3-2017

A walk on the wild side: Disturbance dynamics and the conservation and management of European mountain forest ecosystems

Dominik Kulakowski
Clark University, DKulakowski@clarku.edu

Rupert Seidl
Universitat fur Bodenkultur Wien

Jan Holeksa
Uniwersytet im. Adama Mickiewicza w Poznaniu

Timo Kuuluvainen
Helsingin Yliopisto

Thomas A. Nagel
Univerza v Ljubljani

See next page for additional authors

Published in final edited form as:
For Ecol Manage. 2017 March 15; 388: 120–131. doi:10.1016/j.foreco.2016.07.037.

A walk on the wild side: Disturbance dynamics and the conservation and management of European mountain forest ecosystems☆

Dominik Kulakowski[a,b,*], **Rupert Seidl**[c], **Jan Holeksa**[d], **Timo Kuuluvainen**[e], **Thomas A. Nagel**[f], **Momchil Panayotov**[g], **Miroslav Svoboda**[h], **Simon Thorn**[i], **Giorgio Vacchiano**[j], **Cathy Whitlock**[k], **Thomas Wohlgemuth**[l], and **Peter Bebi**[b]

[a]Graduate School of Geography, Clark University, MA, USA [b]WSL Institute for Snow and Avalanche Research SLF, Davos, Switzerland [c]Institute of Silviculture, Department of Forest- and Soil Sciences, University of Natural Resources and Life Sciences (BOKU), Vienna, Austria [d]Adam Mickiewicz University, Faculty of Biology, Department of Plant Ecology and Environment Protection, Umultowska 89, 61-614 Poznań, Poland [e]Department of Forest Sciences, University of Helsinki, Helsinki, Finland [f]Department of Forestry and Renewable Forest Resources, University of Ljubljana, Slovenia [g]Dendrology Department, University of Forestry, 1797 Sofia, Bulgaria [h]Faculty of Forestry and Wood Sciences, Czech University of Life Sciences, Prague, Czech Republic [i]Field Station Fabrikschleichach, Biocenter, University of Würzburg, Glashüttenstraße 5, 96181 Rauhenebrach, Germany [j]Università degli Studi di Torino, DISAFA, Largo Braccini 2, 10095 Grugliasco (TO), Italy [k]Montana Institute on Ecosystems, Montana State University, Bozeman, MT, USA [l]Swiss Federal Institute for Forest, Snow and Landscape Research WSL, Birmensdorf, Switzerland

Abstract

Mountain forests are among the most important ecosystems in Europe as they support numerous ecological, hydrological, climatic, social, and economic functions. They are unique relatively natural ecosystems consisting of long-lived species in an otherwise densely populated human landscape. Despite this, centuries of intensive forest management in many of these forests have eclipsed evidence of natural processes, especially the role of disturbances in long-term forest dynamics. Recent trends of land abandonment and establishment of protected forests have coincided with a growing interest in managing forests in more natural states. At the same time, the importance of past disturbances highlighted in an emerging body of literature, and recent increasing disturbances due to climate change are challenging long-held views of dynamics in these ecosystems. Here, we synthesize aspects of this *Special Issue* on the ecology of mountain forest ecosystems in Europe in the context of broader discussions in the field, to present a new perspective on these ecosystems and their natural disturbance regimes. Most mountain forests in Europe, for which long-term data are available, show a strong and long-term effect of not only human land use but also of natural disturbances that vary by orders of magnitude in size and

*Corresponding author at: Graduate School of Geography, Clark University, MA, USA. dkulakowski@clarku.edu (D. Kulakowski).
☆This article is part of the special issue: "Ecology of Mountain Forest Ecosystems in Europe" published in the journal Forest Ecology and Management 388, 2017.

Europe PMC Funders Author Manuscripts

frequency. Although these disturbances may kill many trees, the forests themselves have not been threatened. The relative importance of natural disturbances, land use, and climate change for ecosystem dynamics varies across space and time. Across the continent, changing climate and land use are altering forest cover, forest structure, tree demography, and natural disturbances, including fires, insect outbreaks, avalanches, and wind disturbances. Projected continued increases in forest area and biomass along with continued warming are likely to further promote forest disturbances. Episodic disturbances may foster ecosystem adaptation to the effects of ongoing and future climatic change. Increasing disturbances, along with trends of less intense land use, will promote further increases in coarse woody debris, with cascading positive effects on biodiversity, edaphic conditions, biogeochemical cycles, and increased heterogeneity across a range of spatial scales. Together, this may translate to disturbance-mediated resilience of forest landscapes and increased biodiversity, as long as climate and disturbance regimes remain within the tolerance of relevant species. Understanding ecological variability, even imperfectly, is integral to anticipating vulnerabilities and promoting ecological resilience, especially under growing uncertainty. Allowing some forests to be shaped by natural processes may be congruent with multiple goals of forest management, even in densely settled and developed countries.

Keywords

Disturbance regimes; Socioecological systems; Temperate forests; Range of variability; Resilience; Wilderness

1 Introduction

The magnitude and direction of environmental changes vary globally with biophysical, economic, political, and sociological setting. In Europe, long-term intensive land use has been a dominant driver of ecological dynamics for centuries to millennia. However, since the nineteenth century, many European landscapes increasingly reflect abandonment of agriculture and other high-intensity land uses (Navarro and Pereira, 2012), as well as the establishment of protected areas (Motta et al., 2015), which together have contributed to an expansion of forest area (Rudel et al., 2005; Naudts et al., 2016). This recent expansion of forest has coincided with an increase in natural disturbances, partly as a result of these very changes in forest cover, structure, and composition, and partly as a result of changes in climate (Seidl et al., 2011). At the same time, an emerging body of literature highlights the historical importance of large infrequent disturbances in Europe (e.g., *articles in this issue*), even in ecosystems long thought to be shaped by fine-scale short-term processes. These changes in ecological dynamics and ecological understanding are concurrent with growing public interest in managing forests in more natural states, especially in places where other desired ecosystem services (e.g., carbon storage, nutrient cycling, water and air purification, maintenance of wildlife habitat, social and cultural benefits such as recreation, protection against natural hazards, supply of forest products, etc.) are not compromised (Meeus, 1995; Kräuchi et al., 2000). Consequently, natural disturbances and other natural processes have been increasingly allowed to shape the structure and dynamics of some forest ecosystems, but in others, the effects of natural disturbance continue to be intensively managed (Duncker et al., 2012).

Europe PMC Funders Author Manuscripts

In order to inform adaptive management strategies and science-based scenarios of future forest development, important priorities for forest ecology and management in Europe include contextualizing recent ecological dynamics within what can be expected to be a normal range of variation; recognizing spatiotemporal patterns and trends; and understanding the ecological, social, and economic consequences of recent trajectories. Here we synthesize aspects of this *Special Issue* on the ecology of mountain forest ecosystems in Europe in the context of other relevant literature to present a new perspective on European mountain forests and their natural disturbance regimes. We especially focus on mountain forests of the Balkan Peninsula (Panayotov et al., 2017; Nagel et al., 2017), the Apennines (Vacchiano et al., 2017), the Alps (Bebi et al., 2017; Conedera et al., 2017; Seidl et al., 2017), Bavaria (Thorn et al., 2017), the Carpathians (Holeksa et al., 2017; Janda et al., 2017), and the North Fennoscandian Mountains (Kuuluvainen et al., 2017) (Fig. 1). We explore ecological factors that underlie variability, resilience, and vulnerabilities of mountain forest ecosystems in Europe. We also compare similarities and differences of forest dynamics and disturbance regimes across these ecosystems, discuss future scenarios of an emerging new ecological reality of altered climate and altered disturbance regimes, and suggest ways of accommodating natural ecological dynamics in the management of Europe's mountain forests.

Mountain forest ecosystems in Europe are in a relatively natural state compared with the more developed matrix in which they occur (EEA, 2010) (Fig. 1). Although the landscape structure of these mountain forests is heterogeneous, that mosaic is often less fragmented by human activity in comparison to lowland forests. Therefore, mountain forests serve as important refugia for genetic, species, habitat, and ecosystem diversity. The long-term history of European mountain forests varies across regions and is largely contingent on patterns of human settlement, land use, and socioeconomic development. In many forests near dense human settlements, land use has been more important than climate in determining forest extent and dynamics, in some cases even for the past 6000–8000 years (Conedera et al., 2017; Bebi et al., 2017; Vacchiano et al., 2017). The paleoecological record from central Europe shows a history of deforestation, deliberate burning and selective forest management since Neolithic times, with the most intense land use during the Medieval Period. Brief periods of forest recovery occurred as a result of land abandonment at the end of the Roman Period and during the last century. In some areas, such as those of the Alps and the Apennine Mountains, intensive agriculture, grazing, and logging were widespread also at high elevations until the mid-19th century, which reduced forest extent and forest density below topographically and climatically-determined limits (e.g., Bebi et al., 2017; Vacchiano et al., 2017). In contrast, land use history has been shorter and less intense in the forests of eastern Europe (Kaplan et al., 2009), including the Carpathian Mountains (Janda et al., 2017; Holeksa et al., 2017), southeastern Europe, including the Balkan Peninsula (Nagel et al., 2017; Panayotov et al., 2017), and northern Europe, including the North Fennoscandian Mountains (Kuuluvainen et al., 2017). Since the onset of industrialization in the mid-19th century, reduced agriculture, and secondarily reduced demand for wood, active reforestation, and active afforestation, have resulted in expanded forest cover in many regions across Europe (Table 1).

Much research on European mountain forests has focused on understanding the dynamics of the last decades to century and relatively few studies have examined the longer history of these forests (but see Section 4). Although forest dynamics of the recent past are important, many dominant species (e.g., Norway spruce, European larch, stone pine, etc.) have longevities of 200–500 years and forest dynamics are likely to fluctuate over many centuries. Present-day 100 to 150-year-old forests can actually be considered young relative to their maximum lifespan, and a perspective of a century is short for describing a natural range of variability. Understanding natural system dynamics is a key prerequisite of ecosystem management, yet the full spectrum of system dynamics cannot be understood without a longer perspective.

2 Concepts of variability

The benefits of understanding and using concepts of variability in ecosystem management have been reviewed extensively (e.g., Landres et al., 1999). They provide operational flexibility for management actions and protocols (Landres et al., 1999) and allow a coarse filter approach for sustaining a wide range of taxa with diverse and often poorly understood species requirements (Lindenmayer and Franklin, 2002). Managing within the boundaries of natural variability is also often easier and less expensive than trying to manage outside of natural system boundaries (Allen and Hoekstra, 1992; Landres et al., 1999). For example, retaining windthrow in avalanche or rockfall protection forests utilizes the protective capacity of increased surface roughness (due to increased logs and pit and mound topography), is easier and less expensive than active management, and often maintains adequate protection against rockfall or avalanches (Schönenberger et al., 2005). Incorporating natural variability into management strategies ensures that ecosystem processes that sustain ecosystems are more likely to be maintained, even if not all their respective drivers are perfectly understood. Dendroecology, paleoecology, documentary sources, and other data can help describe key components of past variability, and remote sensing and simulation modeling can describe important ecosystem processes and characteristics (e.g., patch sizes, deadwood; Cyr et al., 2009; Nonaka and Spies, 2005) in the past as well as the future.

Natural conditions and processes provide a useful guideline for sustainable ecosystem management and often highlight that natural disturbances are vital attributes of most ecological systems. The concept of the Historical Range of Variability (HRV) describes the spectrum of natural patterns and processes that exist in the absence of major anthropogenic modification and has been used to guide ecosystem management in North America and elsewhere (e.g., Landres et al., 1999; Tinker et al., 2003; Gustafson et al., 2010; Storaunet et al., 2013; Caldera et al., 2015). HRV is most useful where major human modification of ecosystem structure and function is fairly recent or limited. Ecosystems with a long history of intense human modification may be better served by the concept of Natural Range of Variability, which is based on more than historical observation and can also be based on comparisons to other similar ecosystems as well as theoretical considerations.

Criticisms of using concepts of variability in ecosystem management include the fact that there are many possible goals of ecosystem management, including maximizing timber

Europe PMC Funders Author Manuscripts

production and protecting human settlements and infrastructure from natural hazards, which might not be optimally fulfilled by variability-based management. Furthermore, it may be unreasonable or unrealistic to manage ecosystems in states in which they existed centuries ago. Other concerns include the fact that climatic conditions are substantially different now than they were during reference periods for which ranges of variability were established. These points are less relevant if concepts of variability are not used as prescriptive goals, but rather as (1) indicators of the fact that some amount of variability and disturbance is normal, (2) examples of the importance and effects of disturbance legacies (e.g., Long, 2009); (3) reminders of the dynamic character of ecosystems, and (4) potential baselines against which recent changes due to climate change or land use can be assessed (e.g., Jarvis and Kulakowski, 2015; Whitlock et al., 2015).

The possibility of understanding past variability and applying it to contemporary management depends in part on past and current forest conditions. Fairly extensive areas of natural or primary forests exist in eastern, southeastern and northern Europe (Holeksa et al., 2017; Janda et al., 2017; Panayotov et al., 2017; Nagel et al., 2017; Kuuluvainen et al., 2017). But for forest ecosystems that exist in areas that have been intensively managed or unforested for centuries, such as in parts of central and western Europe, one might question whether a range of variability can be established at all, and if so, whether it is relevant for understanding and managing these regions. Ecosystems in which centuries of heavy human influence has shifted the baseline (Papworth et al., 2009) of what is considered “normal” or “natural” may require more flexible definitions of variability. For example, one could posit a Recent Range of Variability (RRV), to refer to the range of conditions and dynamics that have characterized an ecosystem over the last few decades. This conceptualization would likely underestimate the overall variability inherent to a system, but still may be useful in highlighting the dynamic nature of ecosystems where only short-term dynamics are known. Additionally, by recognizing that for some ecosystems we only know the recent range of variability (RRV) but not the HRV, we more explicitly acknowledge “known unknowns”. One could also conceive of a Future Range of Variability (FRV), describing the expected range of conditions under future climate and land use (Duncan et al., 2010; Seidl et al., 2016b). The utility of all variability concepts is ultimately that they stress ecosystem dynamics rather than stationarity or optimization of forest structure or composition. These approaches also have the benefit of distinguishing between changes that fall within the natural dynamics of the system and those that are novel (see Radeloff et al., 2015). In contrast, disregarding natural variation altogether, and expecting newly forested areas or mature forests not to be disturbed and not to change, is inconsistent with contemporary ecological understanding. Ignoring variation renders the natural dynamics of forests as an “unknown unknown” in the context of management. Understanding ecological variability, even imperfectly, is integral to anticipating vulnerabilities and promoting ecological resilience, especially under growing uncertainty (Carpenter et al., 2006; Seidl, 2014). Indeed, concepts of variability are particularly useful in assessing whether current and future disturbance regimes fall within a range that will not compromise ecological resilience or ecosystem services (Seidl et al., 2016b).

Europe PMC Funders Author Manuscripts

3 Resilience and vulnerabilities

The concept of resilience (the ability of a system to recover from and tolerate perturbations without shifting to a different state controlled by different processes) has become central in discussions of global environmental change (Folke et al., 2004; Biggs et al., 2012; Reyer et al., 2015; Seidl et al., 2016b; Müller et al., 2016; Seidl et al., 2017). Resilience may refer to the ability of an ecosystem to return to a functionally equivalent structure (e.g., multiple-aged stands), a functionally equivalent forest type (e.g., spruce forests), or a functionally equivalent vegetation type (e.g., forests) following disturbance at stand or landscape scales. Given this breadth of possible criteria, it logically follows that definitions of resilience affect assessments of ecological change. The broader the range of conditions that are considered normal, the less natural dynamics and disturbances can be perceived as substantially altering (or destroying) ecosystems. Therefore, key issues for ecosystem management focus on metrics of resilience, identification of critical disturbance processes, and the relationships between resilience and disturbances (Carpenter et al., 2001; Seidl et al., 2016b).

A long-term dynamic view of mountain forest ecosystems in Europe is offered by dendroecological, paleoecological, and documentary records that show that forests can exist in a range of states and regenerate following a range of disturbances, even severe ones (Svoboda et al., 2012; Svoboda et al., 2014; Dobrowolska, 2015; Nagel et al., 2016; Panayotov et al., 2015; Čada et al., 2016; Janda et al., 2017). For example, severe outbreaks of bark beetles in the Carpathian Mountains have altered forest structure for decades or longer, but post-disturbance regeneration is usually composed of the same set of species that dominated prior to disturbance (Wild et al., 2014; Zeppenfeld et al., 2015). Over time, both structure and composition remain within a dynamic equilibrium, even in forests affected by severe outbreaks, meaning that even by narrow definitions, forests have been resilient. Of course, if disturbances are too large, severe, frequent, or novel in type, resilience will break down and forests can tip to new stable states (Johnstone et al., in press).

Ecological disturbances can create spatial heterogeneity (e.g., variation in the amount and arrangement of surviving forest patches or trees) that often promotes biodiversity (Rixen et al., 2007), primary production (Silva Pedro et al., 2016), wildlife habitat, hydrogeologic protection (Dorren et al., 2004), and ecosystem resilience (Loreau et al., 2003; Turner et al., 2012; Seidl et al., 2014a). Furthermore, variability of tree, stand, and landscape patch conditions can modulate disturbance size and severity and can increase the likelihood of survival of individual or groups of trees (e.g., Kulakowski and Veblen, 2002; Kulakowski et al., 2003) that subsequently can be important in post-disturbance regeneration. By contributing to forest resilience, spatial heterogeneity also facilitates ecological adaptation to future environmental change and helps sustain important ecosystem services (Turner et al., 2012). Consequently, a common goal of recent management in Europe and elsewhere is to increase structural diversity and other attributes of heterogeneity, in part as a safeguard for future conditions (e.g. Schütz, 2002).

Stand-replacing disturbances (that leave no or few surviving trees) often create relatively homogenous forest structure in the decades that follow, unless underlying environmental heterogeneity is substantial (Oliver, 1981; Palmer, 1994; Wohlgemuth et al., 2002). More generally, post-disturbance regeneration varies with disturbance severity, pre-disturbance forest structure, and biophysical setting (e.g. Kulakowski et al., 2013; Vacchiano et al., 2014; Turner et al., 2016). Post-disturbance development is more rapid on sites with adequate seed source and suitable temperature and moisture availability, and as stands develop, heterogeneity gradually increases (Oliver, 1981). While stand development is slow, natural disturbances, such as insect outbreaks and wind storms, can greatly accelerate the creation of structural and compositional complexity at stand and landscape scales, especially in stands that are in early stages of development (Panayotov et al., 2011; Silva Pedro et al., 2016; Janda et al., 2017). Stands in latter stages of structural development are likely to have more abundant seedlings, saplings, and small trees (Burrascano et al., 2013) that tend to survive even very severe wind and insect disturbances and promote fairly rapid post-disturbance development. Post-disturbance logging, a common practice in Europe following wind and insect disturbance, normally limits potential disturbance-created heterogeneity (Thorn et al., 2017) and reduces natural post-disturbance regeneration (e.g. Beghin et al., 2010).

Importantly, if disturbances are too large, severe, or frequent, legacies of the pre-disturbance system may be lost and the ability of affected ecosystems to regenerate may be compromised (Kuuluvainen et al., 2017). This loss can shift ecosystems to alternate stable states, sometimes over extensive areas (Reyer et al., 2015; Johnstone et al., 2017). Consequently, a critical research need is to understand the range of variability of disturbances that promote resilience, as well as identify the threshold beyond which disturbances may compromise it (Scheffer et al., 2015). Similarly, it is important to understand how resilience may be changing as a result of climate change (Seidl et al., 2017). Increased warming may intensify disturbance events, alter post-disturbance regeneration, and result in novel ecosystems including even non-forest alternate stable states. Tipping points are most likely to be crossed as a result of extreme climate events that increase the size, frequency, and intensity of disturbances (e.g. Allen et al., 2010), and post-disturbance climatic conditions that hinder post-disturbance regeneration (see e.g., Rigling et al., 2013; Harvey et al., 2016). Disturbance size and frequency have increased across Europe in recent decades (Schelhaas et al., 2003; Seidl et al., 2014b). The highest potential for disturbance-mediated tipping points will likely be at climatically-defined range limits (Seidl et al., 2017; Kuuluvainen et al., 2017), although marginal populations may also have genetic traits to survive severe climatic conditions (Hampe and Petit 2005; Eckert et al., 2008). Questions of whether and how current and future changes in climate and disturbance will result in critical transitions in Europe’s mountain forests remain unanswered and should be a focus of new research. A first important step towards this goal is to better understand past and current disturbance regimes in these systems.

4 Disturbances in European mountain forests

A long-standing view of European forests has held that large severe disturbances are directly or indirectly caused by human activity, including forest management practices that simplified forest structure (Klimo et al., 2000; Hansen and Spiecker, 2004). To test this view, a number of dendroecological studies have explored the dynamics of old-growth remnants in mountain forests in recent years, with some studies reconstructing dynamics back to the end of the 18th century (Piovesan et al., 2005; Firm et al., 2009; Motta et al., 2011; Panayotov et al., 2011; Nagel et al., 2014; Holeksa et al., 2016). These studies have been limited by the fact that preservation of forest lands has been contingent on patterns of human settlement and land use such that easily accessible forests have been more modified than remote ones. Evidence of long-term forest dynamics has been preferentially retained in sparsely populated regions and less accessible sites. As a result, well-preserved and well-studied sites are not necessarily representative of the larger landscape. Nevertheless, studies in remnant old-growth forests provide the best available view into long-term dynamics and important insights can be derived from retrospective studies of old, remnant patches of unmanaged forests, even while recognizing that these studies represent a conservative estimate of the importance of disturbances (e.g., Janda et al., 2017; Panayotov et al., 2017; Nagel et al., 2017).

Most studies of long-term forest dynamics rely on documentary, dendroecological, or paleoecological data. Documentary records provide a fairly accurate and reliable – but often short-term – view of ecological change (e.g., Seidl et al., 2011; Thom et al., 2013; Vacchiano et al., 2016) and at best, they provide information on a recent range of variability. In contrast, dendroecological records provide information that spans several centuries (e.g., Svoboda et al., 2012; Janda et al., 2014; Čada et al., 2016), but are spatially limited to the stand- or landscape scale. Longer term perspectives, covering centuries to millennia, come from pollen, plant macrofossil, and charcoal records preserved in the sediments of lakes and wetlands. These data provide information on forest dynamics linked to past changes in climate, land-use, and disturbances. In some settings, they can be used to infer stand-level history, but more often they offer landscape-scale reconstructions (Conedera et al., 2017).

Based on these multiple sources of information, the most common natural disturbances across Europe's mountain forests are caused by windstorms, insect outbreaks, fires, and avalanches (Table 1; Fig. 2). Dominant types of disturbances vary regionally across Europe with forest type, location, climate, the degree of cultural landscape modification, and topographic setting (Table 1, Fig. 2). Below we briefly review these disturbances and refer to relevant articles in this *Special Issue* and beyond that describe regional disturbance regimes in greater detail.

4.1 Wind

Wind disturbances are and have been over the past several centuries, the most ubiquitous and important disturbances in European mountain forests, yet there are key differences among mountain ranges (Table 1, Fig. 2). Wind damage related to summer thunderstorms is common across most European mountain ranges, but usually results in relatively small areas of wind disturbance. In the Dinaric Mountains, the wind regime is dominated by frequent small-scale summer thunderstorms that tend to create small patches of intermediate to severe damage (Nagel et al., 2017). In contrast, winter storm systems in mountain ranges of central and northwestern Europe affect larger forest areas than any other disturbance. Notable examples of these extra-tropical cyclones include the storms Vivian in February 1990 and Lothar in December 1999, both of which caused damage across large regions of the Alps (Bebi et al., 2017) and central Europe. Other intense wind storms have caused large and severe disturbances in the Carpathians (Holeksa et al., 2017; Janda et al., 2017), mountains of the Balkan Peninsula (Panayotov et al., 2017), and Pyrenees. Wind disturbance is less important in the forests of the relatively low latitude and low elevation Apennines (Vacchiano et al., 2017), which lie outside of major winter storm tracks, are less susceptible to winter storms (Della-Marta et al., 2009), and are more sheltered from strong winds by neighboring mountain ranges. Similarly, forests in the North Fennoscandian Mountains are less affected by strong storms (Kuuluvainen et al., 2017).

Short-term records suggest that the total European forest area disturbed by wind (Schelhaas et al., 2003; Seidl et al., 2014b) and in mountains specifically (e.g., Panayotov et al., 2017) has increased over the past decades, especially where forest area and growing stock have increased (e.g., Bebi et al., 2017). Trends of increasing wind disturbances may result from changing forest structure or improved and more complete reporting of wind damage over time. In the Swiss Alps where forest area has substantially increased, the trend is evident even where reporting has been consistent over the last 150 years (Usbeck et al., 2010a). It is important to put recent wind disturbances in the context of the long-term development of mountain forests. Tree-ring records indicate that large and severe wind disturbances have occurred over the last several centuries in virtually every mountain range across Europe for which long-term disturbance histories exist (e.g., Holeksa et al., 2017; Janda et al., 2017; Panayotov et al., 2017), suggesting that wind disturbances have long been an important natural driver of mountain forest dynamics in Europe. Windstorms are irregular events, and no long-term trend in storms has been identified in Europe (Holeksa et al., 2016); nonetheless, the circulation features associated with projected climate change will likely result in increased peak wind speeds and possible shifts in storm tracks (Ulbrich and Christoph, 1999; Usbeck et al., 2010b; Pryor et al., 2012).

4.2 Insects

Outbreaks of bark beetles and defoliators across Europe affect forests dominated by spruce, pine, fir, and other species (Table 1, Fig. 2). In North Fennoscandia, mass outbreaks of defoliators such as *Eppirita autumnata* have severely affected birch forests (Kuuluvainen et al., 2017). In the Balkans and in other pine forests, outbreaks of the defoliators *Thaumetopoea pityocampa* have like-wise been ecologically important. But across the continent, the most important insect outbreaks are those of the European spruce bark beetle (*Ips typographus* L.) attacking Norway spruce (*Picea abies* (L.) Karst.). As recently felled trees provide optimal habitat for growth of spruce bark beetle populations, outbreaks often follow wind disturbance, especially where weather conditions support the reproduction and survival of beetles. As with wind disturbances, large severe bark beetle outbreaks have occurred over the past decades across virtually every mountain range across Europe, except where low temperatures or poor forest connectivity have prevented such outbreaks (Thom et al., 2013; Stadelmann et al., 2013; Panayotov et al., 2015; Holeksa et al., 2017; Janda et al., 2017). The fragmentary records that are available suggest that past bark beetle outbreaks and windstorms may have been synchronous at regional to continental scales, but this possibility warrants further investigation (see e.g., Donat et al., 2010; Seidl et al., 2016a). In any case, there is a clear recent trend of larger and more frequent outbreaks, as climate change is making mountain forests (in which beetle development was previously limited by low temperatures) increasingly favorable to outbreaks (Jönsson et al., 2009; Netherer and Schopf, 2010).

4.3 Fire

Fire is the largest, most severe and most important natural disturbance in the Apennine Mountains (Vacchiano et al., 2017) and also plays an important role in shaping some forest types in the Southern and Central Alps, Dinaric Mountains, Pyrenees, and Mountains of the Balkan Peninsula (Perez-Sanz et al., 2013; Bebi et al., 2017; Nagel et al., 2017; Panayotov et al., 2017). It is also prevalent at xeric sites in the North Fennoscandian Mountains (Kuuluvainen et al., 2017) (Table 1, Fig. 2). Fires historically have been less important in cool mesic spruce forests that occupy mountain ranges in many other parts of Europe.

Anthropogenic fires were widespread during the Neolithic Age (ca. 4200–7500 BP) in association with agriculture and forest clearance (Conedera et al., 2017). From the Bronze and Iron Age onwards (since ca. 4000 BP), fires were used extensively for various land-use practices, including charcoal production and pasture clearance (Bebi et al., 2017; Conedera et al., 2017). With widespread human settlement in the Medieval and Historic periods, mountain forests became more restricted and managed, with consequent effects on vegetation structure, composition, and function (Conedera et al., 2017). Long-term trends in fires vary among regions (e.g., Navarro et al., 2015), but in general the size and frequency of fires has declined in recent centuries with increased forest fragmentation and active fire management (Conedera et al., 2017; Table 1). Presently, human-set ignition and land use determine fire occurrence in most mountain regions, with the possible exception of remote forests on the Balkan Peninsula where fires are primarily driven by climate (e.g., Panayotov et al., 2017). Despite the strong human influence in many regions, recent warming has increased fire hazard, fire frequency, and forest area burned across Europe (Seidl et al., 2011) and in mountain forests specifically (e.g., Panayotov et al., 2017).

4.4 Avalanche, snow and ice

Avalanches are a prominent disturbance agent that affect forest structure and dynamics in the Alps (Bebi et al., 2017), Carpathians (Holeksa et al., 2017), Pyrenees (Camarero et al., 2000), and the Mountains on the Balkan Peninsula (Panayotov et al., 2017). Avalanches are primarily controlled by topography and climate, but are also strongly affected by land use. Prior to the 20th century, avalanches were more frequent in the Alps as a result of reduced tree cover, especially where the upper treeline was depressed due to grazing in high-elevation pastures, which enlarged avalanche initiation areas. Over the past century, expansion of forest and construction of snow-supporting structures in avalanche starting zones have reduced the frequency and severity of avalanches in many areas (Bebi et al., 2009). During the last decades, these changes in alpine and subalpine land use have coincided with increasing temperatures, and decreasing snow and weather conditions favorable for avalanche releases below tree line (Teich et al., 2012). Over the past decades, decreased avalanche frequency has accelerated tree growth and reduced the fragmentation of forest landscapes (Kulakowski et al., 2006, 2011), and this in turn has affected carbon sequestration and biodiversity (Rixen et al., 2007; Vacchiano et al., 2015). As the climate continues to warm, it is likely that avalanches will become less important as a disturbance

Europe PMC Funders Author Manuscripts

agent in forest ecosystems of the Alps and elsewhere, at least at lower elevations, (Castebrunet et al., 2014) and relative to wind, insect outbreaks, and fires, which are all projected to increase in frequency or severity. In addition to avalanches, extreme precipitation events also cause snow breakage across Europe (Wallentin and Nilsson, 2014; Bebi et al., 2017), especially where trees are not adapted to heavy snow loads (Hlasny et al., 2011), where snow is heavy and wet, and where precipitation is in the form of freezing rain (Carrière et al., 2000; Nagel et al., 2016; Nagel et al., 2017).

4.5 Synthesis of disturbance patterns

Disturbances of varying size and severity characterize all European mountain forest ecosystems (Table 1; Fig. 2). Their occurrence is not outside the natural range of variability, nor is it likely to threaten the long-term persistence of forest ecosystems. This insight is supported not only by historical reconstructions, but also by observations that forests have regenerated after recent extensive and severe disturbances, even in the absence of human intervention (e.g., Zeppenfeld et al., 2015). As forest area and biomass continue to increase and forests age, the cumulative area affected by disturbances will also increase. Indeed, the extent of forest disturbances is increasing partly as a consequence of expanding forest area (Schelhaas et al., 2003; Seidl et al., 2011), which highlights the fact that disturbances are inseparable from forested landscapes. Furthermore, little or no discernable trend in disturbance frequency and size is evident where total forest cover, structure, and composition have not changed substantially in the last two centuries (e.g., Holeksa et al., 2017) – until recent climate warming has increased the size and frequency of natural disturbances (e.g., Janda et al., 2017; Panayotov et al., 2017).

Ecological patterns can persist and can entrain other ecosystem processes over long periods (Peterson, 2002). Across European mountain ranges, topographic setting and landscape connectivity contribute to key differences in disturbance characteristics. The maximum size of disturbances appears to be inversely proportional to topographic complexity and fragmentation. For example, wind disturbances are much larger on the southern flanks of the Carpathian Mountains in contrast to the more topographically complex northern flanks, due to differences in wind speed and turbulence, as well as structure of the exposed forest stands (e.g., Holeksa et al., 2017). As in other parts of the world, small disturbances affect the largest cumulative area during most years (e.g., Schüepp et al., 1994; Nagel et al., 2017), but it is the infrequent large events that account for the largest cumulative disturbed area over longer periods (Nagel et al., 2017; Panayotov et al., 2017). Thus, infrequent large events are especially important for shaping landscape pattern and should be considered in estimates of historical range of variability.

Disturbance severity (as measured by percent of all trees, saplings and seedlings in a stand that are damaged or killed) is generally determined by disturbance type, forest composition, and forest structure. The maximum severity of fires (e.g., Vacchiano et al., 2017) is greater than that of windstorms and bark beetle outbreaks in stands of mixed species composition and heterogeneous size structure (e.g., Holeksa et al., 2017; Janda et al., 2017; Panayotov et al., 2017). Maximum severity from fires, windstorms and insect outbreaks, in turn, is normally higher than that of ice storms (e.g., Nagel et al., 2017). However, all other things being equal maximum severity of windstorms and outbreaks depends on stand structure and is highest in homogenous stands in which all trees are equally susceptible.

5 Potential future trajectories

Considered together, the view of European mountain forest ecosystems that emerges from this *Special Issue*, as well as other recent research, has implications for projected future ecological trajectories and associated management strategies. It is likely that the frequency and extent of forest disturbances will continue to increase with projected warming, forest expansion, and forest closure (e.g., Seidl et al., 2014b; Millar and Stephenson, 2015). For example, future outbreaks of spruce bark beetle may start to affect forests at high elevations that are currently too cold to support climate-sensitive beetle populations. Increasing natural disturbances, coupled with reduced land use (Bebi et al., 2017; Vacchiano et al., 2017) likely will increase coarse woody debris and structural heterogeneity, with cascading effects on biodiversity, edaphic conditions, and biogeochemical cycles. Increased heterogeneity across a range of spatial scales may also translate to disturbance-mediated resilience of forest landscapes (see Thom et al., 2017). At the same time, increased size, frequency, or severity of forest disturbance could eventually present a challenge for the provisioning of important ecosystem services, such as timber production (Thom and Seidl, 2017). Furthermore, if severe disturbances will become large relative to the size of the affected forest, they will be more likely to compromise regeneration, biodiversity, and other ecological functions and services – possibly for long periods of time after the actual disturbance event.

As disturbances increase in frequency, size, and severity, the probability that individual forest stands will be affected by multiple disturbances becomes greater and interactions with linked effects (in which one disturbance changes the likelihood of subsequent disturbances) or compounded effects (in which an ecosystem is affected by cumulative and potentially nonlinear effects of two or more interacting disturbances) may lead to unexpected consequences (e.g., Buma, 2015; Kulakowski and Veblen, 2015). Research in Europe has already shown that wind disturbances can increase the risk of subsequent outbreaks of bark beetles (Schroeder and Lindelöw, 2002), especially during extreme heat-waves, such as the one that followed the 1999 Lothar wind storm (Stadelmann et al., 2013). As climate continues to warm, these links between wind and beetle disturbances may tighten as postwind-throw conditions become more favorable for development of beetle populations (Seidl and Rammer, 2017). Indeed, outbreaks may already be more likely to follow wind disturbances in forests on warmer aspects (Holeksa et al., 2017). Additionally, changing fuel loads and fuel continuity created by other disturbances may alter fire regimes in some European forests, as they have in North America and elsewhere (e.g., Kulakowski and Veblen, 2007). Such disturbance interactions are likely to become increasingly important in shaping the future structure, composition, and dynamics of European mountain forests. Understanding these interactions is thus an important goal for new research.

6 Learning to coexist with natural forest disturbances in Europe

The ecological benefits of disturbances are well known (e.g., DellaSala et al., 2006; Stephens et al., 2013). For example, wind throw and insect outbreaks increase dead wood

Europe PMC Funders Author Manuscripts

and light availability and, as a consequence, increase the abundance and diversity of many insect, plant, bird, and mammal species (Thom et al., 2017; Thorn et al., 2017). Disturbances also introduce structural complexity in regions where long and intensive land use has homogenized landscapes and reduced the extent of structurally complex old-growth forests. The role of natural disturbances in restoration has long been recognized in many different ecosystems (Angelstam, 1998; Turner et al., 2003; Noss et al., 2006). Restoration activities to create old-growth conditions frequently involve felling and girdling trees to create snags – mimicking some of the effects of natural disturbances (Halme et al., 2013; Seibold et al., 2015). Selective post-disturbance logging (Priewasser et al., 2013) can maintain some ecologically important structural characteristics, however, soil compaction, soil nutrients, coarse woody debris, structural diversity, biological legacies, amount of surviving post-disturbance regeneration, and establishment of new post-disturbance regeneration are substantially different in most forests that have been clear-cut or logged following natural disturbance compared with forests that have been affected only by natural disturbance (Lindenmayer and Noss, 2006; Lindenmayer et al., 2008). Therefore, post-disturbance management should weigh the economic benefits of timber production versus the ecological benefits of disturbance-created complexity (Lindenmayer et al., 2008).

Although disturbances have become larger, more frequent, or more severe across Europe as a result of recent changes in land use and climate (Schelhaas et al., 2003; Seidl et al., 2011), they do not, in and of themselves, threaten forest persistence. Disturbances can, however, pose a risk to human populations and challenge forest management. For example, some ecosystem services such as timber production and natural hazard mitigation can be affected negatively by natural disturbances (Thom and Seidl, 2017; Vacchiano et al., 2016). Furthermore, potential risk to human populations associated with natural disturbances are intensified by urban expansion into forested areas as well as forest expansion into urban areas. Consequently, in spite of advances in the fields of ecology and forestry, there is strong legal and social pressure to continue to suppress disturbances and control the natural dynamics of disturbed forests (see e.g., Fares et al., 2015). This command-and control approach to forest management will become increasingly difficult to implement in the future as disturbances increase in size, frequency, and severity. This suggests that an intensified conversation about how societies can coexist with disturbances is needed in Europe’s mountain forests (see e.g., Moritz et al., 2014).

Despite centuries of production forestry in Europe, efforts to eradicate natural disturbance from the landscape have not succeed (cf. Table 1). Working with, rather than against, natural processes in managing forests is of paramount importance, especially in light of projected changes in climate. Given the inevitability of disturbances in forest ecosystems, the relatively remote nature of many mountain forests, and the ecological benefits of disturbances, a key question is whether it is feasible to allow disturbances in some European mountain forests to operate as natural ecological processes and if so, how to optimize their ecological benefit while protecting human safety and well-being and maintaining other desired ecosystem services.

Approaches to forest management vary in intensity from passive management to intensive agro-forestry timber production (Duncker et al., 2012). Forest management needs to balance

Europe PMC Funders Author Manuscripts

promoting natural processes while meeting societal needs for timber, fiber, and other raw materials (Kuuluvainen and Grenfell, 2012). In Europe, recent policy decisions promote emergence of a bioeconomy (EC, 2012; Pülzl et al., 2014), aimed at development of more sustainable societies while concurrently increasing the demands on local natural resources. But in other forests, the objectives of passive management center on allowing natural processes to shape forest dynamics without intensive intervention (Duncker et al., 2012). This approach maintains ecologically valuable habitats and biodiversity, which, in turn, provide a reference for close-to-nature silviculture (e.g., Brang et al., 2014). Passive management schemes require an understanding of ecosystem variability in order to define acceptable limits of change. It is important to identify areas where letting natural processes shape forest ecosystems is compatible with other desired ecosystem services (e.g., Vacchiano et al., 2016). Studies such as those in this *Special Issue* present important information on forest variability and disturbance ecology from which baselines for management strategies may be developed. Although passive management of all disturbed forests is neither feasible nor desirable, allowing disturbances, even large ones, to shape some European mountain forest ecosystems may promote ecological resilience in the face of climatic and environmental change. Finally, acceptance and appreciation of natural disturbances by the general public, especially in the tightly couple human-natural systems of Europe, is critical for land managers and policy makers to maintain forests in more natural states.

7 Conclusions

The articles in this *Special Issue*, along with other studies that highlight long-term variability of disturbance regimes in Europe, help contextualize recent trends of increasing natural disturbance. Without such information, it is difficult to determine whether recent disturbances are unprecedented events that may threaten the persistence of forests. Although limited information is available on long-term natural disturbance regimes in European mountain forest ecosystems, it is clear that natural disturbances, especially wind throw, insect outbreaks, avalanches, and fires have long been important for the dynamics of these forests and are normal components of these systems. In and of themselves, these disturbances, as long as they are within a range of size, severity, and frequency to which ecosystems are adapted (i.e., within a range that shaped these or similar forests over past centuries), do not threaten forests, but rather promote heterogeneity across multiple spatial scales from the individual tree to entire landscapes, which in turn promotes ecological resilience across spatial and temporal scales. Disturbances kill trees, not forests.

We maintain that learning from natural processes and retaining a range of natural variation are important goals for ecosystem management. In some areas, containment of natural hazards may be of paramount social or economic importance, requiring management to minimize their impacts. In other areas where goals include both production and conservation, a dynamic view of forests that includes gradual as well as abrupt change, and fine as well as large-scale disturbances provides guiding principles. A shift in management focus from only the stand level to stand, landscape, regional, and continental scales (Lindenmayer et al., 2010) requires cooperation across jurisdictions, including national jurisdictions. As natural disturbance regimes contain both large and small patches, a less rigid and more dynamic approach to managing forests (cf. Nagel et al., 2014) might not only benefit a broad variety of taxa in the context of conservation but also increase flexibility in the provisioning of forest products. Allowing some forests to be shaped by natural processes may meet multiple goals of forest use, even in densely settled and developed countries.

Acknowledgments

For research assistance we thank L. Ramstein and C. Eschmann. D. Kulakowski was supported by a fellowship from the Swiss Federal Institute for Forest, Snow, and Landscape Research (WSL). M. Panayotov acknowledges funding from SNSF Project IZEBZO143109. M. Svoboda was supported by GACR project no. 15-14840S. R. Seidl acknowledges funding from an Austrian Science Fund (FWF) START grant (Y895-B25). C. Whitlock was supported by fellowships from the Oeschger Centre for Climate Change Research and Sigrist Foundation (University of Bern) and Swiss Federal Institute for Forest, Snow, and Landscape Research (WSL).

References

Allen, TFH., Hoekstra, TW. Toward a Unified Ecology. University of Columbia Press; New York: 1992.

Allen CD, Macalady AK, Chenchouni H, Bachelet D, McDowell N, Vennetier M, Kitzberger T, Rigling A, Breshears DD, Hogg ET, Gonzalez P. A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. For Ecol Manage. 2010; 259:660–684.

Angelstam PK. Maintaining and restoring biodiversity in European boreal forests by developing natural disturbance regimes. J Veg Sci. 1998; 9:593–602.

Bebi P, Kulakowski D, Rixen C. Snow avalanche disturbances in forest ecosystems – state of research and implications for management. For Ecol Manage. 2009; 257:1883–1892.

Bebi P, Seidl R, Motta R, Fuhr M, Firm D, Krumm F, Conedera M, Ginzler C, Wohlgemuth T, Kulakowski D. Changes of forest cover and disturbance regimes in the mountain forests of the Alps. For Ecol Manage. 2017; 388:43–56.

Beghin R, Lingua E, Garbarino M, Lonati M, Bovio G, Motta R, Marzano R. Pinus sylvestris forest regeneration under different post-fire restoration practices in the northwestern Italian Alps. Ecol Eng. 2010; 36:1365–1372.

Biggs R, Schlüter M, Biggs D, Bohensky EL, BurnSilver S, Cundill G, Dakos V, Daw TM, Evans LS, Kotschy K, Leitch AM, et al. Toward principles for enhancing the resilience of ecosystem services. Annu Rev Environ Resour. 2012; 37:421–448.

Brang P, Spathelf P, Larsen JB, Bauhus J, Boncčìna A, Chauvin C, Drössler L, García-Güemes C, Heiri C, Kerr G, Lexer MJ, et al. Suitability of close-to-nature silviculture for adapting temperate European forests to climate change. Forestry. 2014; 87:492–503.

Buma B. Disturbance interactions: characterization, prediction, and the potential for cascading effects. Ecosphere. 2015; 6 art.70.

Burrascano S, Keeton WS, Sabatini FM, Blasi C. Commonality and variability in the structural attributes of moist temperate old-growth forests: a global review. For Ecol Manage. 2013; 291:458–479.

Čada V, Morrissey RC, Michalová Z, Bače R, Janda P, Svoboda M. Frequent severe natural disturbances and non-equilibrium landscape dynamics shaped the mountain spruce forest in central Europe. For Ecol Manage. 2016; 363:169–178.

Caldera WJ, Parker D, Stopka CJ, Jiménez-Moreno G, Shumana BN. Medieval warming initiated exceptionally large wildfire outbreaks in the Rocky Mountains. Proc Natl Acad Sci. 2015; 112:13261–13266. [PubMed: 26438834]

Camarero JJ, Gutiérrez E, Fortin MJ. Spatial pattern of subalpine forest-alpine grassland ecotones in the Spanish Central Pyrenees. For Ecol Manage. 2000; 134:1–16.

Carpenter S, Walker B, Anderies JM, Abel N. From metaphor to measurement: resilience of what to what? Ecosystems. 2001; 4:765–781.

Europe PMC Funders Author Manuscripts

Carpenter SR, Bennett EM, Peterson GD. Scenarios for ecosystem services: an overview. Ecol Soc. 2006; 11:29.

Carrière JM, Lainard C, Le Bot C, Robart F. A climatological study of surface freezing precipitation in Europe. Meteorol Appl. 2000; 7:229–238.

Castebrunet H, Eckert N, Giraud G, Durand Y, Morin S. Projected changes of snow conditions and avalanche activity in a warming climate: the French Alps over the 2020–2050 and 2070–2100 periods. Cryosphere. 2014; 8:1673–1697.

Conedera M, Colombaroli D, Whitlock C, Tinner W. Insights about past forest dynamics as a tool or present and future forest management in Switzerland. For Ecol Manage. 2017; 388:100–112.

Cyr D, Gauthier S, Bergeron Y, Carcaillet C. Forest management is driving the eastern North American boreal forest outside its natural range of variability. Front Ecol Environ. 2009; 7:519–524.

Della-Marta PM, Mathis H, Frei C, Liniger MA, Kleinn J, Appenzeller C. The return period of wind storms over Europe. Int J Climatol. 2009; 29:437–459.

DellaSala D, Karr J, Schoennagel T, Perry D, Noss R, Lindenmayer D, Beschta R, Hutto R, Swanson M, Evans J. Post-disturbance logging debate ignores many issues. Science. 2006; 314:51–52. [PubMed: 17023633]

Dobrowolska D. Forest regeneration in northeastern Poland following a catastrophic blowdown. Can J For Res. 2015; 45:1172–1182.

Donat MG, Leckebusch GC, Pinto JG, Ulbrich U. Examination of wind storms over Central Europe with respect to circulation weather types and NAO phases. Int J Climatol. 2010; 30:1289–1300.

Dorren LKA, Berger F, Imeson AC, Maier B, Rey F. Integrity, stability and management of protection forests in the European Alps. For Ecol Manage. 2004; 195:165–176.

Duncan SL, McComb BC, Johnson KN. Integrating ecological and social ranges of variability in conservation of biodiversity: past, present, and future. Ecol Soc. 2010; 15 art.5.

Duncker PS, Barreiro SM, Hengeveld GM, Lind T, Mason WL, Ambrozy S, Spiecker H. Classification of forest management approaches: a new conceptual framework and its applicability to European forestry. Ecol Soc. 2012; 17:51.

EC. Communication from the Commission to the European Parliament, the Council, the European Economic and Social Committee and the Committee of the Regions. Innovating for sustainable growth: a bioeconomy for Europe. European Commission; Brussles: 2012.

Eckert CG, Samis KE, Lougheed SC. Genetic variation across species' geographical ranges: the central-marginal hypothesis and beyond. Mol Ecol. 2008; 17:1170–1188. [PubMed: 18302683]

EEA. Europe's Ecological Backbone: Recognising the True Value of Our Mountains. European Environmental Agency; Copenhagen: 2010.

Fares S, Scarascia-Mugnozza GE, Corona P, Palahí M. Five steps for managing Europe's forests. Nature. 2015; 519:407–409. [PubMed: 25810187]

Firm D, Nagel TA, Diaci J. Disturbance history and dynamics of an old-growth mixed species mountain forest in the Slovenian Alps. For Ecol Manage. 2009; 257:1893–1901.

Folke C, Carpenter S, Walker B, Scheffer M, Elmqvist T, Gunderson L, Holling CS. Regime shifts, resilience, and biodiversity in ecosystem management. Annu Rev Ecol Evol Syst. 2004; 35:557–581.

Gustafson EJ, Shvidenko AZ, Sturtevant BR, Scheller RM. Predicting global change effects on forest biomass and composition in south-central Siberia. Ecol Appl. 2010; 20:700–715. [PubMed: 20437957]

Halme P, Allen KA, Aunins A, Bradshaw RHW, Brumelis G, Čada V, Clear JL, Eriksson A-M, Hannon G, Hyvärinen E, Ikauniece S, et al. Challenges of ecological restoration: lessons from forests in northern Europe. Biol Conserv. 2013; 167:248–256.

Hampe A, Petit RJ. Conserving biodiversity under climate change: the rear edge matters. Ecol Lett. 2005; 8:461–467. [PubMed: 21352449]

Hansen, J., Spiecker, H. Conversion of Norway spruce (Picea abies [L.] Karst.) forests in Europe. Restoration of Boreal and Temperate Forests. Stanturf, JA., Madsen, P., editors. CRC Press; 2004. p. 339-347.

Europe PMC Funders Author Manuscripts

Harvey BJ, Donato DC, Turner MG. High and dry: postfire drought and large stand-replacing burn patches reduce postfire tree regeneration in subalpine forests. Glob Ecol Biogeogr. 2016; 25:655–669.

Hlasny T, Kristek S, Holusa J, Trombik J, Urbancova N. Snow disturbances in secondary Norway spruce forests in Central Europe: regression modeling and its implications for forest management. For Ecol Manage. 2011; 262:2151–2161.

Holeksa J, Jaloviar P, Kucbel S, Saniga M, Svoboda M, Szewczyk J, Szwagrzyk J, Zielonka T, Żywiec M. Models of disturbance driven dynamics in the West Carpathian spruce forests. For Ecol Manage. 2017; 388:79–89.

Holeksa J, Zielonka T, Żywiec M, Fleischer P. Identifying the disturbance history over a large area of larch-spruce mountain forest in Central Europe. For Ecol Manage. 2016; 361:318–327.

Janda P, Bače R, Trotsiuk V, Mikoláš M, Nagel T, Seidel R, Mrhalová H, Morrisey RC, Matějů L, Lábusová J, Kucbel S, et al. The historical disturbance regime of mountain Norway spruce forests in the Western Carpathians and its influence on current forest structure and composition. For Ecol Manage. 2017; 388:67–78.

Janda P, Svoboda M, Bace R, Čada V, Peck JE. Three hundred years of spatio-temporal development in a primary mountain Norway spruce stand in the Bohemian Forest, central Europe. For Ecol Manage. 2014; 330:304–311.

Jarvis D, Kulakowski D. Long-term history and synchrony of mountain pine beetle outbreaks. J Biogeogr. 2015; 42:1029–1039.

Johnstone JF, Allen CD, Franklin JF, Frelich LE, Harvey BJ, Higuera PE, Mack MC, Meentemeyer RK, Metz MR, Perry GLW, Schoennagel T, et al. Changing disturbance regimes, ecological memory, and forest resilience. Front Ecol Environ. 2017 In press.

Jönsson A, Appelberg G, Harding S, Bärring L. Spatio-temporal impact of climate change on the activity and voltinism of the spruce bark beetle, Ips typographus. Glob Change Biol. 2009; 15:486–499.

Klimo E, Hager H, Kulhavý J. Spruce monocultures in Central Europe – problems and perspectives. European Forest Institute Proceedings. 2000; 33

Kaplan JO, Krumhardt KM, Zimmermann N. The prehistoric and preindustrial deforestation of Europe. Quaternary Sci Rev. 2009; 28:3016–3034.

Kulakowski D, Bebi P, Rixen C. The interacting effects of land use change, climate change, and suppression of disturbances on landscape forest structure in the Swiss Alps. Oikos. 2011; 120:216–225.

Kulakowski D, Matthews C, Jarvis D, Veblen TT. Compounded disturbances in subalpine forests in western Colorado favor future dominance by quaking aspen (*Populus tremuloides*). J Veg Sci. 2013; 24:168–176.

Kulakowski D, Rixen C, Bebi P. Changes in forest structure and in the relative importance of climatic stress as a result of suppression of avalanche disturbances. For Ecol Manage. 2006; 223:66–74.

Kulakowski D, Veblen TT. Influences of fire history and topography on the pattern of a severe wind blowdown in a Colorado subalpine forest. J Ecol. 2002; 90:806–819.

Kulakowski D, Veblen TT. Effect of prior disturbances on the extent and severity of wildfire in Colorado subalpine forests. Ecology. 2007; 88:759–769. [PubMed: 17503603]

Kulakowski, D., Veblen, TT. Bark beetles and high-severity fires in rocky mountain subalpine forests. Mixed-High Severity Fires: Ecosystem Processes and Biodiversity. DellaSalla, D., Hanson, C., editors. Elsevier; San Francisco, CA: 2015. p. 149-174.409 pages

Kulakowski D, Veblen TT, Bebi P. Effects of fire and spruce beetle outbreak legacies on the disturbance regime of a subalpine forest in Colorado. J Biogeogr. 2003; 30:1445–1456.

Kuuluvainen T, Grenfell R. Natural disturbance emulation in boreal forest ecosystem management – theories, strategies, and a comparison with conventional even-aged management. Can J For Res. 2012; 42:1185–1203.

Kuuluvainen T, Hofgaard A, Aakala T, Jonsson BG. North Fennoscandian mountain forests: history, composition, disturbance dynamics and the unpredictable future. For Ecol Manage. 2017; 388:90–99.

Kräuchi N, Brang P, Schönenberger W. Forests of mountainous regions: gaps in knowledge and research needs. For Ecol Manage. 2000; 132:73–82.

Landres PR, Morgand P, Swanson FJ. Overview of the use of natural variability concepts in managing ecological systems. Ecol Appl. 1999; 9:1179–1188.

Lindenmayer, DB., Burton, PJ., Franklin, JF. Salvage Logging and Its Ecological Consequences. Island Press; Washington: 2008.

Lindenmayer, DB., Franklin, JF. Conserving Forest Biodiversity. A Comprehensive Multiscaled Approach. Island Press; Washington DC, USA: 2002.

Lindenmayer DB, Likens GE, Franklin JF. Rapid responses to facilitate ecological discoveries from major disturbances. Front Ecol Environ. 2010; 8:527–532. DOI: 10.1890/090184

Lindenmayer DB, Noss RF. Salvage logging, ecosystem processes, and biodiversity conservation. Conserv Biol. 2006; 20:949–958. [PubMed: 16922212]

Long JN. Emulating natural disturbance regimes as a basis for forest management: a North American view. For Ecol Manage. 2009; 257:1868–1873.

Loreau M, Mouquet N, Gonzalez A. Biodiversity as spatial insurance in heterogeneous landscapes. Proc Natl Acad Sci. 2003; 100:12765–12770. [PubMed: 14569008]

Meeus J. Pan-European landscapes. Landscape Urban Plan. 1995; 31:57–79.

Millar CI, Stephenson NL. Temperate forest health in an era of emerging megadisturbance. Science. 2015; 349:823–826. [PubMed: 26293954]

Moritz MA, Batllori E, Bradstock RA, Gill AM, Handmer J, Hessburg PF, Leonard J, McCaffrey S, Odion DC, Schoennagel T, Syphard AD. Learning to Coexist with Wildfire. Nature. 2014; doi: 10.1038/nature13946

Motta R, Berretti R, Castagneri D, Dukić V, Garbarino M, Govedar Z, Lingua E, Maunaga Z, Meloni F. Toward a definition of the range of variability of central European mixed Fagus–Abies–Picea forests: the nearly steady-state forest of Lom (Bosnia and Herzegovina). Can J For Res. 2011; 41:1871–1884.

Motta R, Garbarino M, Berretti R, Meloni F, Nosenzo A, Vacchiano G. Development of old-growth characteristics in uneven-aged forests of the Italian Alps. Eur J Forest Res. 2015; 134:19–31.

Navarro LM, Pereira HM. Rewilding abandoned landscapes in Europe. Ecosystems. 2012; 15:900–912.

Müller F, Bergmann M, Dannowski R, Dippner JW, Gnauck A, Haase P, Jochimsen MC, Kasprzak P, Kröncke I, Kümmerlin R, Küster M, et al. Assessing resilience in long-term ecological data sets. Ecol Ind. 2016; 65:10–43.

Nagel TA, Firm D, Rozenbergar D, Kobal M. Patterns and drivers of ice storm damage in temperate forests of Central Europe. Eur J Forest Res. 2016; 135:519–530.

Nagel TA, Mikac S, Dolinar M, Klopcic M, Keren S, Svoboda M, Diaci J, Boncina A. The natural disturbance regime in forests of the Dinaric Mountains: a synthesis of evidence. For Ecol Manage. 2017; 388:29–42.

Nagel TA, Svoboda M, Kobal M. Disturbance, life history traits, and dynamics in an old-growth forest landscape of southeastern Europe. Ecol Appl. 2014; 24:663–679. [PubMed: 24988767]

Naudts K, Chen Y, McGrath MJ, Ryder J, Valade A, Otto J, Luyssaert S. Europe's forest management did not mitigate climate warming. Science. 2016; 351:597–601. [PubMed: 26912701]

Navarro, ML., Proença, V., Kaplan, JO., Pereira, MH. Maintaining disturbance-dependent habitats. Rewilding European Landscapes. Pereira, MH., Navarro, ML., editors. Springer International Publishing; Cham: 2015. p. 143-167.

Netherer S, Schopf A. Potential effects of climate change on insect herbivores in European forests—general aspects and the pine processionary moth as specific example. For Ecol Manage. 2010; 259:831–838.

Nonaka E, Spies TA. Historical range of variability in landscape structure: a simulation study in Oregon, USA. Ecol Appl. 2005; 15:1727–1746.

Noss RF, Beier P, Covington WW, Grumbine RE, Lindenmayer DB, Prather JW, Schmiegelow F, Sisk TD, Vosick DJ. Recommendations for integrating restoration ecology and conservation biology in ponderosa pine forests of the southwestern United States. Restor Ecol. 2006; 14:4–10. DOI: 10.10.1111/j.1526-100X.2006.00099.x

Oliver CD. Forest development in North America following major disturbances. For Ecol Manage. 1981; 3:153–168.

Palmer MW. Variation in species richness – towards a unification of hypotheses. Geobotanica. 1994; 29:511–530.

Panayotov M, Kulakowski D, Laranjeiro Dos Santos L, Bebi P. Wind disturbances shape old Norway spruce forests in Bulgaria. For Ecol Manage. 2011; 262:470–481.

Panayotov M, Bebi P, Tsvetanov N, Alexandrov N, Laranjeiro L, Kulakowski D. The disturbance regime of Norway spruce forests in Bulgaria. Can J For Res. 2015; 45:1143–1153.

Panayotov M, Gogushev G, Tsavkov E, Vassileva P, Tsvetanov N, Kulakowski D, Bebi P. Abiotic disturbances in Bulgarian mountain coniferous forests – an overview. For Ecol and Manage. 2017; 388:13–28.

Papworth SK, Rist J, Coad L, Milner-Gulland EJ. Evidence for shifting baseline syndrome in conservation. Conserv Lett. 2009; 2:93–100.

Perez-Sanz A, Gonzalez-Samperiz P, Moreno A, Valero-Garces B, Gil-Romera G, Rieradevall M, et al. Holocene climate variability, vegetation dynamics and fire regime in the central Pyrenees: the Basa de la Mora sequence (NE Spain). Quatern Sci Rev. 2013; 73:149–169.

Peterson GD. Contagious disturbance, ecological memory, and the emergence of landscape pattern. Ecosystems. 2002; 5:329–338.

Piovesan G, Di Filippo A, Alessandrini A, Biondi F, Schirone B. Structure, dynamics and dendroecology of an old-growth Fagus forest in the Apennines. J Veg Sci. 2005; 16:13–28.

Priewasser K, Brang P, Bachofen H, Bugmann H, Wohlgemuth T. Impacts of salvage-logging on the status of deadwood after windthrow in Swiss forests. Eur J For Res. 2013; 132:231–240.

Pryor SC, Barthelmie RJ, Clausen NE, Drews M, MacKellar N, Kjellström E. Analyses of possible changes in intense and extreme wind speeds over northern Europe under climate change scenarios. Clim Dyn. 2012; 38:189–208.

Pülzl H, Kleinschmit D, Arts B. Bioeconomy – an emerging meta-discourse affecting forest discourses? Scand J For Res. 2014; 29:386–393.

Radeloff VC, Williams JW, Bateman BL, Burke KD, Sarah CK, Childress ES, Cromwell KJ, Gratton C, Hasley AO, Kraemer BM, Latzka AW, et al. The rise of novelty in ecosystems. Ecol Appl. 2015; 25:2051–2068. [PubMed: 26910939]

Reyer CP, Brouwers N, Rammig A, Brook BW, Epila J, Grant RF, Holmgren M, Langerwisch F, Leuzinger S, Lucht W, Medlyn B. Forest resilience and tipping points at different spatio-temporal scales: approaches and challenges. J Ecol. 2015; 103:5–15.

Rigling A, Bigler C, Eilmann B, Feldmeyer-Christe E, Gimmi U, Ginzler C, Graf U, Mayer P, Vacchiano G, Weber P, Wohlgemuth T. Driving factors of a vegetation shift from Scots pine to pubescent oak in dry Alpine forests. Glob Change Biol. 2013; 19:229–240.

Rixen C, Haag S, Kulakowski D, Bebi P. Natural disturbance modulates plant diversity and species composition in subalpine forest. J Veg Sci. 2007; 18:735–742.

Rudel TK, Coomes OT, Moran E, Achard F, Angelsen A, Xu J, Lambin E. Forest transitions: towards a global understanding of land use change. Global Environ Change. 2005; 15:23–31.

Scheffer M, Barrett S, Carpenter SR, Folke C, Green AJ, Holmgren M, Hughes TP, Kosten S, van de Leemput IA, Nepstad DC, van Nes EH, et al. Creating a safe operating space for iconic ecosystems. Science. 2015; 347:1317–1319. [PubMed: 25792318]

Schelhaas MJ, Nabuurs G, Schuck A. Natural disturbances in the European forests in the 19th and 20th centuries. Glob Change Biol. 2003; 9:1620–1633.

Schneider A, Friedl MA, McIver DK, Woodcock CE. Mapping urban areas by fusing multiple sources of coarse resolution remotely sensed data. Photogramm Eng Remote Sens. 2003; 69:1377–1386.

Schroeder LM, Lindelöw Å. Attacks on living spruce trees by the bark beetle Ips typographus (Col. Scolytidae) following a storm-felling: a comparison between stands with and without removal of wind-felled trees. Agric For Entomol. 2002; 4:47–56.

Schönenberger W, Noack A, Thee P. Effect of timber removal from windthrow slopes on the risk of snow avalanches and rockfall. For Ecol Manage. 2005; 213:197–208.

Schütz JP. Silvicultural tools to develop irregular and diverse forest structures. Forestry. 2002; 75:329–337.

Schüepp M, Schiesser HH, Huntrieser H, Scherrer HU, Schmidtke H. The winterstorm “Vivian” of 27 February 1990: about the meteorological development, wind forces and damage situation in the forests of Switzerland. Theor Appl Climatol. 1994; 49:183–200.

Seidl R. The shape of ecosystem management to come: anticipating risks and fostering resilience. Bioscience. 2014; 64:1159–1169. [PubMed: 25729079]

Seidl R, Müller J, Hothorn T, Bässler C, Heurich M, Kautz M. Small beetle, large-scale drivers: how regional and landscape factors affect outbreaks of the European spruce bark beetle. J Appl Ecol. 2016a; 53:530–540.

Seidl R, Rammer W. Climate change amplifies the interactions between wind and bark beetle disturbance in forest landscapes. Landsc Ecol. in press.

Seidl R, Rammer W, Spies TA. Disturbance legacies increase the resilience of forest ecosystem structure, composition, and functioning. Ecol Appl. 2014a; 24:2063–2077. [PubMed: 27053913]

Seidl R, Schelhaas M-J, Lexer MJ. Unraveling the drivers of intensifying forest disturbance regimes in Europe. Glob Change Biol. 2011; 17:2842–2852.

Seidl R, Schelhaas M-J, Rammer W, Verkerk PJ. Increasing forest disturbances in Europe and their impact on carbon storage. Nat Clim Change. 2014b; 4:806–810.

Seidl R, Spies TA, Peterson DL, Stephens SL, Hicke JA. Searching for resilience: addressing the impacts of changing disturbance regimes on forest ecosystem services. J Appl Ecol. 2016b; 53:120–129. [PubMed: 26966320]

Seidl R, Vigl F, Rössler G, Neumann M, Rammer W. Assessing the resilience of Norway spruce forests through a model-based reanalysis of thinning trials. For Ecol Manage. 2017; 388:3–12.

Seibold S, Bassler C, Brandl R, Gossner MM, Thorn S, Ulyshen MD, Muller J. Experimental studies of dead-wood biodiversity – a review identifying global gaps in knowledge. Biol Conserv. 2015; 191:139–149.

Silva Pedro M, Rammer W, Seidl R. A disturbance-induced increase in tree species diversity facilitates forest productivity. Landscape Ecol. 2016; 31:989–1004.

Stadelmann G, Bugmann H, Wermelinger B, Meier F, Bigler C. A predictive framework to assess spatio-temporal variability of infestations by the European spruce bark beetle. Ecography. 2013; 36:1208–1217.

Stephens SL, Agee JK, Fulé PZ, North MP, Romme WH, Swetnam TW, Turner MG. Managing forests and fire in changing climates. Science. 2013; 342:41–42. [PubMed: 24092714]

Storaunet K, Rolstad J, Toeneiet M, Blanck Y-L. Strong anthropogenic signals in historic forest fire regime: a detailed spatiotemporal case study from south-central Norway. Can J For Res. 2013; 43:836–845.

Svoboda M, Janda P, Bace R, Fraver S, Nagel TA, Rejzek J, Mikolas M, Douda J, Boublik K, Samonil P, Čada V, et al. Landscape-level variability in historical disturbance in primary Picea abies mountain forests of the Eastern Carpathians, Romania. J Veg Sci. 2014; 25:386–401.

Svoboda M, Janda P, Nagel TA, Fraver S, Rejzek J, Bace R. Disturbance history of an old-growth sub-alpine Picea abies stand in the Bohemian Forest, Czech Republic. J Veg Sci. 2012; 23:86–97.

Teich M, Marty C, Gollut C, Grêt-Regamey A, Bebi P. Snow and weather conditions associated with avalanche releases in forests: rare situations with decreasing trends during the last 41 years. Cold Reg Sci Technol. 2012; 83–84:77–88.

Thom D, Rammer W, Dirnböck T, Müller J, Kobler J, Katzensteiner K, Helm N, Seidl R. The impacts of climate change and disturbance on spatiotemporal trajectories of biodiversity in a temperate forest landscape. J Appl Ecol. 2017; in press. doi: 10.1111/1365-2664.12644

Thom D, Seidl R. Natural disturbance impacts on ecosystem services and biodiversity in temperate and boreal forests. Biol Rev. 2017; in press. doi: 10.1111/brv.12193

Thom D, Seidl R, Steyrer G, Krehan H, Formayer H. Slow and fast drivers of the natural disturbance regime in Central European forest ecosystems. For Ecol Manage. 2013; 307:293–302.

Thorn S, Bässler C, Svoboda M, Müller J. Effects of natural disturbances and salvage logging on biodiversity – Lessons from the Bohemian Forest. For Ecol Manage. 2017; 388:113–119.

Tinker DB, Romme WH, Despain DG. Historic range of variability in landscape structure in subalpine forests of the greater Yellowstone area, USA. Landscape Ecol. 2003; 18:427–439.

Turner MG, Donato DC, Romme WH. Consequences of spatial heterogeneity for ecosystem services in changing forest landscapes: priorities for future research. Landscape Ecol. 2012; 28:1081–1097.

Turner MG, Romme WH, Tinker DB. Surprises and lessons from the 1988 Yellowstone fires. Front Ecol Environ. 2003; 1:351–358. DOI: 10.1890/1540-9295(2003)001[0351:SALFTY]2.0.CO;2

Turner MG, Whitby TG, Tinker DB, Romme WH. Twenty-four years after the Yellowstone Fires: are postfire lodgepole pine stands converging in structure and function? Ecology. 2016; 97(5):1260–1273. [PubMed: 27349102]

Usbeck T, Wohlgemuth T, Dobbertin M, Pfister C, Bürgi A, Dobbertin M. Increasing storm damage to forests in Switzerland from 1858 to 2007. Agric For Meteorol. 2010a; 150:47–55.

Usbeck T, Wohlgemuth T, Pfister C, Volz R, Beniston M, Dobbertin M. Wind speed measurements and forest damage in Canton Zurich (Central Europe) from 1891 to winter 2007. Int J Climatol. 2010b; 30:347–358.

Ulbrich U, Christoph M. A shift of the NAO and increasing storm track activity over Europe due to anthropogenic greenhouse gas forcing. Clim Dyn. 1999; 15:551–559.

Vacchiano G, Berretti R, Borgogno Mondino E, Meloni F, Motta R. Assessing the effect of disturbances on the functionality of direct protection forests. Mt Res Dev. 2016; 36:41–55. DOI: 10.1659/MRD-JOURNAL-D-15-00075

Vacchiano G, Garbarino M, Lingua E, Motta R. Ecology of mountain forest ecosystems in the Italian Apennines. For Ecol Manage. 2017; 388:57–66.

Vacchiano G, Maggioni M, Perseghin G, Motta R. Effect of avalanche frequency on forest ecosystem services in a spruce–fir mountain forest. Cold Reg Sci Technol. 2015; 115:9–21.

Vacchiano G, Stanchi S, Marinari G, Ascoli D, Zanini E, Motta R. Fire severity, residuals and soil legacies affect regeneration of Scots pine in the Southern Alps. Sci Total Environ. 2014; 472:778–788. [PubMed: 24334000]

Wallentin C, Nilsson U. Storm and snow damage in a Norway spruce thinning experiment in southern Sweden. Forestry. 2014; 87:229–238.

Whitlock C, Mcwethy DB, Tepley AJ, Veblen TT, Holz A, Mcglone MS, Perry GLW, Wilmshurst JM, Wood SW. Past and present vulnerability of closed-canopy temperate forests to altered fire regimes: a comparison of the Pacific Northwest, New Zealand, and Patagonia. Bioscience. 2015; 65:151–163.

Wild J, Kopecky M, Svoboda M, Zenahlikova J, Edwards-Jonasova M, Herben T. Spatial patterns with memory: tree regeneration after stand-replacing disturbance in *Picea abies* mountain forests. J Veg Sci. 2014; 25:1327–1340.

Wohlgemuth T, Bürgi M, Scheidegger C, Schütz M. Dominance reduction of species through disturbance – a proposed management principle for central European forests. For Ecol Manage. 2002; 166:1–15.

Zeppenfeld T, Svoboda M, DeRose RJ, Heurich M, Mueller J, Cizkova P, Stary M, Bace R, Donato DC. Response of mountain *Picea abies* forests to stand-replacing bark beetle outbreaks: neighbourhood effects lead to self-replacement. J Appl Ecol. 2015; 52:1402–1411.

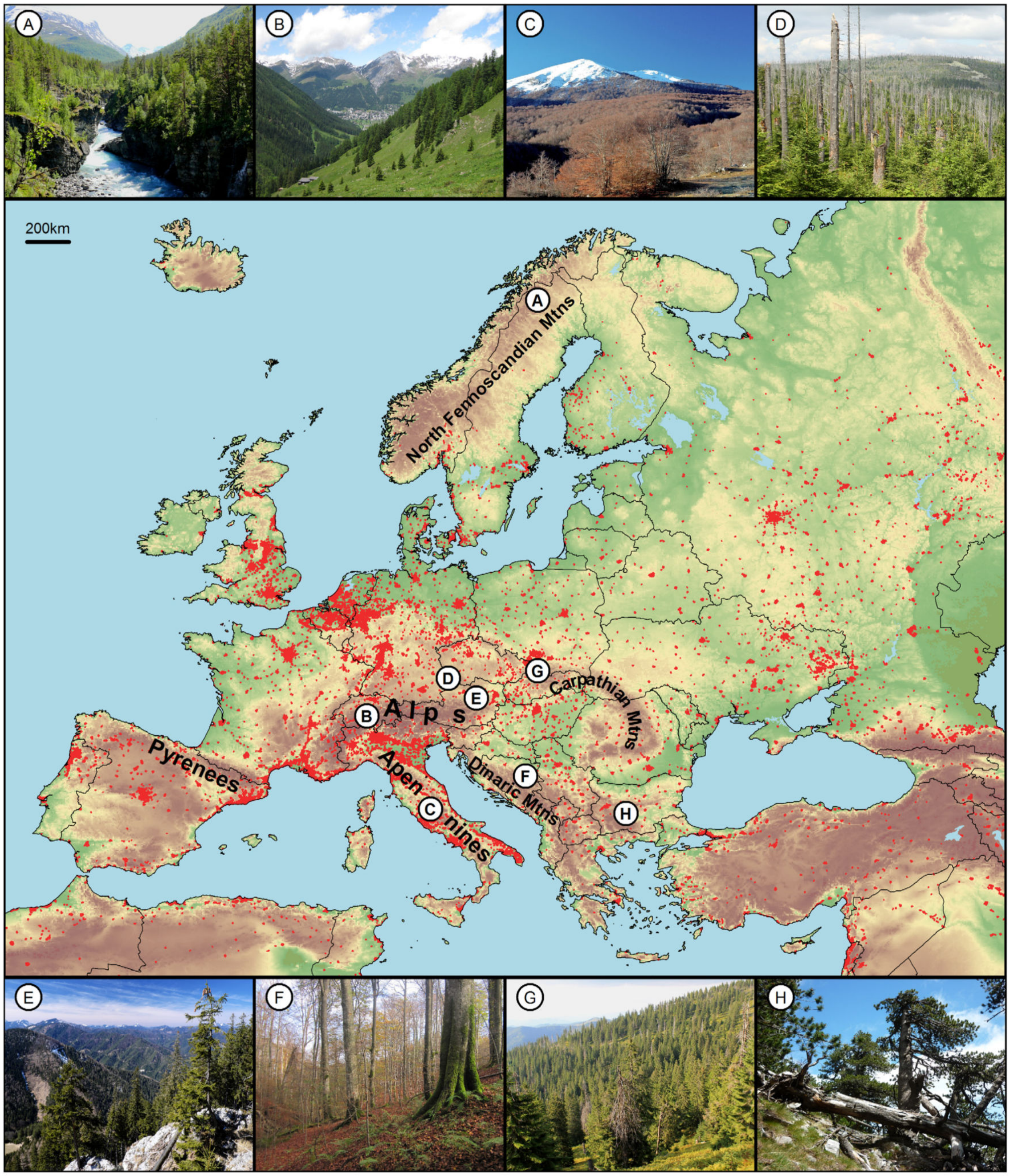

Fig. 1.

Location of major mountain ranges in Europe and general study regions of (A) Kuuluvainen et al. (2017), (B) Bebi et al. (2017) and Conedera et al. (2017), (C) Vacchiano et al. (2017), (D) Thorn et al. (2017), (E) Seidl et al. (2017), (F) Nagel et al. (2017), (G) Holeksa et al. (2017) and Janda et al. (2017), and (H) Panayotov et al. (2017). Urban areas (Schneider et al., 2003) are depicted in red.

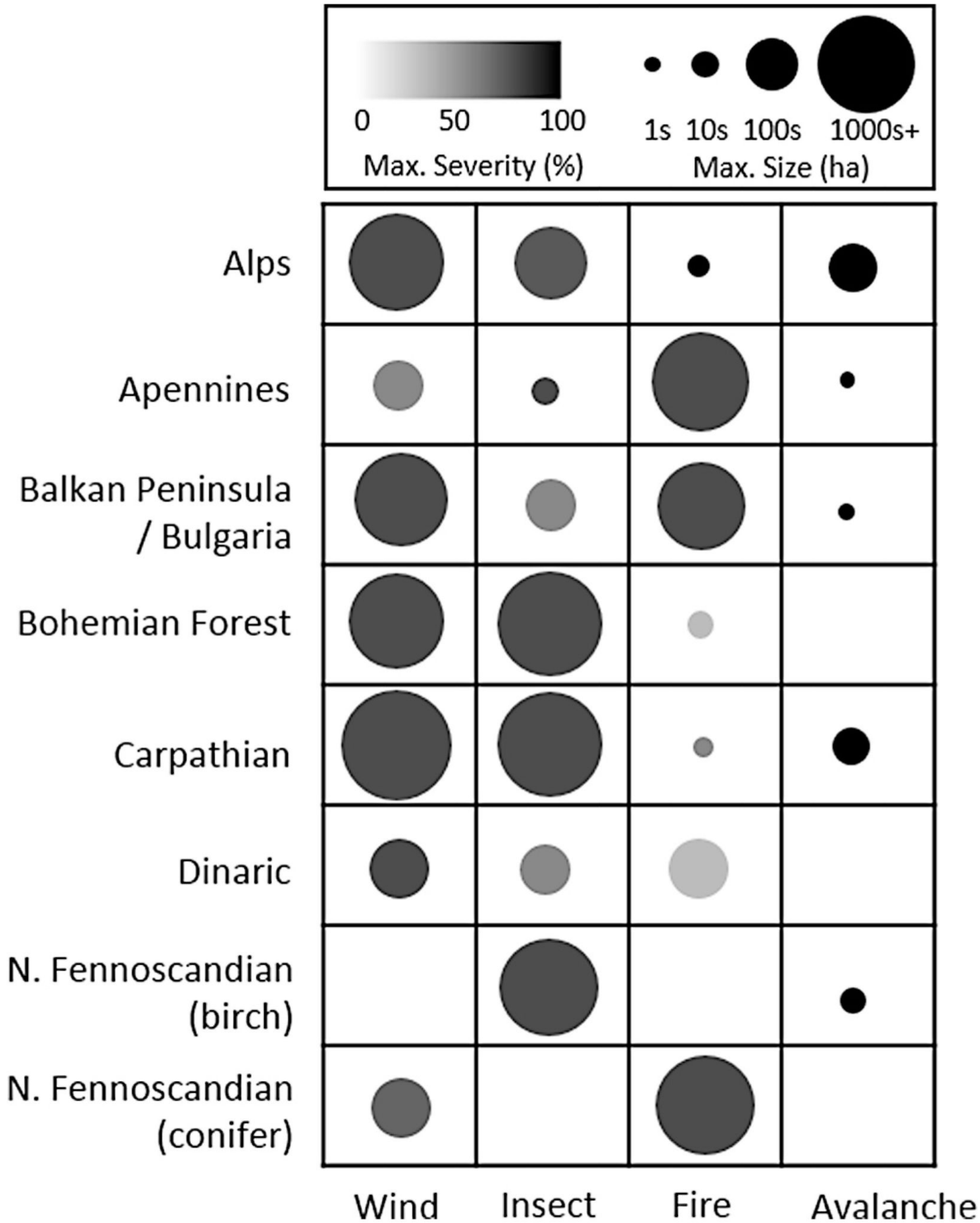

Fig. 2.

Approximate maximum size (total area affected by individual events) and maximum severity (percent of trees killed) of characteristic disturbance regimes across regions for the past c. two centuries. As even large, high-severity disturbances are often patchy and heterogeneous, size represents the cumulative area disturbed by individual events, rather than the size of patches. Frequency is theoretically inversely proportional to disturbance severity. Estimates for the Alps are based on Bebi et al. (2017), Bavaria Forest on Thorn et al. (2017), Balkan Peninsula/Bulgaria on Panayotov et al. (2017), Apennines on Vacchiano et al. (2017), Carpathian Mountains on Holeksa et al. (2017) and on Janda et al. (2017), Dinaric Mountains on Nagel et al. (2017), and North Fennoscandia on Kuuluvainen et al. (2017).

Europe PMC Funders Author Manuscripts

Europe PMC Funders Author Manuscripts

Table 1

Conceptual summary of relationships among forest area, disturbance regimes, land use, and direct effects of climate across regions, forest types, and time periods. Forest area is categorized as increasing (↑), equilibrium (→), or decreasing (↓). Qualitative relative importance of disturbance types, land use, and direct effects of climate on forest dynamics across time and regions are indicated as unknown or minimal (−), minor (+), moderate (++), and major (+++). SI indicates the chapter in this Special Issue on European mountain forests that focuses on respective regions.

Region	SI	Forest type	Time period	Forest area	Wind disturbances	Insect disturbances	Fire disturbances	Avalanche disturbances	Snow & ice disturbances	Land use	Direct effects of climate
Central Balkans	Panayotov et al.	Norway spruce	1850–present	→	+++	++	++	+	−	++	++
Central Balkans	Panayotov et al.	Scots pine	1850–present	↑	++	++	+++	−	++	+++	++
Central Balkans	Panayotov et al.	Black pine	1850–present	↑		++	+++	−	+	+++	++
Central Balkans	Panayotov et al.	Subalpine Balkan pines	1850–present	→	+	−	++	++	−	+	+
Dinaric Mountains	Nagel et al.	Beech; fir-beech	1900	↑	++	++	+	+	++	++	++
Apennines	Vacchiano et al.	Beech	1870–present	↑	++	+	++	++	+	+++	+
Apennines	Vacchiano et al.	Beech	1000–1870	↓	++	+	+	++	+	+++	+
Apennines	Vacchiano et al.	Beech	4000 BCE–1000 CE	↑	++	+	+	++	+	++	++
Apennines	Vacchiano et al.	Fir	5000 BCE–present	↓	+++	+	+	+	++	++	++
Apennines	Vacchiano et al.	Fir	18000 BCE–5000 BCE	↑	+++	+	+	+	++	+	+++
Apennines	Vacchiano et al.	Chestnut	1000–present	↑	+	++	+++	+	+	+++	+
Apennines	Vacchiano et al.	Black and dwarf pine	1870–present	↑	+	++	+++	++	+	++	++
Apennines	Vacchiano et al.	Black and dwarf pine	500–1870	→	+	++	+++	++	+	+	++
Apennines	Vacchiano et al.	Black and dwarf pine	500 BCE–500 CE	↓	+	++	+++	++	+	+++	+
Northern Alps	Bebi et al.	Norway spruce dominated	1850–present	↑	+++	++	+	++	+	++	++
Northern Alps	Bebi et al.	Norway spruce dominated	Pre-1850	↓	++	+	++	+++	+	+++	+
Southern Alps	Bebi et al.	Norway spruce dominated	1850–present	↑	+	+	+	++	+	++	++
Southern Alps	Bebi et al.	Norway spruce dominated	Pre-1850	↓	+	+	+++	+++	+	+++	+
Northern Alps	Bebi et al.	Beech-dominated	1850–present	↑	++	−	−	+	++	++	++
Northern Alps	Bebi et al.	Beech-dominated	Pre-1850	↓	+	−	+	++	++	+++	+
Southern Alps	Bebi et al.	Beech-dominated	1850–present	↑	+	+	++	+	++	+++	+
Southern Alps	Bebi et al.	Beech-dominated	Pre-1850	↓	+	+	++	++	++	+++	+
West Carpathians	Holeksa et al.	Norway spruce	1850–present	→	+++	+++	+	+	+	+	++
West Carpathians	Holeksa et al.	Norway spruce	Pre-1850	→	+++	++	+	+	+	++	++
Carpathians	Janda et al.	Norway spruce	1850–present	↑	+++	+++	+	++	+	−	++
Carpathians	Janda et al.	Beech dominated forests	1850–present	↑	++	−	+	+	+	−	++

Europe PMC Funders Author Manuscripts

Region	SI	Forest type	Time period	Forest area	Wind disturbances	Insect disturbances	Fire disturbances	Avalanche disturbances	Snow & ice disturbances	Land use	Direct effects of climate
Carpathians	Janda et al.	Norway spruce	Pre-1850	↓	+++	++	+	++	+	−	+
Carpathians	Janda et al.	Beech dominated forests	Pre-1850	↓	++	−	+	+	+	−	+
Bohemian Forest	Thorn et al.	Norway Spruce, mixed montane	1800	→	++	+++	+	−	+	++	++
North Fennoscandia	Kuuluvainen et al.	Scots pine	Pre 1850	↓	+	−	+++	−	−	+	++
North Fennoscandia	Kuuluvainen et al.	Scots pine	Post 1850	↑	+	−	+	−	−	+++	+
North Fennoscandia	Kuuluvainen et al.	Norway spruce	Pre 1850	↓	+	−	+	−	+	+	++
North Fennoscandia	Kuuluvainen et al.,	Norway spruce	Post 1850	↑	+	+	−	−	+	+++	+
North Fennoscandia	Kuuluvainen et al.	Mountain birch	Pre 1850	↓	−	+++	−	+	−	++	++
North Fennoscandia	Kuuluvainen et al.	Mountain birch	Post 1850	↑	−	+++	−	+	−	+	++