>
- Huang, Y., Chen, Y., Castro-Izaguirre, N., Baruffol, M., Brezzi, M., Lang, A., Li, Y., Härdtle, W., von Oheimb, G., Yang, X., Liu, X., Pei, K., Both, S., Yang, B. O., Eichenberg, D., Assmann, T., Bauhus, J., Behrens, T., Buscot, F., ... Schmid, B. (2018). Impacts of species richness on productivity in a large-scale subtropical forest experiment. *Science*, 362(6410), 80–83. <https://doi.org/10.1126/science.aat6405>
- Huber, N., Bugmann, H., & Lafond, V. (2020). Capturing ecological processes in dynamic forest models: Why there is no silver bullet to cope with complexity. *Ecosphere*, 11(5). <https://doi.org/10.1002/ecs2.3109>
- Ichii, K., Suzuki, T., Kato, T., Ito, A., Hajima, T., Ueyama, M., Sasai, T., Hirata, R., Saigusa, N., Ohtani, Y., & Takagi, K. (2010). Multi-model analysis of terrestrial carbon cycles in Japan: Limitations and implications of model calibration using eddy flux observations. *Biogeosciences*, 7(7), 2061–2081. <https://doi.org/10.5194/bg-7-2061-2010>
- IPCC. (2014). Climate Change 2014 Synthesis Report. *Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*. <https://doi.org/10.1046/j.1365-2559.2002.1340a.x>
- Jactel, H., Bauhus, J., Boberg, J., Bonal, D., Castagneyrol, B., Gardiner, B., Gonzalez-Olabarria, J. R., Koricheva, J., Meurisse, N., & Brockerhoff, E. G. (2017). Tree diversity drives forest stand resistance to natural disturbances. *Current Forestry Reports*, 3(3), 223–243. <https://doi.org/10.1007/s40725-017-0064-1>
- Johnstone, J. F., Allen, C. D., Franklin, J. F., Frelich, L. E., Harvey, B. J., Higuera, P. E., Mack, M. C., Meentemeyer, R. K., Metz, M. R., Perry, G. L. W., Schoennagel, T., & Turner, M. G. (2016). Changing disturbance regimes, ecological memory, and forest resilience. *Frontiers in Ecology and the Environment*, 14(7), 369–378. <https://doi.org/10.1002/fee.1311>
- Jost, L. (2006). Entropy and diversity. *Opinion*, 2, 363–375.
- Kautz, M., Anthoni, P., Meddens, A. J. H., Pugh, T. A. M., & Arneeth, A. (2018). Simulating the recent impacts of multiple biotic disturbances on forest carbon cycling across the United States. *Global Change Biology*, 24(5), 2079–2092. <https://doi.org/10.1111/gcb.13974>
- Kautz, M., Dworschak, K., Gruppe, A., & Schopf, R. (2011). Quantifying spatio-temporal dispersion of bark beetle infestations in epidemic and non-epidemic conditions. *Forest Ecology and Management*, 262(4), 598–608. <https://doi.org/10.1016/j.foreco.2011.04.023>
- Keane, R. E., McKenzie, D., Falk, D. A., Smithwick, E. A. H., Miller, C., & Kellogg, L. K. B. (2015). Representing climate, disturbance, and vegetation interactions in landscape models. *Ecological Modelling*, 309–310, 33–47. <https://doi.org/10.1016/j.ecolmodel.2015.04.009>
- Kilian, W., Müller, F., & Starlinger, F. (1994). *Die forstlichen Wuchsgebiete Österreichs. Eine Naturraumgliederung nach waldökologischen Gesichtspunkten* (Vol. 82, p. 60). FBVA-Berichte, Schriftenreihe Der Forstlichen Bundesversuchsanstalt Wien.
- Kint, V., Hein, S., Campioli, M., & Muys, B. (2010). Wachstum und Stammqualität in reinen und gemischten Buchenbeständen. *Forest Ecology and Management*, 260(11), 2023–2034. <https://doi.org/10.1016/j.foreco.2010.09.008>
- Knoke, T., Ammer, C., Stimm, B., & Mosandl, R. (2008). Admixing broad-leaved to coniferous tree species: A review on yield, ecological stability and economics. *European Journal of Forest Research*, 127(2), 89–101. <https://doi.org/10.1007/s10342-007-0186-2>
- Kulakowski, D., Seidl, R., Holeksa, J., Kuuluvainen, T., Nagel, T. A., Panayotov, M., Svoboda, M., Thorn, S., Vacchiano, G., Whitlock, C., Wohlgemuth, T., & Bebi, P. (2017). A walk on the wild side: Disturbance dynamics and the conservation and management of European mountain forest ecosystems. *Forest Ecology and Management*, 388, 120–131. <https://doi.org/10.1016/j.foreco.2016.07.037>
- Lamy, T., Liss, K. N., Gonzalez, A., & Bennett, E. M. (2016). Landscape structure affects the provision of multiple ecosystem services. *Environmental Research Letters*, 11(12), 1–9. <https://doi.org/10.1088/1748-9326/11/12/124017>
- Larocque, G. R., Luckai, N., Adhikary, S. N., Groot, A., Bell, F. W., & Sharma, M. (2013). Competition theory-science and application in mixed forest stands: Review of experimental and modelling methods and suggestions for future research. *Environmental Reviews*, 21(2), 71–84. <https://doi.org/10.1139/er-2012-0033>
- Lebourgeois, F., Gomez, N., Pinto, P., & Mérian, P. (2013). Mixed stands reduce *Abies alba* tree-ring sensitivity to summer drought in the Vosges mountains, western Europe. *Forest Ecology and Management*, 303, 61–71. <https://doi.org/10.1016/j.foreco.2013.04.003>
- McDowell, N. G., Allen, C. D., Anderson-Teixeira, K., Aukema, B. H., Bond-Lamberty, B., Chini, L., Clark, J. S., Dietze, M., Grossiord, C., Hanbury-Brown, A., Hurr, G. C., Jackson, R. B., Johnson, D. J., Kueppers, L., Lichstein, J. W., Ogle, K., Poulter, B., Pugh, T. A. M., Seidl, R., ... Xu, C. (2020). Pervasive shifts in forest dynamics in a changing world. *Science (New York, NY)*, 368(6494). <https://doi.org/10.1126/science.aaz9463>
- McDowell, N. G., Fisher, R. A., Xu, C., Domec, J. C., Hölttä, T., Mackay, D. S., Sperry, J. S., Boutz, A., Dickman, L., Gehres, N., Limousin, J. M., Macalady, A., Martínez-Vilalta, J., Mencuccini, M., Plaut, J. A., Ogée,

- J., Pangle, R. E., Rasse, D. P., Ryan, M. G., ... Pockman, W. T. (2013). Evaluating theories of drought-induced vegetation mortality using a multimodel-experiment framework. *New Phytologist*, 200(2), 304–321. <https://doi.org/10.1111/nph.12465>
- Menzel, A., Sparks, T. H., Estrella, N., Koch, E., Aasa, A., Ahas, R., Alm-kübler, K., Bissolli, P., Braslavská, O'lga, Briede, A., Chmielewski, F. M., Crepinsek, Z., Curnel, Y., Dahl, Å., Defila, C., Donnelly, A., Filella, Y., Jatczak, K., Måge, F., ... Zust, A. (2006). European phenological response to climate change matches the warming pattern. *Global Change Biology*, 12(10), 1969–1976. <https://doi.org/10.1111/j.1365-2486.2006.01193.x>
- Messier, C., Puettmann, K., Chazdon, R., Andersson, K. P., Angers, V. A., Brotons, L., Filotas, E., Tittler, R., Parrott, L., & Levin, S. A. (2015). From management to stewardship: Viewing forests as complex adaptive systems in an uncertain world. *Conservation Letters*, 8(5), 368–377. <https://doi.org/10.1111/conl.12156>
- Metz, J., Annighöfer, P., Schall, P., Zimmermann, J., Kahl, T., Schulze, E. D., & Ammer, C. (2016). Site-adapted admixed tree species reduce drought susceptibility of mature European beech. *Global Change Biology*, 22(2), 903–920. <https://doi.org/10.1111/gcb.13113>
- Mezei, P., Grodzki, W., Blaženec, M., & Jakuš, R. (2014). Factors influencing the wind-bark beetles' disturbance system in the course of an *Ips typographus* outbreak in the Tatra Mountains. *Forest Ecology and Management*, 312, 67–77. <https://doi.org/10.1016/j.foreco.2013.10.020>
- Millar, C. I., Stephenson, N. L., & Stephens, S. L. (2007). Climate change and forests of the future: Managing in the face of uncertainty. *Ecological Applications*, 17(8), 2145–2151. <https://doi.org/10.1890/06-1715.1>
- Mina, M., Bugmann, H., Cordonnier, T., Irauschek, F., Klopčič, M., Pardos, M., & Cailleret, M. (2017). Future ecosystem services from European mountain forests under climate change. *Journal of Applied Ecology*, 54(2), 389–401. <https://doi.org/10.1111/1365-2664.12772>
- Mori, A. S., Furukawa, T., & Sasaki, T. (2013). Response diversity determines the resilience of ecosystems to environmental change. *Biological Reviews*, 88(2), 349–364. <https://doi.org/10.1111/brv.12004>
- Mori, A. S., Isbell, F., & Seidl, R. (2018). β -diversity, community assembly, and ecosystem functioning. *Trends in Ecology & Evolution*, 33(7), 549–564. <https://doi.org/10.1016/j.tree.2018.04.012>
- Morin, X., Fahse, L., Jactel, H., Scherer-Lorenzen, M., García-Valdés, R., & Bugmann, H. (2018). Long-term response of forest productivity to climate change is mostly driven by change in tree species composition. *Scientific Reports*, 8(1), 1–12. <https://doi.org/10.1038/s41598-018-23763-y>
- Neuner, S., Albrecht, A., Cullmann, D., Engels, F., Griess, V. C., Hahn, W. A., Hanewinkel, M., Härtl, F., Kölling, C., Staupendahl, K., & Knoke, T. (2015). Survival of Norway spruce remains higher in mixed stands under a dryer and warmer climate. *Global Change Biology*, 21(2), 935–946. <https://doi.org/10.1111/gcb.12751>
- Peterson, G., Allen, C. R., & Holling, C. S. (1998). Ecological resilience, biodiversity, and scale. *Ecosystems*, 1(1), 6–18. <https://doi.org/10.2307/3658701>
- Petter, G., Mairota, P., Albrich, K., Bebi, P., Bruna, J., Bugmann, H., Haffenden, A., Scheller, R. M., Schmatz, D. R., Seidl, R., Speich, M., Vacchiano, G., & Lischke, H. (2020). How robust are future projections of forest landscape dynamics? Insights from a systematic comparison of four forest landscape models. *Environmental Modelling & Software*, 134, 104844. <https://doi.org/10.1016/j.envsoft.2020.104844>
- Phillips, J. D. (2007). The perfect landscape. *Geomorphology*, 84, 159–169. <https://doi.org/10.1016/j.geomorph.2006.01.039>
- Plas, F., Ratcliffe, S., Ruiz-Benito, P., Scherer-Lorenzen, M., Verheyen, K., Wirth, C., Zavala, M. A., Ampoorter, E., Baeten, L., Barbaro, L., Bastias, C. C., Bauhus, J., Benavides, R., Benneter, A., Bonal, D., Bouriaud, O., Brulheide, H., Bussotti, F., Carnol, M., ... Allan, E. (2018). Continental mapping of forest ecosystem functions reveals a high but unrealised potential for forest multifunctionality. *Ecology Letters*, 21(1), 31–42. <https://doi.org/10.1111/ele.12868>
- Pretzsch, H., Schütze, G., & Uhl, E. (2013). Resistance of European tree species to drought stress in mixed versus pure forests: Evidence of stress release by inter-specific facilitation. *Plant Biology*, 15(3), 483–495. <https://doi.org/10.1111/j.1438-8677.2012.00670.x>
- R Core Team. (2020). *R: A language and environment for statistical computing*. Retrieved from <https://www.r-project.org/>
- Renwick, K. M., Curtis, C., Kleinhesselink, A. R., Schlaepfer, D., Bradley, B. A., Aldridge, C. L., Poulter, B., & Adler, P. B. (2018). Multi-model comparison highlights consistency in predicted effect of warming on a semi-arid shrub. *Global Change Biology*, 24(1), 424–438. <https://doi.org/10.1111/gcb.13900>
- Reyer, C. P. O., Bathgate, S., Blennow, K., Borges, J. G., Bugmann, H., Delzon, S., Faia, S. P., Garcia-Gonzalo, J., Gardiner, B., Gonzalez-Olabarria, J. R., Gracia, C., Hernández, J. G., Kellomäki, S., Kramer, K., Lexer, M. J., Lindner, M., van der Maaten, E., Maroschek, M., Muys, B., ... Hanewinkel, M. (2017). Are forest disturbances amplifying or canceling out climate change-induced productivity changes in European forests? *Environmental Research Letters*, 12(3). <https://doi.org/10.1088/1748-9326/aa5ef1>
- Rothe, A., & Binkley, D. (2001). Nutritional interactions in mixed species forests: A synthesis. *Canadian Journal of Forest Research*, 31(11), 1855–1870. <https://doi.org/10.1139/cjfr-31-11-1855>
- Schall, P., Gossner, M. M., Heinrichs, S., Fischer, M., Boch, S., Prati, D., Jung, K., Baumgartner, V., Blaser, S., Böhm, S., Buscot, F., Daniel, R., Goldmann, K., Kaiser, K., Kahl, T., Lange, M., Müller, J., Overmann, J., Renner, S. C., ... Ammer, C. (2018). The impact of even-aged and uneven-aged forest management on regional biodiversity of multiple taxa in European beech forests. *Journal of Applied Ecology*, 55(1), 267–278. <https://doi.org/10.1111/1365-2664.12950>
- Schelhaas, M.-J., Nabuurs, G.-J., & Schuck, A. (2003). Natural disturbances in the European forests in the 19th and 20th centuries. *Global Change Biology*, 9(11), 1620–1633. <https://doi.org/10.1046/j.1529-8817.2003.00684.x>
- Scheller, R. M., & Mladenoff, D. J. (2007). An ecological classification of forest landscape simulation models: Tools and strategies for understanding broad-scale forested ecosystems. *Landscape Ecology*, 22(4), 491–505. <https://doi.org/10.1007/s10980-006-9048-4>
- Schmidt, M., Hanewinkel, M., Kändler, G., Kublin, E., & Kohnle, U. (2010). An inventory-based approach for modeling singletree storm damage - experiences with the winter storm of 1999 in southwestern Germany. *Canadian Journal of Forest Research*, 40(8), 1636–1652. <https://doi.org/10.1139/X10-099>
- Schuler, L. J., Bugmann, H., Petter, G., & Snell, R. S. (2019). How multiple and interacting disturbances shape tree diversity in European mountain landscapes. *Landscape Ecology*, 34(6), 1279–1294. <https://doi.org/10.1007/s10980-019-00838-3>
- Schuler, L. J., Bugmann, H., & Snell, R. S. (2017). From monocultures to mixed-species forests: Is tree diversity key for providing ecosystem services at the landscape scale? *Landscape Ecology*, 32(7), 1499–1516. <https://doi.org/10.1007/s10980-016-0422-6>
- Schumacher, S., & Bugmann, H. (2006). The relative importance of climatic effects, wildfires and management for future forest landscape dynamics in the Swiss Alps. *Global Change Biology*, 12(8), 1435–1450. <https://doi.org/10.1111/j.1365-2486.2006.01188.x>
- Schumacher, S., Bugmann, H., & Mladenoff, D. J. (2004). Improving the formulation of tree growth and succession in a spatially explicit landscape model. *Ecological Modelling*, 180(1), 175–194. <https://doi.org/10.1016/j.ecolmodel.2003.12.055>
- Schumacher, S., Reineking, B., Sibold, J., & Bugmann, H. (2006). Modeling the impact of climate and vegetation on fire regimes in mountain landscapes. *Landscape Ecology*, 21(4), 539–554. <https://doi.org/10.1007/s10980-005-2165-7>

- Schwarz, B., Dietrich, C., Cesarz, S., Scherer-Lorenzen, M., Auge, H., Schulz, E., & Eisenhauer, N. (2015). Non-significant tree diversity but significant identity effects on earthworm communities in three tree diversity experiments. *European Journal of Soil Biology*, 67, 17–26. <https://doi.org/10.1016/j.ejsobi.2015.01.001>
- Sebald, J., Thrippleton, T., Rammer, W., Bugmann, H., & Seidl, R. (2021). Data from: Mixing tree species at different spatial scales: The effect of alpha, beta and gamma diversity on disturbance impacts under climate change. *Zenodo Digital Repository*, <https://doi.org/10.5281/zenodo.4739037>
- Seidl, R., Albrich, K., Erb, K., Formayer, H., Leidinger, D., Leitinger, G., Tappeiner, U., Tasser, E., & Rammer, W. (2019). What drives the future supply of regulating ecosystem services in a mountain forest landscape? *Forest Ecology and Management*, 445, 37–47. <https://doi.org/10.1016/j.foreco.2019.03.047>
- Seidl, R., Honkaniemi, J., Aakala, T., Aleinikov, A., Angelstam, P., Bouchard, M., Boulanger, Y., Burton, P. J., De Grandpré, L., Gauthier, S., Hansen, W. D., Jepsen, J. U., Jögi, K., Kneeshaw, D. D., Kuuluvainen, T., Lisitsyna, O., Makoto, K., Mori, A. S., Pureswaran, D. S., ... Senf, C. (2020). Globally consistent climate sensitivity of natural disturbances across boreal and temperate forest ecosystems. *Ecography*, 43(7), 967–978. <https://doi.org/10.1111/ecog.04995>
- Seidl, R., Rammer, W., Scheller, R. M., & Spies, T. A. (2012). An individual-based process model to simulate landscape-scale forest ecosystem dynamics. *Ecological Modelling*, 231, 87–100. <https://doi.org/10.1016/j.ecolmodel.2012.02.015>
- Seidl, R., Schelhaas, M. J., Rammer, W., & Verkerk, P. J. (2014). Increasing forest disturbances in Europe and their impact on carbon storage. *Nature Climate Change*, 4(9), 806–810. <https://doi.org/10.1038/nclimate2318>
- Seidl, R., Thom, D., Kautz, M., Martin-Benito, D., Peltoniemi, M., Vacchiano, G., Wild, J., Ascoli, D., Petr, M., Honkaniemi, J., Lexer, M. J., Trotsiuk, V., Mairota, P., Svoboda, M., Fabrika, M., Nagel, T. A., & Rey, C. P. O. (2017). Forest disturbances under climate change. *Nature Climate Change*, 7(6), 395–402. <https://doi.org/10.1038/nclimate3303>
- Senf, C., Pflugmacher, D., Hostert, P., & Seidl, R. (2017). Using Landsat time series for characterizing forest disturbance dynamics in the coupled human and natural systems of Central Europe. *ISPRS Journal of Photogrammetry and Remote Sensing*, 130, 453–463. <https://doi.org/10.1016/j.isprsjprs.2017.07.004>
- Senf, C., & Seidl, R. (2021). Mapping the forest disturbance regimes of Europe. *Nature Sustainability*, 4(1), 63–70. <https://doi.org/10.1038/s41893-020-00609-y>
- Silva Pedro, M., Rammer, W., & Seidl, R. (2015). Tree species diversity mitigates disturbance impacts on the forest carbon cycle. *Oecologia*, 177(3), 619–630. <https://doi.org/10.1007/s00442-014-3150-0>
- Sommerfeld, A., Senf, C., Buma, B., D'Amato, A. W., Després, T., Díaz-Hormazábal, I., Fraver, S., Frelich, L. E., Gutiérrez, Á. G., Hart, S. J., Harvey, B. J., He, H. S., Hlásny, T., Holz, A., Kitzberger, T., Kulakowski, D., Lindenmayer, D., Mori, A. S., Müller, J., ... Seidl, R. (2018). Patterns and drivers of recent disturbances across the temperate forest biome. *Nature Communications*, 9(1), 4355. <https://doi.org/10.1038/s41467-018-06788-9>
- Tebaldi, C., & Knutti, R. (2007). The use of the multi-model ensemble in probabilistic climate projections. *Philosophical Transactions of the Royal Society A: Mathematical, Physical and Engineering Sciences*, 365(1857), 2053–2075. <https://doi.org/10.1098/rsta.2007.2076>
- Temperli, C., Bugmann, H., & Elkin, C. (2013). Cross-scale interactions among bark beetles, climate change, and wind disturbances: A landscape modeling approach. *Ecological Monographs*, 83(3), 383–402. <https://doi.org/10.1890/12-1503.1>
- Thom, D., Rammer, W., Dirnböck, T., Müller, J., Kobler, J., Katzensteiner, K., Helm, N., & Seidl, R. (2017). The impacts of climate change and disturbance on spatio-temporal trajectories of biodiversity in a temperate forest landscape. *Journal of Applied Ecology*, 54(1), 28–38. <https://doi.org/10.1111/1365-2664.12644>
- Thom, D., Seidl, R., Steyrer, G., Krehan, H., & Formayer, H. (2013). Slow and fast drivers of the natural disturbance regime in Central European forest ecosystems. *Forest Ecology and Management*, 307, 293–302. <https://doi.org/10.1016/j.foreco.2013.07.017>
- Thrippleton, T., Bugmann, H., Kramer-Priewasser, K., & Snell, R. S. (2016). Herbaceous understorey: An overlooked player in forest landscape dynamics? *Ecosystems*, 19(7), 1240–1254. <https://doi.org/10.1007/s10021-016-9999-5>
- Trumbore, S., Brando, P., & Hartmann, H. (2015). Forest health and global change. *Science*, 349(6250), 814–819. <https://doi.org/10.1126/science.aaa9092>
- Turner, M. G. (2010). Disturbance and landscape dynamics in a changing world. *Ecology*, 91(10), 2833–2849. <https://doi.org/10.1890/10-0097.1>
- Urban, D. L., Neill, R. V. O., & Shugart, H. H. (1987). Ecology landscape spatial patterns. *BioScience*, 37(2), 119–127.
- Valle, D., Staudhammer, C. L., Cropper, W. P., & Van Gardingen, P. R. (2009). The importance of multimodel projections to assess uncertainty in projections from simulation models. *Ecological Applications*, 19(7), 1680–1692. <https://doi.org/10.1890/08-1579.1>
- van der Plas, F., Manning, P., Soliveres, S., Allan, E., Scherer-Lorenzen, M., Verheyen, K., Wirth, C., Zavala, M. A., Ampoorter, E., Baeten, L., Barbaro, L., Bauhus, J., Benavides, R., Benneter, A., Bonal, D., Bouriaud, O., Bruelheide, H., Bussotti, F., Carnol, M., ... Fischer, M. (2016). Biotic homogenization can decrease landscape-scale forest multifunctionality. *Proceedings of the National Academy of Sciences of the United States of America*, 113(13), 3557–3562. <https://doi.org/10.1073/pnas.1517903113>
- Yachi, S., & Loreau, M. (1999). Biodiversity and ecosystem productivity in a fluctuating environment: The insurance hypothesis. *Proceedings of the National Academy of Sciences of the United States of America*, 96(4), 1463–1468. <https://doi.org/10.1073/pnas.96.4.1463>
- Zimová, S., Dobor, L., Hlásny, T., Rammer, W., & Seidl, R. (2020). Reducing rotation age to address increasing disturbances in Central Europe: Potential and limitations. *Forest Ecology and Management*, 475(July), 118408. <https://doi.org/10.1016/j.foreco.2020.118408>
- Zingg, A., & Ramp, B. (1997). Wachstum und Stammqualität in reinen und gemischten Buchenbeständen. In *Deutscher Verband Forstlicher Forschungsanstalten. Sektion Ertragskunde. Jahrestagung 1997, Grünberg* (pp. 152–164). Deutscher Verband Forstlicher Forschungsanstalten.

SUPPORTING INFORMATION

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

How to cite this article: Sebald J, Thrippleton T, Rammer W, Bugmann H, Seidl R. Mixing tree species at different spatial scales: The effect of alpha, beta and gamma diversity on disturbance impacts under climate change. *J Appl Ecol*. 2021;00:1–15. <https://doi.org/10.1111/1365-2664.13912>

Appendix D: Curriculum Vitae

Education

03/2018 – 09/2021	PhD in Forest Science University of Natural Resources and Life Sciences, Vienna
10/2015 – 02/2018	MSc in Forest Science (with distinction) University of Natural Resources and Life Sciences, Vienna Thesis title: Störungsanalyse für Österreichs Wald anhand von Satellitendaten der Jahre 1986 bis 2016
10/2011 – 07/2015	BEng in Forest Engineering University of Applied Sciences Weihenstephan, Freising Thesis title: Vom Altersklassenwald zum gemischten Dauerwald: Untersuchung mit Hilfe von Dauerbeobachtungsflächen

Professional Experience

11/2020 –	Specialist Austrian Federal Forests (ÖBf AG), Hall, Tyrol
03/2018 – 07/2021	Research Assistant University of Natural Resources and Life Sciences, Vienna
03/2017 – 02/2018	Student Research Assistant University of Natural Resources and Life Sciences, Vienna

Awards

2019	Klaus Fischer Innovationspreis für Technik und Umwelt
2018	Preis des Fonds 120 Jahre Universität für Bodenkultur

Publications

Academic

2021

Sebald, J., Senf, C., Seidl, R., 2021. Human or natural? Landscape context improves the attribution of forest disturbances mapped from Landsat in Central Europe. *Remote Sensing of Environment*.

Sebald, J., Thrippleton, T., Rammer, W., Bugmann, H., Seidl, R., 2021. Mixing tree species at different spatial scales: the effect of alpha, beta and gamma diversity on disturbance impacts under climate change. *Journal of Applied Ecology*.

Senf, C., **Sebald, J.**, Seidl, R., 2021. Increasing canopy mortality and their impact on the demographic structure of Europe`s forests. *One Earth*.

2020

Thom, D., Sommerfeld, A., **Sebald, J.**, Hagge, J., Müller, J., Seidl, R., 2020. Effects of disturbance patterns and deadwood on the microclimate in European beech forests. *Agriculture and Forest Meteorology* 291.

2019

Sebald, J., Senf, C., Heiser, M., Scheidl, C., Pflugmacher, D., Seidl, R., 2019. The effects of forest cover and disturbance on torrential hazards: Large-scale evidence from the Eastern Alps. *Environmental Research Letters*.

2018

Senf, C., Pflugmacher, D., Zhiqiang, Y., **Sebald, J.**, Knorn, J., Neumann, M., Hostert, P., Seidl, R., 2018. Canopy mortality has doubled in Europe's temperate forests over the last three decades. *Nature Communications* 9, 4978

Popular science

Sebald, J., Senf, C., Seidl, R., 2020. Einfluss von Störungen auf Wildbachereignisse. *Österreichische Forstzeitung*, 05/2020, 10-12

Academic presentations

Sebald, J., 2020. Forest management for climate robust mountain landscapes. *Seminar on Silviculture, Ecosystem Dynamics and Forest Management, Freising, Germany*

Sebald, J., Rammer, W., Seidl, R., 2020. The role of alpha and beta diversity in buffering the effects of intensifying disturbance regimes under climate change. *Managing forest in the 21st century, Potsdam, Germany*

Sebald, J., Senf, C., Heiser, M., Scheidl, C., Pflugmacher, D., Seidl, R., 2019. Are forested landscape protecting against torrential hazards? Empirical large-scale evidence from the Alps. *International Association for Landscape Ecology – World congress, Milano, Italy*

Sebald, J., Senf, C., Heiser, M., Scheidl, C., Pflugmacher, D., Seidl, R., 2019. Forest disturbances increase the risk from torrential hazards in mountain regions. *European Geosciences union (EGU) – General Assembly, Vienna, Austria*

Sebald, J., Senf, C., Seidl, R., 2019. Mapping forest disturbances to quantify effects of forest cover and disturbance on natural hazard probability in the Eastern Alps. *Seminar on forest disturbances at LUKE, Helsinki, Finland*

Sebald, J., Rammer, W., Seidl, R., 2019. P:E:T:S.- The Permanent Evaluation and Test Suite for iLand. *Forest modelling symposium at UFZ, Leipzig, Germany*

Reviewer for Scientific Journals

Environmental Research Letters, Global Change Biology

Teaching

2018 Grundlagen der Waldbewirtschaftung (Basics of Forest Management), practical exercises, University of Natural Resources and Life Sciences, Vienna