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ABSTRACT

Natural disturbances, such as avalanches, snow breakage, insect outbreaks, windthrow or fires are shaping mountain forests globally. However, over the past centuries human activities have modulated the legacies of past natural disturbances in many regions, thus limiting our current understanding of natural ecological processes. In this contribution we shortly review the current understanding on changes in forest cover, forest structure, and disturbance regimes in the mountain forests across the European Alps over the past millennia. We also quantify changes in forest cover across the entire Alps based on inventory data over the past century. In addition, using the Swiss Alps as an example, we conduct an in-depth analysis of changes in forest cover and forest structure and their effect on patterns of fire and wind disturbances, based on digital historic maps from 1880, modern forest cover maps, inventory data on current forest structure, topographical data, and spatially explicit data on disturbances. During the Holocene natural disturbances were reduced by fire suppression and land-use, which resulted in decreased forest cover and the extraction of large amounts of dead wood. More recently, forest cover has increased again across the entire Alps (on average +4% per decade over the past 25 to 115 years). Also, live tree volume (+ 10% per decade) and dead tree volume (mean +59% per decade) have increased over the last 15-40 years in all regions for which data were available. In the Swiss Alps secondary forests that established after 1880 constitute approximately 41% of the forest cover. Compared to forests established previously, post-1880 forests are situated primarily on steep slopes (>30 °). They have lower biomass, a more aggregated forest structure (primarily stem-exclusion stage), and have been more strongly affected by fires, but less affected by wind disturbance in the 20th century. More broadly, an increase in growing stock and expanding forest areas since the mid-19th century have - along with climatic changes - contributed to an increasing frequency and size of disturbances in the Alps. Although many areas remain intensively managed, the extent, structure, and dynamics of the forests of the Alps reflect natural drivers more strongly today than at any time in the past millennium.

Keywords: land-use history, secondary succession, disturbance interactions, European Alps, snow avalanches, windthrow, forest fire

1. Introduction

Mountain forests globally are undergoing major changes driven by factors related to climate, land-use, and natural disturbances (Dale et al. 2001, Kulakowski et al. 2012). While the understanding of all three of these driving forces has greatly increased, interactions between them are still difficult to disentangle. Natural disturbances such as fire, wind, insect outbreaks and avalanches are strongly affected by forest cover, forest structure, climate, and land-use (Seidl et al. 2011a, Kulakowski et al. 2011, Puerta-Piñero et al. 2012, Liu et al. 2015, Flatley et al. 2013). Especially in mountainous areas, forming a complex biophysical template for these drivers, the spatiotemporal complexities of these dynamics are not yet well understood.

Forest cover has substantially increased since the 19th century in several mountain ranges of the world (Wear and Bolstad 1998, Bunce 1991, Kozak 2003), mainly as a result of reduced or abandoned agricultural areas (Baldock et al. 1996, Gellrich et al. 2007). As past land-use can have multiple and long-term impacts on forest soils and successional pattern (Foster et al. 1992, Körner et al. 1997, Dambrine et al. 2006, Spohn et al. 2016), we can expect important differences between post-agricultural forests compared to areas that did not undergo land-use change (Flinn and Vellend 2005, Foster et al. 2003). In addition to forest expansion, changes in climate and extensification of forest management have contributed to widespread changes in forest structure and biomass stocks, which in turn have contributed to increased disturbances by wind, bark beetles, and wildfires over the past decades across large parts of Europe (Seidl et al. 2014). However, in the specific context of the Alps it is not clear whether recent trends in disturbance regimes are primarily related to successional dynamics in newly established secondary forest, or to increasing biomass levels in previously established forests, and how strongly these changes are mediated by the ongoing climatic changes. It is thus helpful to examine long-term trends to obtain better insights into the effect of these various drivers of mountain forest dynamics.

Reliable data on forest cover changes and disturbance history is much more limited before the 19th century than for recent periods in the Alps, but paleoecological, dendroecological and historical records can provide insights into forest development and species shifts over longer time periods (Kaplan et al. 2009). In particular paleoecological data provide evidence of how forest cover has decreased under the increasing pressure of human land-use, and how fire regimes have changed in response to climate and land-use (Tinner 2005, Conedera et al., this issue.). Evidence of past forest development and the historic variation of different disturbances regimes is often provided by dendroecological reconstructions of disturbance regimes (e.g., Janda et al. this issue; Panayotov et al. this issue), but in some regions the influence of human management over past centuries was strong, obscuring the evidence of natural disturbances (Kulakowski and Bebi 2004). In contrast to the forest history since the 19th century, which has been characterized by increasing biomass and disturbances (e.g. Usbeck et al. 2010), we have a relatively fragmentary picture of the processes which have contributed to the massive decreases of forest cover and biomass prior to the 19th century (Kaplan et al. 2009, Küster 2010). Consequently, our long-term understanding of the variability in disturbance regimes remains cursory for forest ecosystems such as those in the European Alps, which have a long and intensive management history (Bätzing 2003, Mathieu et al. 2016). As a result, no long-term and broad-scale overview on natural disturbance regimes of the Alps exists to date.

In this contribution we synthesize the available information on long-term forest cover changes and disturbance regimes in the Alps. We combine this information with analyses of forest inventory data for the entire mountain range and detailed data on forest cover, structure, and disturbance development since the 19th century for the Swiss Alps (Ginzler et al. 2012). Based on these sources of information we address the following main questions: (1) What are the recent trends in forest cover, structure, and disturbance regimes since the 19th century, and how do they relate to the long-term context of forest development? (2) How do secondary forests that established since the 19th century differ from older forests in terms of stand structure and natural disturbance regimes?

2. Long term forest composition and land use changes

The European Alps extend over approximately 1000 km, from the French and Italian Mediterranean coast across Switzerland, southern Bavaria, northern Italy, Austria and Slovenia, and have a total population of 14 million people (Chartré et al. 2010). The mountain peaks reach elevations of more than 4000 m asl and are intersected with deep valleys, some of which are more than 100 km long and divide the mountain range into major massifs. The Alps are a relatively young mountain system, whose "step-like" morphology was contoured by the pleistocenic glaciation. Bedrocks can be divided into calcareous and crystalline material. The climate is characterized by strong environmental gradients ranging from oceanic to dry climate. The most widespread forest types are mixed European beech (*Fagus sylvatica* L.) and silver fir (*Abies alba* Mill.), pure Norway spruce (*Picea abies* (L.) H. Karst.), and mountain pine (*Pinus mugo* Turra s.l.) in the front ranges, while European larch (*Larix decidua* Mill.), Swiss stone pine (*Pinus cembra* Mill.) and Scots pine (*Pinus sylvestris* L.) may replace them in the dry central Alps.

Early changes in forest cover and forest composition since the late glacial-Holocene transition have been reconstructed based on paleoecological records (Kral 1995, Tinner and Kaltenrieder 2005; Conedera et al., this issue). These records show evidence of a relatively rapid invasion of pioneer species like European larch, and different pine species, occurring as early as 11’400 years before present (y BP) and extending as far as the current subalpine belt (Blarquez et al. 2009, Tinner and Kaltenrieder 2005). Major current tree species of the Alps like silver fir (glacial refugia in the south), Norway spruce (refugia in the east), and European beech (different refugia in the south, west and east) immigrated after 9000 y BP (Kral 1995, van der Knaap et al. 2005).

Land-use has influenced forest dynamics at least in parts of the Alps since ca. 6500 y BP, when neolithic herdsmen started to use fire to expand pastures for grazing in mountain forests (Schwörer et al. 2015, Winckler 2012). These early human impacts and the intense use of fire have not only changed forest cover and forest density in some regions of the Alps, but have also shifted species composition. For example, anthropogenic fires combined with successive intensive browsing facilitated expansion of *P. abies* into areas formerly occupied by *A. alba,* which is more sensitive to disturbances (Schwörer et al. 2015, Conedera et al., this issue). A second (between 5000 and 3500 y BP) and a third (between 1200 and 700 y BP) wave of increase in the human population and migration into the Alps led to permanent settlements in higher elevation areas, resulting in major and wide spread human impacts on mountain forests (Schuler 1988, Winkler 2012). Accelerated slash and burn management during this time reduced forest cover in central Europe, which was already below or comparable to current levels (Hauser 1964, Bork et al. 2001).

With an increasing awareness of trade-offs between deforestation and the occurrence of natural hazards the first written regulations against further exploitation of protection forests were released in the 13th and 14th centuries (Price 1988). In spite of such regulations, people continued to intensively exploit mountain forests and their products for energy and construction materials as well as extracting litter and pasturing over the following centuries (Mathieu et al. 2016). Deforestation and exploitation were partly slowed due to the Black Death and the ensuing decline in the human population in the 16th and 17th century (McEvedy and Jones, 1978). There is strong evidence of accelerated deforestation across most of the Alps for the late 18th and early 19th century, when human population again increased and the demand of wood resources was strongly boosted by industrialization (Mather et al. 1999, Bätzing 2003).

Multiple factors acting simultaneously finally halted forest exploitation in the Alps in the mid-19th century, with the importance of these factors varying from region to region. In some regions, such as the French Alps and the SW parts of the Italian Alps, regional depopulation (partly amplified by unfavorable climatic conditions) resulted in an expansion of forest cover (Bätzing 2003, Motta et al. 2006). In contrast, heavy flooding (especially in the 1860s) and a generally increasing awareness of the protection effect of mountain forests against natural hazards contributed to afforestation, stricter laws, and adapted management in mountain forests of the Northern Swiss and Bavarian Alps (Matter and Fairbairn 2000), the Austrian and Slovenian Alps, and parts of the French Alps (Sonnier 1991). Additionally, the combination of increasing agricultural efficiency and a gradual replacement of fuel-wood by coal and other fossil energy sources decreased the pressure on forests towards the end of the 19th century (Matter and Fairbairn 2000). The increasing globalization (transport, trade) also contributed to a reduced use and exploitation of forests, which in turn contributed to denser forests and larger areas with progressing secondary succession (Fig 1).

3. Forest disturbance regimes previous to forest records

Natural disturbances (i.e. discrete large pulses of tree mortality from agents such as avalanches, fires, winds or insect outbreaks) have been important drivers of the ecology of the mountain forests of the Alps for millennia. Snow avalanches and other snow-related disturbances have been integral in the mountain forests of the Alps, which is evidenced by (1) reconstructions of the snowline during the Holocene (Patzelt and Bortenschlager 1973, (2) long-term historical avalanche records of the past centuries (Latenser and Pfister 1997), and (3) adaptations of tree species in snow-rich environments to snow related disturbances (Bebi et al. 2009). As steep mountain peaks in large parts of the Alps exceed the current elevation of the treeline (1750 – 2350 m a.s.l., Paulsen and Körner 2001) and accumulate large snow packs during winter, snow avalanches frequently intersect forested areas in the Alps and contribute to a heterogeneous forest structure (Bebi et al. 2009, Vacchiano et al. 2015). Extensive areas that had been deforested since the beginning of human settlement in the Alps changed avalanche frequency by creating new release areas in formerly forested terrain resulting in a long-term absence of forest cover due to repeated avalanche disturbance (Küttel 1990).

In addition to avalanches, snow breakage across different spatial scales has been a widespread disturbance in the forests of the Alps (Coaz 1887, Weigl 1997, Rottmann 1985, Klopcic et al. 2009). Damage to trees that are not well adapted to large snow loads can be considerable, particularly in mid-elevation areas and/or during exceptionally wet and heavy snow events (Hlasny et al. 2011). Although different attributes of stand structure may modulate the susceptibility to snow breakage, the long-term variation in disturbance from snow breakage is, like for avalanches, mainly driven by climate.

Fire regimes in the Alps are highly heterogeneous, with a clear difference between the high fire frequency in the southern Alps, due to a convergence of environmental and climatic factors that enhance fire ignition and spread, and lower fire frequency in the northern Alps (Fig. 2, Wastl et al. 2013). In contrast to fire activity on the southern slopes of the Alps, which peak in the relatively dry winter season and which are mainly influenced by human ignitions, forest fires are most frequent in summer in Central Alpine valleys, which are characterized by persistent snow cover, dominance of coniferous forests (especially highly ignitable Scots pines, *Pinus sylvestris* L.), and relatively high proportion of lightning-induced forest fires (Cesti *et al.* 2005; Conedera *et al.* 2006). An elevated probability for lightning-caused fires also exists along the eastern and south-eastern rim of the Alps in Austria (Müller et al. 2012). Besides such environmental and climatological influences and their changes over time, human activity has been, by far, the main cause of fires for at least 6500 years in many regions of the Alps (Tinner et al. 2005, Arndt et al. 2013).

Slash and burn management decreased forest cover in many parts of the Alps and shifted tree species composition. This effect is particularly evident in the Southern Alps, where human-caused fires strongly reduced the abundance of fire-sensitive species (Tinner et al. 1999). Management by fire also played an important role in the Northern Alps during the same time period, but fire frequencies were too low to result in the disappearance of entire forest communities (Tinner et al. 2005). Where natural fire frequency was historically high (e.g. in dry zones of the Central Alps), forest vegetation has been more fire adapted and changed less in response to human-induced increases in fire frequencies (Stähli et al. 2006). Since the Roman Times (ca. 2000 y BP), fire use has been less extensive, but has persisted as an important ecosystem management tool (Conedera et al. 2007) and as driver of landscape change in many regions of the Alps (Valese et al. 2014).

Data about disturbance from windthrow and bark beetle outbreaks stem mostly from records going back only to the mid-19th century (Usbeck et al. 2010, Bottero et al. 2013, Seidl et al. 2014), and suggest strong spatio-temporal variations in occurrence and extent. In the Alps strong winds with potentially damaging effects on forests occur mainly due to westerly or northerly winter storms (Gardiner et al. 2010, Usbeck et al. 2015). Consequently, exposed forests of the Northern and North-Western Alps are more prone to large-scale wind disturbance compared to mountain forests in the inner Alpine valleys and the Southern Alps, which are generally protected from strong winds by the northern front range (Usbeck 2010). However, foehn winds can also result in large wind disturbances in the central and eastern parts of the mountain range. Bark beetle outbreaks are highly correlated with spruce abundance and standing volume, growing season temperature, drought stress, and preceding disturbances of which windthrow is the most important, as it creates large amounts of virtually defenseless breeding material for beetle development (Thom et al. 2013, Stadelmann et al. 2014). Historical records on windthrow events and bark beetle outbreaks before the 19th century are widely missing (Pfister 1988) and dendroecological reconstructions of these disturbance events are difficult in forests with intensive management history (Kulakowski and Bebi 2004). Our knowledge of the historical range of variability of these disturbance agents in the Alps is thus very limited (Vacchiano *et al.*, 2016, Kulakowski et al., this issue), and can only vaguely be deduced from a relative short observation period and from analogies with similar mountain forest ecosystems.

4. Analyzing forest cover dynamics since the 19th century

To analyze forest dynamics in the Alps, we compiled and analyzed available records on forest cover change and forest structural change (including living and dead timber volume, as well as the growing stock of relevant tree species) for all Alpine countries (Austria, Germany, France, Italy, Liechtenstein, Slovenia, Switzerland). Changes of forest cover and other attributes were computed as average rates of changes per decade based on the back-calculated values at the beginning of each decade (Fig. 3). In addition, we analyzed forest cover changes under different topographical settings in the Swiss Alps, and compared forests that established after the mid-19th century with older forests. We joined digitized historical land-use maps with 2363 plots of the Swiss National Forest Inventory (NFI; regular 1.4 km grid), resulting in data for the Northern Prealps, Central Alps and Southern Alps for the years 1880, 1915, 1940 and 2000 (Ginzler 2011). NFI stand structural data were recorded (1) by field crews in two concentric circles with sizes of 200 m^2 (inner circle) and 500 m^2 (outer circle), and (2) for an area of 50*50 m surrounding the study plot, where additional variables on stand structure and management history were assessed based on aerial photo interpretation, field surveys and surveys by regional foresters (Keller 2005). Based on these data, we derived forest presence/absence for each time step mentioned above. We used GIS (*ArcGIS* version 10.1) to define the distance from the potential treeline (as defined by Paulsen and Körner 2009), as well as the presence of wind and fire disturbances in these plots. We derived wind disturbances from remotely sensed forest damage data from the winter storms Vivian (in 1990) and Lothar (in 1999) (Usbeck et al. 2012) and digitized an inventory of 487 fires of the Canton of Grisons between 1971 and 2015 (Pezzatti et al. 2010). We analyzed data on forest structure and past forest management based on the most recent NFI surveys (1982/86, 1993/95 and 2004/06, 2009/15 (Abegg et al. 2014). In order to compare post-1880 versus pre-1880 forests in terms of their spatial distribution under different environmental settings, their occurrence in stands affected by windthrow and fire, and in terms of current forest attributes and forest development according the most recent NFI-surveys (and 2004/06 and 2009/15), we applied spatial overlay analysis. Pearson's Chi-squared tests (with Yates' continuity correction) were used to test associations with binary variables and Wilcoxon-Mann-Whitney tests for associations with continuous variables (R core Team, 2013).

5. Results on forest cover dynamics since the 19th century

5.1 Forest trends in the Alps

All available data sets – both ground inventory and repeated forest cover maps based on remote sensing – across all regions of the Alps indicate an increase in forest cover in recent decades. However the rates of forest cover change since the availability of forest cover data in the late 19th or early 20th century varied considerably, both spatially and temporally, and range from +25 to +150% (Fig. 3). Forest cover expanded most significantly in parts of the Italian Alps (e.g. +8.7% per decade since 1962 in Val Masino, Sondrio (Martinelli et al., unpublished data), +6.2% per decade since 1954 in Val Vigezzo, Verbania (Vacchiano, 2008)), in the Southern Swiss Alps (average rate of +7.3% per decade since 1880), and in the Austrian province of Salzburg (+7.0% per decade since 1928, BFW, 2016, Weigl 1997). Forest cover expanded less rapidly in Bavaria (Germany; +0.7% per decade since 1900), in the French Prealps (+3.5 % per decade between 1850 and 1990) and the Northern Swiss Alps (+2.1% per decade between 1880 and 2013). On average (mean of all reported values), forest area across the Alps increased by +3.7% per decade since 1930 and +4.3% per decade since 1990.

Live and dead biomass also strongly increased since the end of the 19th century and continues to increase. Based on inventory data of different countries in the Alps (since 1973 for the Northern French Alps, since 1992/96 for Austria and since 1993/95 for the Swiss Alps), the total live wood volume increased in all regions of the Alps, averaging +10.0% of growing stock per decade, and ranging from +0.4% per decade in the northern Swiss Alps to +16.9% per decade in the eastern Slovenian Alps to +17.1% per decade in the Southern Swiss Alps (Table 1). Dead wood volume increased even more in the same time period, with rises between +39.3% and +105.8% per decade (Table 1). Species shifts differ across the Alps, and include an increased share of silver fir on the total growing stock in parts of the Western and Central Alps (+11.0 % in the French Alps, +18.5% in the central Swiss Alps) that contrasts with a decrease in parts of the Eastern Alps (e.g. -2.6% per decade in Vorarlberg (Austria) and the eastern Slovenian Alps and -3.8% in Liechtenstein, Table 1).

5.2 Detailed analysis of forest change in Switzerland

Forest cover change varied across natural gradients: It was more pronounced on slopes > 30° compared to more gentle slopes, in particular in the Central Alps, where more than 96% of the forest cover increase occurred on slopes with a steepness of > 30°. The highest rates of change since 1880 occurred near the treeline ecotone (0-200 m below the potential treeline), but also areas that are more than 800 m below the current potential treeline changed considerably (Fig. 4b).

Secondary forests (i.e. areas not identified as forests in the 1880 forest cover maps) make up ca. 41% of all current forests in the Swiss Alps, and differed distinctly from pre-1880-forests in the most recent forest inventory (Table 2). Post 1880-forests have lower biomass (both living and dead stock volume), are more often characterized by low diameters (between 10 and 30 cm DBH) and less represented in large diameter (>50 cm DBH) classes. Since the forest inventory of 1993/95, total wood volume increased more strongly in secondary forests, but dead volume increased more strongly in pre-1880 forests (these changes were however highly variable and therefore not statistically significant, Table 2). In spite of strongly increasing growing stocks in secondary forests, they were still less dense (lower crown closure) but more spatially aggregated (open forests with interspersed dense patches), especially in areas that have been grazed, but otherwise not actively managed over the last 50 years. Spruce, fir, and beech were more often the dominant tree species in primary forests, while larch and miscellaneous broadleaved species were more likely to dominate in secondary forests.

Forests that established after 1880 were less affected by the two largest storms of the 20th century, namely Vivian (in the year 1990) and Lothar (in the year 1999), compared to forests established before 1880 ($p = 0.005$, Chi-square test, Fig. 5). Based on a record of 487 fires in the Swiss Canton Graubünden the density of fires that occurred between 1971 and 2015 was higher in secondary forests ($p = 0.00013$, Chi-square test) (Fig. 6).

6. Discussion

Our review of forest cover changes prior to the 19th century and our analysis of spatial data since the 19th century indicate that forest cover changes in the Alps during the last millennium have been strongly related to changes in land-use. Forest cover across the Alps has dramatically increased at approximately +4% per decade after a minimum during the mid-19th century. The rates of forest cover change have varied considerably in response to local socio-economic and environmental factors (Bätzing 2003, Gellrich et al. 2007), but a general increase is evident across the entire European Alps. While both live and dead biomass has increased across different regions of the Alps (Table 1, Abegg 2014, BFW 2016), changes in species composition follow more regional patterns and are influenced by a variety of factors. For example, regionally diverging trends in silver fir share have been attributed to different levels of ungulate browsing (Ammer 1996, Didion et al. 2009, Klopcic and Boncina 2011), while strong expansion of the same species in the French Alps (Chauchard et al. 2010) and of European Larch in the western Italian Alps (Motta et al. 2006, Garbarino et al. 2011) have been mainly attributed to an extensification of livestock grazing during the 20th century.

Furthermore, our in-depth analysis of forest cover change in the Swiss Alps comparing maps from 1880 to more recent maps (Ginzler et al. 2012) confirmed strong regional differences as well as the decisive role of topography and land-use history for forest development (Fig. 3). Major increases in forest cover before 1940, particularly near the upper treeline, may in part be artifacts of slightly different criteria for the assessment of forest cover in the different maps analyzed here (Ginzler 2012), but are likely to reflect decreasing land-use intensity, starting at the most remote high elevation sites. This is consistent with other research showing that forest expansion near the treeline in the Alps during the late 20th century has mainly been a bounce-back from a treeline depressed by previous anthropogenic activity, rather than a climatically induced advance of the treeline (Gehring-Fasel et al. 2007). This further suggests that warmer temperatures during the last decades probably had a relatively minor effect on the expansion of forest cover since the end of the 19th century so far (Kulakowski et al. 2011).

The specific land-use history of the Alps is also reflected in the current forest structure of secondary forests that established after 1880 compared to pre 1880-forests. After the decrease in grazing pressure these forests are either still in an early stage of stand initiation (apparent in the higher proportion of scattered and clustered forest structures) or they are already in more dense stages of forest development with increasing competition and stem-exclusion (Krumm et al. 2012). The initial conditions for these secondary forests were characterized by a high availability of light, exposed mineral soil in grazed areas, and an absence of structural heterogeneity typical for naturally disturbed sites (e.g., remnant large trees, logs, and pit-and-mound topography). Long-lasting legacies of past land-use also have been reported for soil nutrient concentrations (Spohn et al. 2016) and seed banks (Plue et al. 2008). The timing of forest establishment likely influences also the species composition. Late successional species are more abundant in pre-1880 forests, while early successional and light-demanding species *(Larix decidua*) occur more frequently in post-1880 forests (Table 2). However, such differences between pre- and post-1880 forests have to be interpreted carefully because of differences in environmental drivers, and because also most of the pre-1880-forests of the Alps have a long-term management history. However, our analyses confirm that secondary forests which established after 1880 may –at least partly – follow different successional trajectories as a result of altered starting conditions compared to their primary counterparts.

In contrast to our increasingly clear view of the large-scale patterns of forest development after 1880, temporal development of forest cover changes before the 19th century can only be cursorily characterized based on available historical records and paleoecological data. The potentially large variation in the timing and intensity of anthropogenic forest cover change and forest exploitation across the Alps prior to 1880 is difficult to show based on available evidence. Nevertheless, studies suggest that intensive land use has affected most forests in the European Alps, has strongly reduced forest cover and created open forest structures by the late 18th century (Landolt 1862, Kaplan et al. 2009). Similarly, decreasing biomass until the 19th century and a subsequent fast recovery of biomass also has been documented for forests outside of the Alps which were subject to similar changes in land use (e.g. Foster et al. 1992, Mather et al. 1999). The effects of forest cover changes prior to the 19th century on historical disturbance regimes are difficult to assess, not only because of uncertainties in timing and intensity of forest cover changes but also because of obvious difficulties in reconstructing natural disturbances in intensively managed forest landscapes (Kulakowski and Bebi 2004). Our knowledge about the historical range of variability of disturbance regimes in the Alps (cf. Kulakowski et al., this issue) has thus to be deduced from a synthesis of (1) disturbances occurring since the 19th century and (2) our fragmentary picture of forest cover change and disturbance regimes before this forest transition.

Avalanches

Forest expansion in the Alps since the 19th century has mostly occurred on steep slopes above 30 degrees, and has thus led to a decreased avalanche activity in many areas (Bebi et al. 2009). This recent trend has partially compensated for the increasing avalanche activity due to deforestation and forest degradation before the 19th century. However, compensation of former increases in avalanche disturbance has not occurred where anthropogenic deforestation (partly combined with climatic shifts during the little ice age) allowed the development of new avalanches, which continue to disturb exposed forests and inhibit their growth and development. For example, a reforestation of large parts of the Urseren Valley (Switzerland), where the original forest had been reduced to four small dispersed fragments by a combination of land-use and avalanches, has not been possible under the current conditions of climate and avalanche disturbances (Föhn 1978), even though paleoecological records indicate that this valley was forested during most of the Holocene (Küttel 1990). Warmer winter temperatures and decreasing days with minimum snow depth required for avalanche will probably further reduce the importance of avalanche disturbances in forested terrain in the future, and will further promote shifts from dry avalanche regimes to wet avalanche regimes (Castebrunet et al. 2014). However, where avalanche release zones are above the current treeline and forests are shaped preliminary by recurring avalanche disturbance, avalanches will likely continue to disturb forests - as they have throughout most of the Holocene.

Snow breakage

Forest structural characteristics such as large proportions of pole stage stands and high h/d-ratios increase susceptibility to snow breakage (Rotmann 1985, Nykänen et al. 1997, Hlasny et al. 2011). Such structural characteristics are typical for stands that established after 1880 (Table 2) and are likely to become more widespread with increasing crown closure and competition in these stands (Krumm et al. 2012). However, snow breakage events are primarily related to specific weather events, and climate warming is likely to reduce snow fall and thus compensate for potentially increased susceptibility to snow breakage due to changes in forest structure, particularly in lower elevations (Bebi et al. 2012).

Fires

The increase in forest cover and biomass since the 19th century has resulted in more fuel available for fires. Retrospective analysis from the 20th century showed that an increase of fire frequencies in the Southern and Central Alps (Valais) was mainly related to an increase in fuel availability due to a decrease of agricultural land-use in lower elevations (Zumbrunnen et al. 2009), whereas warming and earlier spring seem to be more important in higher elevations and regions with less change in forest-cover (Zumbrunnen et al. 2009, Westerling et al. 2009).

We found higher fire densities in secondary forests that established after 1880 compared to older forests. This suggests that increased forest cover and connectivity between potentially burnable forest patches may have substantially contributed to the observed increase of forest fires in the Alps (Zumbrunnen et al. 2009). These relationships vary strongly across different elevational zones and forest types, and may also be influenced by other human factors such as firefighting techniques or fire-inducing activities at the wildland-urban interface (Conedera et al. 2015). Thus, future research should test whether the increase in fires in these younger forests is due to the structure of the forests, or rather a factor of their location.

For the future we can expect that the ongoing forest cover increase and build-up of biomass (Table 2, Abegg et al. 2014) will continue and provide fuels for potential fires. Furthermore, while the complex topographical template influencing fire regimes in mountain regions will remain constant, increasing temperatures, summer droughts, and shorter snow duration will increase the probability for forest fires in the Alps (Arpaci et al. 2015), even in relatively mesic forests in which fires have not been historically important. Particularly in areas where forest vegetation is less adapted to frequent fires (Tinner et al. 2005), this may lead to drastic vegetation shifts (Moser et al. 2010). In the southern Alps, we also can expect an increase in the fires at higher elevations and in forest types that until now have only been marginally affected by fires (Ascoli et al. 2013). Improved strategies to prevent fire and fire brigades better prepared to suppress and contain fires once ignited may counteract an increasing fire risk under climate change (e.g., Wohlgemuth et al. 2015).

Windthrow

Forests that established after 1880 have been less affected by recent windthrows in 1990 and 1999 compared to older forests. This may be explained by higher susceptibility of older forests with taller trees and higher biomass (Kulakowski and Veblen 2002, Gardiner et al. 2010, Thom et al. 2013, Usbeck 2016) and suggests that the observed increase in storm damage during the 20th century across Europe (Schelhaas et al. 2003) could be explained, to a considerable degree, by the aging of pre-1880 forests rather than by the establishment of new forests (see also Seidl et al. 2011a). At the same time, however, storms with critical wind speed have become more frequent since the 1940s (Usbeck 2010a, with particular consequences for forests with high stock rates (Usbeck et al. 2010b). Alternatively, given that post-1880 forests are located preferentially in topographic settings that were preferable for agriculture, lower damage levels in recent wind storms may also reflect differences in topographic exposure. Thus, future research should test whether differential wind damage in pre- and post-1880 forest is due to differences in forest structure or topographic exposure.

Because of lacking data, assessments on storm damage before the 19th century remain difficult. However, extratropical cyclones have likely led to winter storms that are similar to those that affect the Alps today for a long time (Kraus and Ebel 2003), and historical wind damage in other mountain ranges of Europe (Kulakowski et al. this issue) also suggest that wind disturbances were likely common before significant human influence. Based on known process understanding of the relationships between growing stock, forest structure, and storm damage (Dobbertin 2002, Gardiner et al. 2010) we can assume that historic land-use and management in the Alps have partly downscaled the effects of wind disturbances of different size, but that wind has been among the most relevant forest disturbance agents long before the 19th century.

Whether wind disturbance – currently the single most important disturbance agent in the Alps – will cause even more damage in the future remains highly uncertain, not least because projections of future wind dynamics remain challenging. However, with mountain forests responding to longer growing seasons, higher mean temperatures and, to some extent, CO_2 fertilization, increasing stocking levels can be expected to make forests more prone to wind disturbance (Seidl et al. 2011b). Furthermore, as most wind disturbances in the Alps occur in winter, and as tree stability is highly sensitive to soil frost (Usbeck et al. 2010), a decreasing period of soil frost could further increase forest susceptibility to wind in the future.

Insect outbreaks

Based on current knowledge - which is mainly derived from data collected since the 19th century - bark beetles (and here primarily *Ips typographus*) are the most relevant biotic disturbances in the mountain forests of the Alps. Beetle outbreaks are often strongly linked to wind disturbances and have similarly increased over the last decades, mainly as a function of increasing volume of potential host trees (i.e., mainly *P. abies*), increasing summer and winter temperatures, and preceding wind disturbances (Seidl et al. 2014, Stadelmann et al. 2014). However, in contrast to evidence of regular outbreaks of e.g., larch budworm (*Zeiraphera diniana*), obtained from dendroecological reconstructions (Büntgen et al. 2009), we have almost no direct information about bark beetle outbreaks prior to the 19th century. A detection of earlier outbreaks with dendroecological methods (Cada et al. 2016) is not reliable in the Alps because of the overwhelming influence of forest management. Historical documents for periods prior to the 19th century are hardly specific enough to clearly identify bark beetle outbreaks (Pfister 1988).

Because of this missing information and due to interactions between different drivers of beetle outbreaks, assumptions about the historical range of variability of bark beetle disturbances remain challenging. However, based on information on the rigorous exploitation of living and dead biomass in mountain forests in earlier periods as well as analogies with similar mountain ecosystems in Europe (Kulakowski et al., this issue) we can assume that bark beetle outbreaks are part of the natural disturbance regime in spruce dominated forests in the Alps. Furthermore, it is likely that bark beetle populations (and consequently also the population of their predators) have been kept below their natural levels during periods of most intensive forest use before the 19th century.

In the face of increasing temperature, high and still increasing volume stock of *P. abies* at high elevations, and the aging of relatively young and even-aged forests stands, further increases of bark beetle activities in the future must be expected (Seidl et al. 2009). Furthermore, an increasing propensity for drought events has the potential to trigger bark beetle outbreaks more frequently in the future (Netherer et al. 2015, Seidl et al. 2016). Warmer and drier conditions can also amplify the interaction between wind and bark beetle disturbance, further increasing future disturbances in the mountain forests of the Alps (Seidl and Rammer 2016). Over longer time scales, however, a climatically-induced decrease of Norway spruce at lower elevations may provide a negative feedback on bark beetle outbreaks (Temperli et al. 2013).

Interactions among disturbances

Studying interactions among different disturbances is particularly challenging, but of high societal relevance because disturbance interactions may lead to unexpected, rapid, and nonlinear changes in ecosystems (Paine et al. 1998, Buma 2015), especially under a changing climate (Kulakowski et al. 2012, 2013). One of the most important disturbance interactions in the Alps involves positive feedbacks between the accumulation of fresh deadwood and subsequent insect outbreaks (Bottero et al. 2013, Stadelmann 2014). Other positive feedbacks can result from the removal of biomass due to windthrow, fire, or other disturbance and subsequent gravitational hazards like avalanches, rockfall, or shallow landslides. Such interactions are of particular societal importance in the densely populated Alps, and more knowledge is needed on interactions between a broad range of disturbance agents, in different forest types, and under different management regimes (Conedera et al. 2003, Bebi et al. 2015).

Negative feedbacks between disturbances, leading to lower susceptibility, biomass, and a more fragmented forest cover, and subsequently decreasing disturbance activity, have received less attention in the Alps. The most obvious examples here are avalanche tracks, which may act as fire breaks (Veblen et al. 1994). But also negative feedbacks between the reduction of biomass through windthrow, fire and snow breakage, and the susceptibility to subsequent disturbance (e.g., Kulakowski and Veblen 2002, Kulakowski et al. 2003) may become increasingly important. Individual and interacting disturbances can counteract the general trend of growing biomass across the Alps. The resulting heterogeneity and lower biomass may reduce the risk of even larger disturbances in future. This mechanism may be particularly important in the light of climate change, as disturbances can present opportunities for ecological communities to adapt to new conditions by allowing new, better adapted species to establish (Buma and Wessmann 2013). The importance of both positive and negative feedbacks between different natural disturbances may thus considerably increase in future and should be emphasized more in the future management of mountain forests ecosystems in the Alps.

7. Synthesis and conclusion

Forest changes in the European Alps have been strongly driven by land-use, both before and after a major transition from forest loss to forest gain in the 19th century. The long-standing effects of land-use have had, and continue to have, a strong influence on forest dynamics and the disturbance regimes of mountain forests in the Alps. Human-induced decreases of forest area and density, peaking in the early 19th century, created new avalanche release areas in parts of the Alps. Furthermore, extraction of biomass and the resulting lower stocking levels reduced large-scale disturbances by fire, bark beetle and windthrow before the 20th century. The extensive forest areas in the Alps established after the 19th century on former agricultural land are currently characterized by relatively young stands with a high potential for further biomass accumulation and homogenization of forest structure. Susceptibility to disturbances by bark beetle, fire, and wind is likely to further increase in these areas over the coming decades, particularly in combination with the climatic changes which are expected for the future.

The future management of mountain forest ecosystems in the Alps has to take into account the important and potentially increasing influence of natural disturbances under climate warming, while considering the particular and long-lasting effects of land-use history. It is not possible and, from an ecological perspective, also not desirable to impede these natural disturbances. However, where the protection of forests against natural hazards or other ecosystem services are threatened by disturbances and other natural processes, management may focus on reducing risks and increasing the resilience of mountain forests (Seidl 2014). This can be achieved by disturbance management that allows forests to adapt to future environmental conditions and by counteracting the growing biomass and reduced fragmentation, particularly in secondary stands established after the mid-19th century.

Because of a strong and widespread anthropogenic effect on forest dynamics in the mountain forests of the Alps, assessments of their historical range of variability remain difficult. However, based on the increase of fire, bark beetle, and windthrow disturbances since the 20th century, which has coincided with a recovery of forest area and biomass, and based on analogies with similar ecosystems in Europe, we can assume that the importance of the natural disturbances, which has been dominated by human activities for centuries, is increasing and will be an important driver of mountain forest dynamics in the Alps in future decades.

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