A walk on the wild side: disturbance ecology, conservation and management of European mountain forest ecosystems

Dominik Kulakowski[1,2*], Rupert Seidl[3], Jan Holeksa[4], Thomas A. Nagel[5], Momchil Panayotov[6], Miroslav Svoboda[7], Simon Thorn[8], Giorgio Vacchiano[9], Cathy Whitlock[10], Thomas Wohlgemuth[11], and Peter Bebi[2]

[1] Graduate School of Geography, Clark University, MA, USA

[2] WSL Institute for Snow and Avalanche Research SLF, Davos, Switzerland

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

[4] Adam Mickiewicz University, Faculty of Biology, Department of Plant Ecology and Environment Protection, Umultowska 89, 61-614 Poznań, Poland

[5] Department of Forestry and Renewable Forest Resources, University of Ljubiljana, Slovenia

[6] Dendrology Department, University of Forestry, 1797 Sofia, Bulgaria

[7] Faculty of Forestry and Wood Sciences, Czech University of Life Sciences, Prague, Czech Republic

[9] Università degli Studi di Torino, DISAFA. Largo Braccini 2, 10095 Grugliasco (TO) Italy

[10] Montana Institute on Ecosystems, Montana State University, Bozeman, MT, USA

[11] Swiss Federal Institute for Forest, Snow and Landscape Research WSL, Birmensdorf, Switzerland

[*] corresponding author: dkulakowski@clarku.edu

ABSTRACT:

Mountain forests are among the most important ecosystems in Europe as they support numerous ecological, hydrological, climatic, social, and economic functions. They are also unique in being relatively natural ecosystems consisting of long-lived species in an otherwise densely populated human landscape. Despite this, many of these forests have been intensively managed for centuries, which has eclipsed evidence of natural dynamics, 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 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 the broader discussion 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 frequency. Although these disturbances may kill many trees, the forests themselves have not been threatened. The relative importance of disturbances, land use, and climate change for ecosystem dynamics varies and has varied 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 increases in forest area and biomass along with continued warming in the future are likely to continue to promote forest disturbances. Episodic disturbances may foster ecosystem adaptation to the effects of ongoing and future climatic change. Increasing disturbances, along with likely continuing trends of reduced intensity land use, will promote further increases in coarse woody debris, with cascading effects on biodiversity, edaphic conditions, and biogeochemical cycles, and can increase heterogeneity across a range of spatial scales. Together, this may translate to disturbance-mediated resilience of forest landscapes and increased biodiversity across a range of spatial scales, as long as climate and disturbance regimes remain within the tolerance of relevant species. Allowing some forests to be shaped by natural processes may thus 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 change 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, abandonment of other high-intensity land uses (Navarro and Pereira, 2012), and establishment of protected areas forests (Motta et al., 2015), which together have contributed to an expansion of forest area (Rudel et al., 2009; Naudts et al., 2016). This recent expansion of forest has coincided with an increase in 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 increasingly 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 processes that operate over short periods. 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 are not compromised (Meeus, 1995; Kräuchi et al., 2000). Consequently, natural disturbances and other natural processes have been increasingly allowed to shape forest structure and dynamics in some forests, but in most others disturbances continue to be intensively managed (Duncker et al., 2012).

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 commonalities, differences, 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 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 European mountain forest ecosystems, discuss future scenarios of an emerging new ecological reality of altered climate and 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 to the more developed matrix within which they are found (EEA, 2010) (Figure 1). Although the landscape structure of these forests is a heterogeneous mosaic, that mosaic is often less fragmented by human activity in comparison to lowland forests. Therefore, mountain forests serve as important refuges 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., *this issue*; Bebi et al., *this issue*; Vacchiano et al., *this issue*). 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 in the Medieval Period. Brief periods of forest recovery have 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 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., *this issue*; Vacchiano et al., *this issue*). In contrast, land use has been shorter and less intense in forests in eastern Europe (Kaplan et al., 2010), such as those of the Carpathian Mountains (Janda et al., *this issue;* Holeksa et al., *this issue*), southeastern Europe, including the Balkan Peninsula (Nagel *et al., this issue*; Panayotov et al., *this issue*), and northern Europe, including the North Fennoscandian Mountains (Kuuluvainen et al., *this issue*). Since the onset of industrialization in the mid-19th century, the combination of reduced agriculture, lower demands for wood, active reforestation, and active afforestation has resulted in expanded forest cover in many regions across Europe (Table 1).

Much research on European mountain forests has focused on understanding dynamics of the past 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 certainly 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 are actually relatively young and a perspective of a century is relatively short in 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

Concepts of variability recognize that natural conditions and processes provide a useful guideline for sustainable ecosystem management and that natural disturbances are a vital attribute of most ecological systems (Landres et al., 1999; Keane et al., 2009). The concept of Historical Range of Variability (HRV) describes the spectrum of natural patterns and processes that exists 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 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, based on more than historical observation.

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, not clearing windthrow in avalanche or rockfall protection forests utilizes the protective capacity of increased terrain 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 and services 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) in the past as well as the future.

Criticisms of using concepts of variability in ecosystem management include the fact that there are many possible goals of ecosystem management, including maximizing timber production or protecting human settlements and infrastructure from natural hazards. 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 when concepts of variability are not used as prescriptive goals, but rather serve as (1) indicators of the fact that some amount of variability and disturbance is normal, (2) examples of the importance and effects of various 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).

Fairly extensive areas of natural or primary forests exist in eastern and south-eastern and northern Europe (Holeksa et al., *this issue*; Janda et al., *this issue*; Panayotov et al., *this issue*; Nagel *et al., this issue;* Kuuluvainen et al., *this issue*). But for forest ecosystems that exist in areas that have been intensively managed or un-forested for centuries, such as in parts of Central and Western Europe, an important question is whether a range of variability is even relevant for understanding and managing these forests. These 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. While this would likely underestimate the overall variability inherent to a system, RRV may be useful in highlighting the dynamic nature of ecosystems where it is only possible to determine short-term dynamics. 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 that would be expected 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 and 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 (including size, frequency, severity, etc.) fall within a range that will not compromise ecological resilience or ecosystem services (Seidl et al., 2016b).

3. Resilience and vulnerabilities

Resilience, i.e. the ability of a system to recover from and tolerate perturbation without shifting to a different state controlled by different processes, has emerged as a central concept 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., *this issue*). 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. It logically follows that our definitions of resilience affect our assessment 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 questions for ecosystem management include what is it that we hope will be resilient, what perturbations we are concerned about, and what processes promote and sustains resilience to these perturbations (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; Trotsikuk et al., 2014; Svoboda et al., 2014; Cada et al., 2016; Janda et al., *this issue*; Nagel et al., 2016; Panayotov et al., 2016). For example, severe outbreaks of bark beetles in the Carpathian Mountains have significantly changed forest structure for decades or longer, but post-disturbance regeneration is usually composed of the same pre-disturbance species (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 to outbreaks. Of course if disturbances are too large, severe, frequent, or novel in type, they can tip ecosystems to alternate stable states (Johnstone et al., 2016).

Ecological disturbances have the potential not only to threaten resilience, but also to promote it. Over millennia disturbances act as evolutionary filters and selection pressure agents. The heterogeneity across spatial scales induced by disturbance (e.g., the amount and arrangement of surviving forest patches or trees) has been shown to promote biodiversity (Rixen et al., 2007), primary production, carbon storage, timber production, wildlife habitat, hydrogeologic protection (Dorren et al., 2004), and ultimately foster ecosystem resilience (Loreau et al., 2003; Turner et al., 2013; Seidl et al., 2014a). Furthermore, as tree size, forest structure, and forest composition affect susceptibility to natural disturbances, a range of tree and stand conditions can modulate disturbance severity and increase the likelihood of survival of individual or groups of trees that can subsequently be important in post-disturbance regeneration (e.g., Kulakowski and Veblen 2002; Kulakowski et al., 2003). By contributing to forest resilience, spatial heterogeneity also facilitates ecological adaptation to future environmental change and helps to sustain important ecosystem services (Turner et al., 2013). Consequently, a common goal of recent management in Europe and elsewhere is to increase structural diversity and other attributes of heterogeneity (e.g. Schutz, 2002).

Forest development in the years to decades following stand-replacing disturbances (that leave no or few surviving trees) normally is characterized by a relatively homogenous structure, unless underlying environmental heterogeneity is substantial (Oliver, 1980; Palmer, 1995; Wohlgemuth et al., 2002). Where large areas are affected by an extensive disturbance, the rate of forest recovery is likely to vary with disturbance severity, pre-disturbance forest structure, and biophysical setting (e.g. Vacchiano et al., 2014; Turner et al., 2016). Post-disturbance development typically is more rapid on sites with adequate seed source and suitable temperature and moisture availability. As stands develop, heterogeneity gradually increases (Oliver, 1980), but mixed-severity natural disturbances, such as insect outbreaks and wind storms, greatly accelerate the creation of structural and compositional complexity at stand and landscape scales (Silva Pedro et al., 2016; Janda et al., *this issue*). 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 has been common in Europe following wind and insect disturbance, normally limiting potential disturbance-created heterogeneity (Thorn *et al., this issue*), often also reducing 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 may be compromised. This can shift ecosystems to alternate stable states, even over extensive areas (Reyer et al., 2015; Johnstone et al., 2016). 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., *this issue*). Increased warming may intensify disturbance events, alter normal post-disturbance recovery, and result in 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., Kulakowski et al., 2013; Rigling et al., 2013; Harvey et al., 2016). Disturbances have increased across Europe over the last decades (Schelhaas et al., 2003; Seidl et al., 2014b). If disturbances continue to increase, the highest potential for disturbance-mediated tipping points is most likely to be at range limits, where species may be particularly sensitive to additional climatic stress (Seidl et al., *this issue*; Kuuluvainen et al., *this issue*), though some marginal populations may have adaptive genetic traits that facilitate survival under more 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 future 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 primarily were due to anthropogenic causes, including forest management that simplified forest structure and thereby predisposed stands to wind throw and bark beetle outbreaks (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 18th century (Piovesan et al., 2005; Motta et al., 2011; Nagel et al., 2014; Panayotov et al., 2015; Holeksa et al., 2016). These studies have been limited in part by the fact that preservation of forest lands has been contingent on patterns of human settlement and land use such that easily accessible forests were more modified than remote ones. Evidence of long-term forest dynamics has been preferentially retained in sparsely populated regions and less accessible sites. Given these factors, well preserved sites not influenced by humans 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., *this issue*; Panayotov et al., *this issue*; Nagel et al., *this issue*).

Most studies of long term forest dynamics have relied on documentary, dendroecological, or paleological data. Documentary records can 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; Holeksa et al., *this issue*). But, assessing long-term dynamics based on documentary records alone is difficult or impossible even for the relatively recent past – at best they provide information on a recent range of variability. In contrast, dendroecological records provide longer-term information (e.g., Svoboda et al., 2013; Cada et al., 2016), but normally are spatially limited to the stand- or landscape scale. Longer term perspectives, spanning centuries to millennia, come from pollen, plant macrofossil and charcoal records preserved in the sediments of lakes and wetlands. These data can provide information on forest dynamics linked to past changes in climate, land-use, and fire. In some settings, they can be used to infer stand-level history, but more often they offer landscape-scale reconstructions (Conedera et al., *this issue*).

Based on these multiple sources of information, the most common natural disturbance agents across Europe's mountain forests are windstorms, insect outbreaks, fires, and avalanches (Table 1; Figure 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, Figure 2). Below we briefly review these disturbances and refer to relevant articles in this *Special Issue* 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 many European mountain forests, yet there are key differences among different mountain ranges (Table 1, Figure 2). Wind damage related to summer thunderstorms is common across most European mountain ranges but usually results in relatively small areas of wind throw. In the Dinaric Mountains the wind regime is dominated by frequent small-scale summer thunderstorms that tend to create patches of intermediate to severe damage at smaller scales (Nagel et al., *this issue*). In contrast, winter storm systems in mountain ranges of Central and North-Western Europe affect larger forest areas than any other disturbance. Notable examples of these extra-tropical cyclones include Vivian in February 1990 and Lothar in December 1999, both of which caused damage across large regions of the Alps (Bebi et al., *this issue*) and Central Europe. Other intense winds associated with large-scale synoptic air pressure structures occasionally cause large and severe disturbances in the Carpathians (Holeksa et al., *this issue*; Janda et al., *this issue*), Balkans (Panayotov et al., *this issue*), and Pyrenees (Martín-Alcón et al., 2010). Wind is not a major influence on the forests in the relatively low latitude and low elevation Apennines (Vacchiano et al., *this issue*), nor in the Southern Alps (Conedera et al., *this issue*), which lie outside of major storm tracks that affect Europe, are less susceptible to winter storms (Della-Marta et al., 2009), and may be more sheltered from strong storms by neighboring mountain ranges. Similarly, forests in northern Europe, such as those in the North Fennoscandian Mountains, are less affected by strong storms (Kuuluvainen et al., *this issue*).

Short-term records suggest that the total forest area disturbed by wind across Europe (Schelhaas et al., 2003; Seidl et al., 2014b) and in European mountains specifically (e.g., Panayotov et al., *this issue*) have increased over the past decades, especially where forest area and growing stock have increased (e.g., Bebi et al., *this issue*). Trends of increasing wind disturbances may be associated with changing forest structure or may be associated with improved and more complete reporting of wind damage over time, though in some mountain ranges including those of the Swiss Alps reporting appears to have been consistent over the past century and a half (Usbeck et al., 2010a). In either case, it is important to recognize recent wind disturbances in the context of the long-term development of mountain forests. In this regard it is noteworthy that large and severe wind disturbances have been dendroecologically reconstructed to occur in the past several centuries in virtually every mountain range across Europe for which long-term disturbance histories exist (e.g., Holeksa et al., *this issue*; Janda et al., *this issue*; Panayotov et al., *this issue*) showing that wind disturbances have been and are an important natural driver of mountain forest dynamics in Europe. Windstorms are irregular events, and no long-term trend in storms has been identified (Dorland et al., 1999; Holeksa et al., 2016), but climate change is predicted to intensify peak wind speeds and to shift 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, Figure 2). In North Fennoscandia, mass outbreaks of leaf defoliators such as *Eppirita autumnata* can cause massive damage to birch forests (Kuuluvainen et al., *this issue*). 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 when weather conditions are favorable for the reproduction and survival of beetles. As with wind disturbances, large and 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; Holeksa et al., *this issue*; Janda et al., *this issue*; Panayotov et al., 2016). The fragmentary records that are available may suggest the possibility of past synchronous regional to continental-scale bark beetle outbreaks and windstorms due to common climatic triggers (see e.g., Donat et al., 2010; Seidl et al., 2016a). There is clear trend of larger and more frequent outbreaks, as climate change makes mountain forests (in which beetle development was previously limited by low temperatures) increasingly conducive to outbreaks and promotes the growth of insect populations (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., *this issue*) and also plays an important role in shaping some forest types in the Southern and Central Alps, the Dinaric Mountains, the Pyrenees and Balkan Mountains (Bebi et al., *this issue*; Nagel et al., *this issue*; Panayotov et al., *this issue*; Perez-Sanz *et al.,* 2013) and is prevalent at xeric sites in the North Fennoscandian Mountains (Kuuluvainen et al., *this issue*) (Table 1, Figure 2). Fires have been much less important in the cooler and more mesic spruce forests that occupy other mountain ranges in Europe.

Forest burning in European mountain forests peaked during the Neolithic Age (ca. 4200-7500 BP) when slash-and-burn forest clearance was widespread (Conedera et al., *this issue*). From the Bronze and Iron Age onwards (since ca. 4000 BP) fires were also used extensively for various land-use practices, including charcoal production and pasture clearing near settlements (Bebi et al., *this issue*; Conedera et al., *this issue*). As human settlements became more permanent in mountain regions across Europe, people used fires more carefully, and burned less forests, with consequent effects on vegetation structure, composition, and function (Conedera et al., *this issue*). Recent temporal trends in fires continue to vary spatially, depending on the relative role of people and climate in shaping fire regimes, but the high fragmented of forests, active fire suppression, and reduced anthropogenic burning in many parts of Europe have greatly reduced the size and frequency of fires compared to previous millennia (Conedera et al., *this issue*; Table 1). In densely settled European mountain regions, fire regimes primarily reflect patterns of human land use, whereas fire regimes in remote mountain ranges, such as some of the less accessible forests on the Balkan Peninsula, continue to be primarily driven by climate (e.g., Panayotov et al., *this issue*). Climatic conditions over the past decades have 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., *this issue*).

4.4. Avalanche, snow and ice

Avalanches are a prominent disturbance agent in the forests of the Alps (Bebi et al., *this issue*), and also affect forest structure and dynamics in the Carpathian (Holeksa et al., *this issue*), the Pyrenees (Camarero et al., 2000), and Balkan Mountains (Panayotov et al., *this issue*). Avalanches are primarily controlled by topography and climate, but also have been strongly affected by land use. Prior to the mid-19th century, avalanches were more frequent in the Alps due to reduced tree cover, especially where the upper treeline was depressed due to grazing in high-elevation pastures, resulting in an enlargement of snow accumulation and avalanche initiation areas. Over the past century, forest expansion and the construction of snow-supporting structures in avalanche starting zones has reduced the frequency and ecological effect of avalanches in many areas (Bebi et al., 2009). This has coincided with climatic and snow conditions that are less conducive to avalanches starting within forests (Bebi et al., 2009). Where avalanche frequency has decreased, this has accelerated tree growth and reduced the fragmentation of forest landscapes in areas formerly shaped by avalanches (Kulakowski et al., 2006; 2011) and has affected other forest services such as carbon sequestration and biodiversity (Rixen et al., 2007; Vacchiano et al., 2015). As climate continues to warm, it is likely that snow avalanches will become less important in forest ecosystems compared to insect outbreaks and fires, which will likely increase in importance.

4.5. Synthesis of disturbance patterns

Despite fragmentary information, it is clear that disturbances of varying sizes and severity have been ubiquitous across natural European mountain forest ecosystems (Table 1; Figure 2). A simple but important implication of this fact is that the occurrence of such disturbances is, in and of itself, not outside a natural range of variability, and not likely to threaten the long-term persistence of the respective forest types. This insight is supported by ample regeneration without human intervention following some of the most extensive and severe recent disturbances in Europe (Zeppenfeld et al., 2015). An important caveat of this statement is that if a severe disturbance is large relative to the size of the forest, it is more likely to compromise regeneration, biodiversity, and other ecological functions – even for long periods of time.

It is reasonable to expect that as forest area and biomass continue to increase and forests grow older, the cumulative area affected by disturbances will also increase. Indeed, the extent of forest disturbances is increasing partly due to expanding forest area (Schelhaas et al., 2003; Seidl et al., 2011), which highlights the fact that disturbances are inseparable from forested landscapes. This view is supported also by the fact that little or no discernable trend in disturbances is evident in areas where cover has not changed in the last two centuries (e.g., Holeksa et al., *this issue*). But even in some of these areas, it is clear that recent warming has increased the size and frequency of natural disturbances (e.g., Janda et al., *this issue*).

Ecological pattern can persist and can entrain other ecosystem variables 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., *this issue*). Small disturbances affect the largest cumulative forest area during most years (e.g., Schüepp et al., 1994; Nagel et al., *this issue*), but over longer time periods infrequent large disturbances affect a larger cumulative area (Thorn et al., 2016; Nagel et al., *this issue*; Panayotov et al., *this issue*).

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., *this issue*) 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., *this issue*; Janda et al., *this issue*; Panayotov et al., *this issue*). Maximum severity from fires, windstorms and insect outbreaks, in turn, is normally higher than that of ice storms (e.g., Nagel et al., *this issue*). 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 contextualizing projected future trajectories and developing associated management strategies. It is likely that the frequency and extent of forest disturbances will continue to increase as climatic warming, forest expansion, and forest closure continue (e.g., Seidl et al., 2014b; Millar and Stephenson 2015). For example, outbreaks of spruce bark beetle may affect forests at higher elevations that are currently too cold to support the development of outbreaks. Increasing disturbances, along with likely continuing trends of reduced land use (Bebi et al., *this issue*; Vacchiano et al., *this issue*), likely will promote further increases in coarse woody debris, with cascading effects on biodiversity, edaphic conditions, and biogeochemical cycles. Increasing forest disturbances will likely increase heterogeneity across a range of spatial scales, which may translate to disturbance-mediated resilience of forest landscapes and increase biodiversity (see also Thom et al., 2016). At the same time, a continued increase in forest disturbance could eventually present a challenge for provisioning of some important ecosystem services in some areas (Thom and Seidl 2016).

As disturbances increase in frequency, size, and severity it will be increasingly likely that individual forest stands will be affected by combinations of disturbance within a relatively short interval, setting the stage for interactions among disturbances with possible 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 (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 heatwaves, such as the one that followed the 1999 Lothar wind storm (Stadelmann et al., 2013). As climate continues to warm, the links between wind and beetle disturbances may tighten as post-wind throw conditions become more favorable for development of beetle populations (Seidl and Rammer 2016; Nagel et al., *this issue*). Indeed, outbreaks may already be more likely to follow wind disturbances in forests on warmer aspects (Holeksa et al., *this issue*). Additionally, changing fuel loads and fuel continuity created by other disturbances may affect 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 structure, composition, and dynamics of European mountain forests. Understanding these interactions is an important goal for future 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 and light availability and, as a consequence, increase the abundance and diversity of many insect, plant, bird and mammal species (Thom et al., 2016; Thorn et al., *this issue*). Disturbances also introduce structural complexity in regions where long and intensive land use has homogenized landscapes and reduced the extent of old-growth forests. The role of natural disturbances in restoration has long been recognized in many different ecosystems (Angelstam 1998; Noss et al., 2006; Turner et al., 2003). Restoration activities to create old-growth conditions can involve felling and girdling trees to create snags – mimicking some of the effects of natural disturbances (Halme et al., 2013; Seibold et al., 2015). Although selective post-disturbance logging (Priewasser et al., 2013) can maintain some ecologically important characteristics of disturbed forests, it is also well documented that most forests that have been clear-cut or logged following natural disturbance are substantially different than those only affected by natural disturbance in terms of soil compaction, soil nutrients, coarse woody debris, structural diversity, biological legacies, amount of surviving post-disturbance regeneration, and establishment of new post-disturbance regeneration (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 retaining disturbance-created structures (Lindenmayer et al., 2008).

Although disturbances have become larger or more severe across Europe as a result of recent changes in land use and climate (Schelhaas et al., 2003, Seidl et al., 2011), disturbances do not, in and of themselves, threaten forest persistence. Disturbances do, however, challenge society and forest management. Some ecosystem services such as the provisioning of timber and the continuous protection against natural hazards can be affected negatively by natural disturbances (Thom and Seidl, 2016; Vacchiano et al., 2016). Additional challenges are likely to arise where forest ecosystems lie in close proximity to urban areas. In Europe these challenge are intensified by both urban expansion into forested areas as well as forest expansion into urban areas. 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 (e.g., Fares et al., 2015). This command-and control approach to managing disturbances 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).

In past centuries, production forestry in Europe has aimed to eradicate natural disturbance from the landscape – and did not succeeded (cf. Table 1). This underscores that working with, rather than against, natural processes such as disturbance in managing forests under the new emerging societal and climatic realities is of paramount importance. Forest management needs to balance promoting and incorporating natural processes while providing societally demanded timber, fiber, and other raw materials (Kuuluvainen and Grenfell, 2012) as to avoid leakage to other ecosystems. In Europe, for instance, recent policy decisions promote an emergence of bioeconomy (EC 2012, Pülzl et al., 2014), aiming for a development towards more sustainable societies but at the same time increasing the demands on local natural resources. 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 maintain other desired ecosystem services.

Approaches to forest management vary in intensity from passive management to intensive agro-forestry timber production (Duncker et al., 2012). 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., Parviainen et al., 2000; Brang et al., 2014). Passive management schemes require an understanding of ecosystem variability in order to define acceptable limits of change. It is also important to identify areas where letting natural processes to shape forest ecosystems is compatible with other desired ecosystem services (e.g., Vacchiano et al., 2016). Studies such as the ones in this Special Issue on the ecology of European mountain forest present important views of variability and disturbance ecology from which baselines for management strategies may be derived. 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, it is important to recognize that acceptances and appreciation of natural disturbances by the general public, especially in tightly couple socioecological systems, is critical in making it easier for land managers and policy makers to manage 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 disturbances over the past decades. Without such work it is difficult to determine whether recent disturbances are unprecedented events that may threaten the persistence of forests (Usbeck et al., 2010b; Jarvis and Kulakowski 2015). 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, beetle outbreaks, avalanches, and fires have long been important for the natural dynamics of these forests and are normal components of these systems. In and of themselves, these disturbances, as long as they are within a natural 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 and resilience across multiple spatial scales from the individual tree to entire landscapes. As multi-scale heterogeneity is understood to be an essential component of resilient landscapes (Turner et al., 2013), disturbances likely promote 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 impacts of disturbances. But in areas where a broader suit of multiple goals including production and conservation are desire, a dynamic view of forests that includes both gradual and abrupt, fine and large-scale changes can provide guiding principles. A shift in management from a focus on the stand level to a one that also includes landscape and regional perspectives (Lindenmayer et al., 2010) will require cooperation not only across property boundaries but also across national borders. For commercially managed forests, such an orientation might also allow increased flexibility and a less dogmatic appraisal of what constitutes “close-to-nature” forestry. 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 production of forest products in the context of newly emerging socio-ecological conditions. Allowing some forests to be shaped by natural processes may meet multiple goals of forest use, even in densely settled and developed countries.

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Table

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 BC-1000 CE	↑	++	+	+	++	+	++	++
Apennines	Vacchiano *et al.,*	Fir	5000 BC - present	↓	+++	+	+	+	++	++	++
Apennines	Vacchiano *et al.,*	Fir	18000 BC - 5000 BC	↑	+++	+	+	+	++	+	+++
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 BC-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	↑	++	-	+	+	+	-	++
Carpathians	Janda *et al.,*	Norway	Pre-	↓	+++	++	+	++	+	-	+

		spruce	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	↑	-	+++	-	+	-	+	++