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Long-term change in sub-alpine forest cover, tree line and species composition in the Swiss Alps

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Historical maps; *Larix*; *Picea*; Repeat photography; Sub-alpine forests

Nomenclature
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Abstract

Aims: The 20th century has been marked by dramatic changes in land use, disturbance regimes and climate, which have interacted to affect global ecological patterns and dynamics, including changes in the extent, composition and structure of forest cover. Although much research has highlighted dramatic, short-term ecological change, on-going trends of land-use change and climate change began more than a century ago. Consequently, quantifying and understanding long-term (e.g. centennial) ecological change is critical to contextualizing recent patterns and processes. Here we document changes in the extent, position and composition of sub-alpine forests over the past century in eastern Switzerland.

Location: Davos region of the Swiss Alps, eastern Switzerland.

Methods: Position of tree line, forest cover and forest composition were evaluated using a unique combination of Object-Based Image Classification of an historical (1909) map, recent (2009) aerial photography and repeat terrestrial photography to minimize the inherent bias of each data source, while providing the most robust representation of long-term ecological change.

Results: Over the past century total forest cover expanded by 64.6% and the position of sub-alpine tree line increased on all aspects. Total forest cover also increased at the highest and lowest elevations on all aspects. Dominance of European larch increased at the highest elevations, but decreased at the lowest elevations, where it was replaced by Norway spruce. These patterns suggest land use has been the most important driver of forest change over the past century.

Conclusions: Major changes in the extent, structure and dynamics of sub-alpine forests in the Alps initiated earlier than previously documented and most change occurred prior to the middle of the 20th century. Furthermore, these changes were likely driven primarily by changes in land use, rather than by changes in climate. A combination of data sources and methodological approaches, such as those of the current study, provides a clearer view of long-term changes and minimize the biases associated with any single data source or methodology.

Introduction

Global changes in land use, disturbance regimes and climate have had profound effects on terrestrial and aquatic ecosystems over recent decades (Foley et al. 2005; Krawchuk et al. 2009; Allen et al. 2010, 2015; Moritz et al. 2012). As important and dramatic as these recent ecological changes have been, on-going changes in land use, disturbance regimes and climate began more than a century ago. While many studies have documented ecological changes over the past years to decades, fewer have examined the actual duration and magnitude of these changes. Assessing long-term ecological change is inherently challenging as the availability and quality of data are limited. Yet, over-emphasizing the recent past may contribute to an incomplete understanding of anthropogenic global environmental change and the relative importance of its drivers (Kulakowski et al. 2017).

Ecosystems at high elevations and high latitudes have been particularly vulnerable to recent global environmental change, in part because establishment and growth of alpine and sub-alpine vegetation is strongly limited by

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temperature and therefore especially sensitive to changes in climate (Walther et al. 2005; Holtmeier & Broll 2007; Jurasinski & Kreyling 2007; Harsch et al. 2009), even relatively minor changes (Walther et al. 2005; Wipf et al. 2009, 2013). In contrast, lower elevation limits of forest cover are most often governed by land use, although climate can also be a limiting factor (Gehrig-Fasel et al. 2007). The direct effects of climate change on vegetation near tree line can include changes in plant growth rates (Paulsen et al. 2000; Bugmann 2001), expansion of forest cover and decreased forest fragmentation (Moen et al. 2004), or increased seedling establishment above tree line (Körner & Paulsen 2004). The upward shift of sub-alpine tree line and the increasing density in sub-alpine forests can affect not only local ecosystem structure and function, but can also contribute to critical feedbacks by changing surface albedo and biogeochemical cycles (Grace et al. 2002; Schwaab et al. 2015).

Over the past decades, the sub-alpine forests of the European Alps have been characterized by increases in plant growth rates (Paulsen et al. 2000), tree seedling establishment above tree line (Körner & Paulsen 2004), ecosystem homogeneity (Jurasinski & Kreyling 2007), forest density (Walther et al. 2005) and position of tree line (Moen et al. 2004; Gehrig-Fasel et al. 2007; Kulakowski et al. 2011). These changes have largely been attributed to the individual or interacting effects of a warming climate, abandonment of formerly intensive agriculture and/or changes in disturbance regimes. Despite the ecological and social importance of these dynamics, most studies have focused on changes over the past years to decades and relatively few studies have quantified long-term (e.g. centennial) changes. However, on-going trends in warming, land use and disturbances in many regions, including the European Alps, began around the mid-19th century (Kulakowski et al. 2011).

In the Swiss Alps, mean annual temperature peaked during the 1990s, which was the warmest decade since the beginning of climate measurements in 1959 (Ceppi et al. 2012). However, this warming trend began more than a century ago, and mean annual temperature over the 20th century has increased by 1.35 °C, compared to the global mean annual temperature increase of 0.7 °C (Rebetez & Reinhard 2008).

Since at least the Neolithic Period, human land use, including slash-and-burn management, maintenance of agricultural land, grazing and exploitation of wood resources, has strongly impacted the forests of the Alps (Kasthofer 1825; Landolt 1862; Schuler 1995; Price & Thompson 1997; Schwörer et al. 2015). Since around the 19th century active re-forestation and regulation of grazing practices were implemented in order to maintain the protective functions of mountain forests against natural hazards (Landolt 1862). Furthermore, as in many developed regions, agricultural land use in the European Alps has become less profitable over the past century, which has contributed to less intense agriculture, especially on marginal land, on steep slopes and/or on sites with unfavourable soil conditions (Gellrich & Zimmermann 2007; Gellrich et al. 2007).

The forests of the Alps have long been shaped by avalanches, fires, snow breakage, wind blowdown and insect outbreaks (Seidl et al. 2014). Snow avalanches have been among the most important disturbances and have contributed to the natural fragmentation of the landscape and in some places a suppressed tree line (Bebi et al. 2009). However, over the past century, afforestation and snow-supporting structures have reduced the frequency of avalanches, thus altering the historical disturbance regime as well as ecosystem structure and function (Kulakowski et al. 2006a, 2011; Rixen et al. 2007).

The net effect of changes in climate, land use and disturbance regimes in Europe have resulted in well-documented changes in forest structure and dynamics over the second half of the 20th century (Grace et al. 2002; Gehrig-Fasel et al. 2007; Holtmeier & Broll 2007; Tasser et al. 2007; Harsch et al. 2009; Kulakowski et al. 2011). These changes have included increased forest density, increased elevation of tree line, increased landscape and species homogeneity, and decreased forest fragmentation (Moen et al. 2004; Walther et al. 2005; Jurasinski & Kreyling 2007; Kulakowski et al. 2011). Furthermore, long-term paleo-ecological records, derived from archaeological excavations, pollen, charcoal and tree rings, have revealed extensive and long-term land-use practices, fire histories and vegetation shifts dating back to 3500 yr before present throughout the eastern Swiss Alps (Gobet et al. 2003; Stähli et al. 2006; Röpke et al. 2011; Dietre et al. 2014). However, such records are often not spatially continuous and therefore provide only limited insight into spatial changes in vegetation composition, location and abundance. Despite the fact that the drivers of forest dynamics have been changing over at least the past century, few studies have examined the spatially explicit ecological change over this longer time period (Ginzler et al. 2012), probably due to the scarcity of data on spatial historic vegetation conditions (Pauli et al. 2003a,b) and various limitations of those data.

Here we examine changes in forest extent, forest composition and position of tree line in the Davos region of the Swiss Alps over the past century. We use a unique methodological approach that combines Object-Based Image Classification of an historical (1909) map, recent (2009) aerial photography and repeat terrestrial photography to minimize the inherent bias of each data source, while providing the most robust representation of long-term ecological change.

Methods

Study area

The study area is located in and around Davos, Switzerland, nestled in a high elevation (1080–3146 m a.s.l) alpine and sub-alpine landscape of the eastern Swiss Alps (Fig. 1a). The community of Davos spans a land area of 284 km^2, which is dominated by an urban area in the valley surrounded by rural landscape along the mountainsides. Davos (1560 m a.s.l.) is situated in a transitional boundary between the relatively humid north alpine climate and the more continental climate of the Central Alps. The mean annual temperature between 1889 and 1909 was 0.2 °C compared to the mean annual temperatures between 1889 and 2009 of 2.8 °C (MeteoSwiss 2016). The precipitation in the Davos region averages 1000 mm annually, with the wettest months occurring in July and August.

Forest cover in the study region is dominated by *Picea abies* (Norway spruce; ca. 83% of biomass) and *Larix decidua* (European larch; ca. 13%). The biomass of different pine species (*Pinus cembra*, *Pinus mugo* and *Pinus silvestris*) sums to <5% of the forest biomass. *P. abies* is most dominant at low and mid-elevations, while *L. decidua* is most commonly observed at higher elevation (Brzeziecki et al. 1995; Carrer et al. 2007). The current upper tree line limit in the study region is at ca. 2160 m a.s.l.

Slash and burn management of sub-alpine forests and the subsequent agriculture and pastoral lands have dominated land-use practice of this region since the 13th century. The remaining forests were intensely exploited until the 19th century, mainly for timber production, fire wood extraction, mining (especially between 1513–1848) and grazing by cattle and goats (Günter 1981). Over the past century, the number of farms in the region has decreased by roughly half (Günter 1985; Gellrich et al. 2007; Gellrich & Zimmermann 2007; Lundström et al. 2007), leaving some of the once-cultivated land fallow and abandoned. Therefore, in recent decades the trend has been one of afforestation of abandoned lands, and a homogenization and defragmentation of forested landscape (Moen et al. 2004; Walther et al. 2005; Jurasinski & Kreyling 2007; Kulakowski et al. 2011). Likewise, the exploitation of remaining forests has strongly decreased during recent decades because of a general decrease in cost efficiency and profitability of timber production, increasing job opportunities outside of agriculture and forestry, as well as stricter regulations for grazing practices within forests (Günter 1981; Behre 1988; Wohlgemuth et al. 2002).

Methodology

The methodological approach was based on similar work that has used historical maps to study long-term forest dynamics of forest ecosystems (Bebi et al. 2003; Kulakowski et al. 2004, 2006b, 2011), but built on that methodology by incorporating Object-Based Image

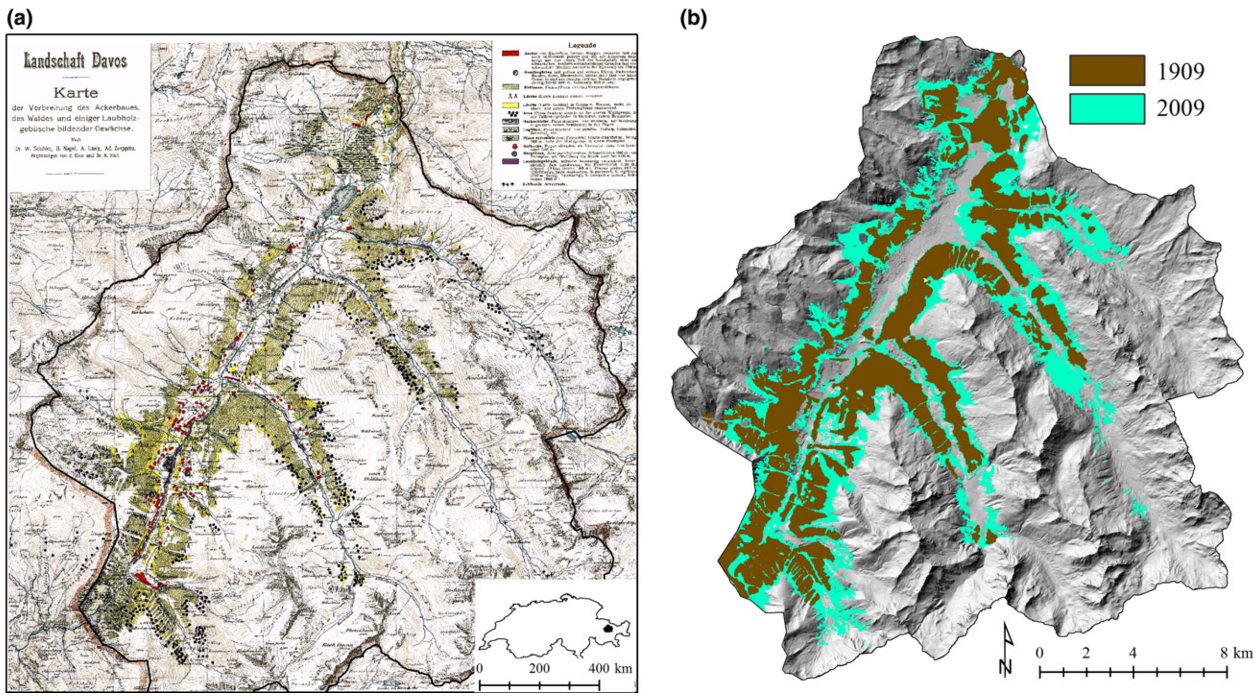

Fig. 1. Study area of Davos, Switzerland as observed in 1909 via the Siegfried map **(a)** and the 1909 and 2009 forest cover extent **(b)**. [Colour figure can be viewed at wileyonlinelibrary.com]

Analysis. In using a more sophisticated classification technique, we were better able to automatically resolve finer features in the historical map that might be otherwise not accounted for using manual classification. Furthermore, we have complemented this landscape-scale analysis of forest cover with an analysis of repeat terrestrial photography to: (1) validate the historical map and (2) assess changes in forest species composition. This novel combination of image classification, repeat terrestrial photography and field-based validation was designed to minimize the inherent bias of historical maps, while providing the most robust representation of long-term ecological change.

Schibler (1909) produced high-resolution maps (1:50 000 scale accurate to ca. 35 m) of forest cover and forest type (i.e. tree species) for parts of Switzerland, including Davos (Fig. 1a; Appendix S1). Although these historical maps did depict forest type according to the dominant tree species, there are uncertainties about the thresholds of these forest type categories. For example, larch is a highly visible deciduous tree species in otherwise evergreen forests. Larch-dominated forests were thus clearly distinguishable in the map, but may have been over-represented in historical documents (Petit & Lambin 2002). The separation of other evergreen tree species with lower abundance was related to even greater uncertainties. Therefore, we used the historical 1909 map only for an analysis of total forest cover and the separation of the two most dominant forest types, larch and spruce, in the Davos region.

The historical map for the Davos region was digitally scanned, georeferenced, georectified and rubber-sheeted in the Arc GIS (ESRI 2012; ESRI, Redlands, CA, US) and IDRISI Selva (Eastman 2012). We georeferenced the historical map by aligning 34 control points (e.g. mountain peaks, river forks and other reference locations) that were identifiable on both the historical maps and modern digital 1:50 000 topographic maps. After georeferencing, the root mean square (RMS) was calculated as an indicator of positional error. The historical map was then rubber-sheeted to further improve its accuracy by correcting geometric distortions that commonly occur in source maps. Prior to analysis, the historical vegetation maps were converted to a 30 m grid, the original minimum mapping unit (Schibler 1909).

Forest cover was derived from aerial photo interpretation (swissimage© 2009, swisstopo; DV 033594). The aerial photographs were captured during leaf-on condition in 2009 and had a spatial resolution of 0.25 m. These data were used to produce a polygon map, where the minimum mapping unit was 30 m, depicting current forest cover in the same area as that covered by the historical map. Both images were classified in eCognition (Definiens 2009) using Object-Based Image Analysis. Automated object-based analysis techniques were used to classify segments as forest or non-forest, followed by manual correction of that classification (Fig. 1b; Appendices S2, S3).

To determine the compositional change of the dominant species, we used information on historical and recent species composition for *L. decidua*, *Pi. abies*, *P. cembra* and *P. mugo*. This information was overlaid in a GIS with the forest composition of the current forest cover based on the most recent forest stand map of the Canton Graubünden (AWN 2014), which contain estimates of species composition (estimation of 10–100% of total forest cover in 10% increments) for each mapped forest stand based on a combination of aerial photographs from 2009 and complementary field surveys.

Polygons of forest change (e.g. from non-forest to forest) were overlaid on a DEM to examine how forest change co-varies with elevation, aspect and slope. Univariate cross-tabulation compared forest change as a function of these physiographic variables. Cross-tabulation analysis tabulates the total area of all values of one variable that occur in each value of a second variable. This observed amount was compared to the expected amount of forest change for each category, which is proportional to the amount of total area in that category. If a given variable does not influence a change in forest extent or dominance, then the amount of change in each class of that variable is expected to be proportional to the amount of change in the whole study area. Thus, a positive departure of the observed from the expected is indicative of increased change, while a negative departure indicates decreased change (e.g. Kulakowski et al. 2011). Significance between observed and expected values for each category are based on 10 000 Monte Carlo simulations and subsequent *t*-tests.

To analyse the historical photographs, we selected 23 historic photographs originating from the same time range as the Schibler map (e.g. ca. 1900–1920) which showed different scenes of the study area (e.g. Fig. 2). For each of these photographs we randomly selected 12 plots (ca. 50 m × 50 m) based on a stratification in order to take into account different topographic site factors (elevation, aspect) and different land-cover categories (no forest, open forest <60% crown cover, closed forest >60% crown cover). We then used the monoplotting tool developed by Bozzini et al. (2012) to georeference historical photographs to temporally match the Schibler map (e.g. 1900–1920). Monoplotting (or monophotogrammetry) involves obtaining measurement following georeferencing of a single oblique unrectified photograph using a digital terrain model (DTM; Bozzini et al. 2012; Scapozza et al. 2014). This method allowed us to produce georeferenced vector data from the 276 selected plots by drawing them directly on the analysed historical photographs.

The degree of landscape fragmentation was examined via key landscape metrics calculated using Fragstats

(McGarrigal & Marks 1993). Patch density refers to the numbers of patches per hectare; edge density equals the sum of all the edge segments that define the patch boundaries, divided by the total landscape area; perimeter to area ratio is a measure of shape complexity that is not standardized to a simple Euclidean shape. Shannon's diversity index was used to assess the landscape heterogeneity (Table 1).

Results

Magnitude of tree cover change

Mean sub-alpine tree line expanded upwards by 83 m over the course of the 20th century and ranged up to 151 m higher, depending on slope (Fig. 3a) and aspect (Fig. 3c). Tree line at the lowest elevations exhibited the largest expansion along slopes <10° (23 m) and southwestern aspects (67 m; Appendix S4). Between the years 1909 and 2009 the total area of forested land increased by 60.7%, from 3219 to 5299 ha. Forest expansion occurred at all elevations, but primarily occurred at the highest (>1900 m) and lowest (<1500 m; Fig. 4a) elevations. High-elevation areas comprise 74% of the total study area and forest expansion here accounted for 44% of the overall increase. Changes at the highest elevations were statistically significant to the 95% CI ($P < 0.001$; Fig. 4b).

Forest expansion and increase in the tree line elevation was also evident based on the analysis of repeated terrestrial photographs. However, this methodology suggested a somewhat lower extent as 31.5% of all plots near existing

Fig. 2. Repeat terrestrial photographs of Davos taken in 1900 (**a,c,e**) and 2015 (**b,d,f**) depicting treeline expansion on upper and lower treeline (**a,b**), upward expansion of treeline and increased forest density at higher elevations (ca. 1900 m a.s.l; **c,d**), and forest densification and treeline increase (**e,f**). [Colour figure can be viewed at wileyonlinelibrary.com]

forest cover (as detected in historical analysis) showed forest expansion with more change than expected occurring at the lowest and highest elevations, as opposed to mid-elevations (Fig. 5a,b). Forest density increased in 44% and decreased in 18% of the plots where repeated photographs were analysed.

Spatial variability of change in tree cover

Based on both analysis of the historical map and of repeat terrestrial photographs, more forest expansion than expected occurred on slopes that are >30° (Figs 3a,b, 5b,c). Mean tree line expansion along the less steep slopes (<30°) was 89 m, and the largest observed tree line shift was at the flattest slopes (<10°) at 145 m (Fig. 3a,b). Mean tree line expansion along the steepest slopes (>30°) was 96 m, while the largest shift in tree line was along slopes of 60° (125 m; Fig. 3a,b). The maximum expansion in tree line occurred on northwest, north and west aspects (151, 103 and 87 m, respectively; Fig. 3c,d). Based on analysis of the historical map, changes in tree line over the past century varied across aspects, but this was not clear on the analysis of repeat photographs, possibly due to the sampling locations. Change in tree line on northeast, east, southeast and south aspects ranged from 53 to 65 m. Tree line changed the least on southwest-facing slopes (51 m). Changes along the north and northwest slopes were statistically significant ($P < 0.001$; Fig. 3d).

Overall expansion of forest cover also varied across slopes but less so than tree line expansion. Forest cover on southern slopes, where tree line increase was smallest, increased by 168 ha (9%) compared to 174–268 ha (10–16%) on all other aspects (Appendix S5a,b). Most (31%) forest expansion occurred on north and northwest slopes. Changes on the steepest and flattest slopes were statistically significant ($P < 0.0001$; Appendix S6b).

Changes in forest composition

Based on analysis of the historical map, changes in forest composition were unique for both *Pi. abies* and *L. decidua*, although trends of increasing abundance were present regardless of species. *Pi. abies* increased across all elevations, but primarily at the highest elevations (>1900 m a.s.l) and secondarily at lowest elevations (<1500 m a.s.l; Fig. 4c,d). Compared to expected values of change, *Pi. abies* increased by 391 ha (183%) at the highest elevations (>1900 m) and 223 ha (178%) at the lowest elevations (<1500 m a.s.l), but less than expected in intermediate elevations between 1500 and 1900 m a.s.l. *Pi. abies* increased 276% (819 ha) more than expected at slopes <30° ($P > 0.0001$; Appendix S5c,d). *Pi. abies* increased (mainly) along the west and southwest slopes, 223 and 225 ha, respectively (Appendix S5c, d).

Larix decidua increased predominately at the moderate (>1500 m a.s.l) and highest (>1900 m a.s.l) elevations, where a 308-ha (906%) and 312-ha (251%) increase was observed compared to expected values, respectively (Fig. 4e,f). *L. decidua* preferentially increased along the steepest slopes (>30°) by 467 ha (378%) compared to expected values, which equated to 86% of the total increase of *L. decidua* (560 ha) observed across the entire study area (Appendix S6e, f). *L. decidua* increased most notably along north- and east-facing slopes, 194 ha (35%) and 138 ha (25%), respectively (Appendix S6e,f).

Based on analysis of historical terrestrial photographs, the change in forest composition was strongly tied to elevation. Over the past century, relative larch dominance increased with increasing elevation, including at the highest elevational zone (Fig. 6). However, across all elevational zones, there were also plots where larch had decreases in total tree cover, in particular <1700 m a.s.l., where 40% of all plots showed decreased larch compared to spruce (Fig. 6).

Discussion

Much recent work has focused on widespread global changes in tree line and forest cover over the past decades (Pauli et al. 1996; Holtmeier & Broll 2007; Jurasinski & Kreyling 2007; Harsch et al. 2009), including in the European Alps (Kulakowski et al. 2011). Importantly, the current study shows such changes in the Swiss Alps began much earlier. The changes documented in the current study across the entire 20th century were much larger (60.7% increase in forest cover) than those documented in the same region during the second half of the 20th century (13.4% increase in forest cover; Kulakowski et al. 2011). These changes reflect the decrease in land-use pressures near upper tree line (Bebi et al. 2017), which accounted for 47.3% of the total forest cover expansion during the first half of the 20th century. The

Table 1. Key landscape fragmentation metrics for total forested areas in 1909 and 2009.

Year	Total Forest Area (ha)	No. of Patches	Patch Density (no.·ha^{-1})	Mean Patch Area (ha)	Parameter to Area Ratio (median)	Shannon Diversity Index
1909	3219	888	27.6	3.6	1640.7	4.1
2009	5299	413	7.8	12.8	1333.3	1.7

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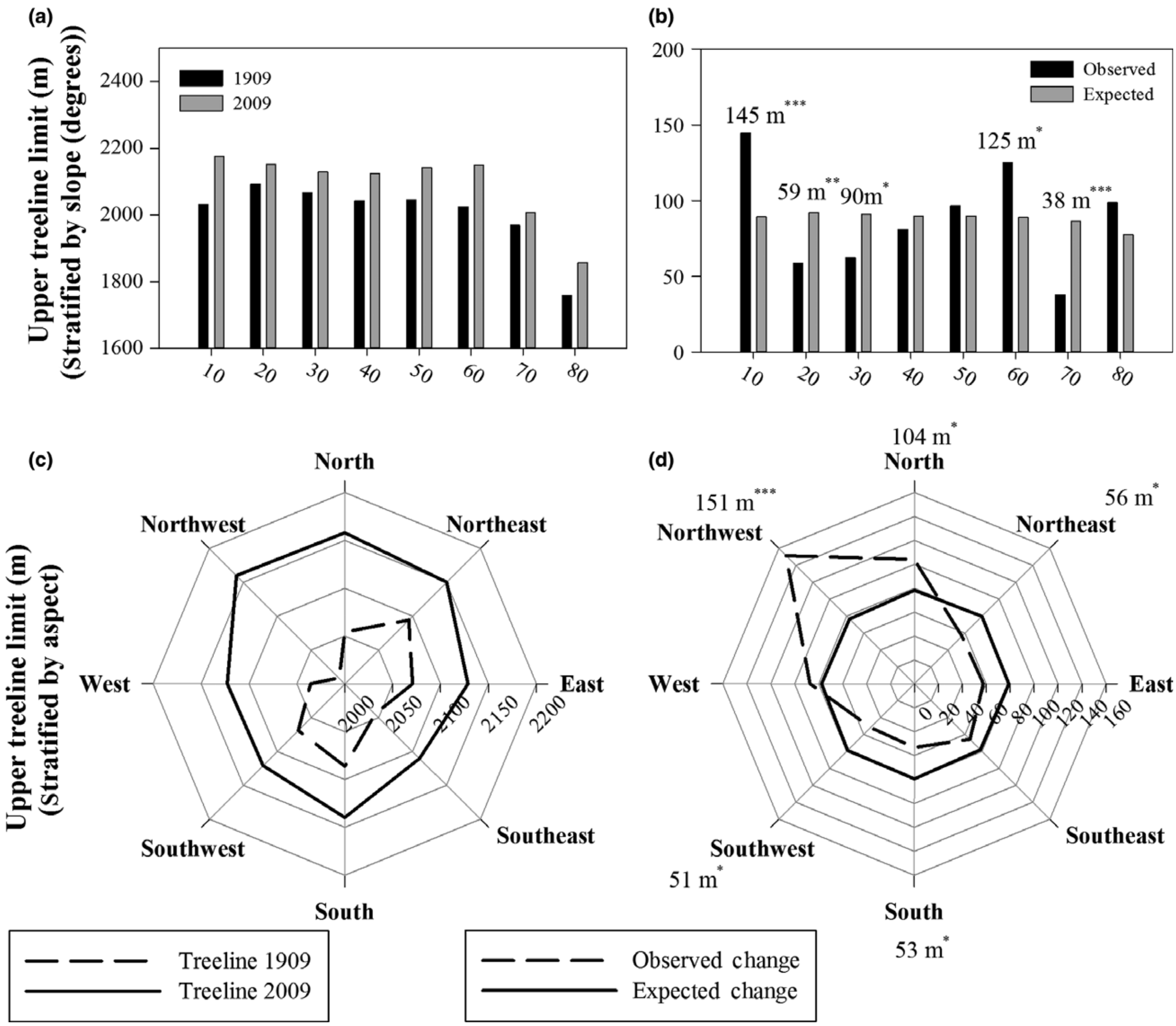

Fig. 3. Total change in treeline per slope in terms of the 99th percentile upper treeline limit (**a**) and the observed and expected treeline change per aspect (**b**). Total change in treeline per aspect in terms of the 99th percentile upper treeline limit (**c**) and the observed and expected treeline change per aspect (**d**). Values above aspect indicate total observed treeline change in meters. Asterisks indicate significant differences (*P = 0.05; **P = 0.01;***P < 0.001) based on 1000 Monte Carlo simulations and subsequent *t*-tests.

current findings suggest that changes in the extent, structure and dynamics of these sub-alpine forests prior to the mid-20th century were likely larger than the changes since then.

The unique methodological approach of the current study allowed us to leverage the advantages of historical maps, aerial photographs and repeat terrestrial photographs in a manner that minimizes the shortcomings of any one of these approaches. Analyses of historical maps can provide a "big picture" of overall forest cover change, but contain uncertainties associated with location accuracy, patch boundary delineation criteria and the definition of forest categories. Furthermore, it is normally impossible to distinguish different forest structures, species composition and forest cover based only on analyses of historical maps. In contrast, analyses of repeat photographs typically offer a view of a limited spatial extent, but within that extent information about changes, including relatively minor increases or decreases of forest density or shifts in species composition, is typically more accurate and detailed.

In the current study, analysis of repeat terrestrial photographs generally confirmed the results of the historical map, but suggested that the latter analysis may overestimate increases in forest cover by as much as 10–30%. The comparison of the two methodological approaches also

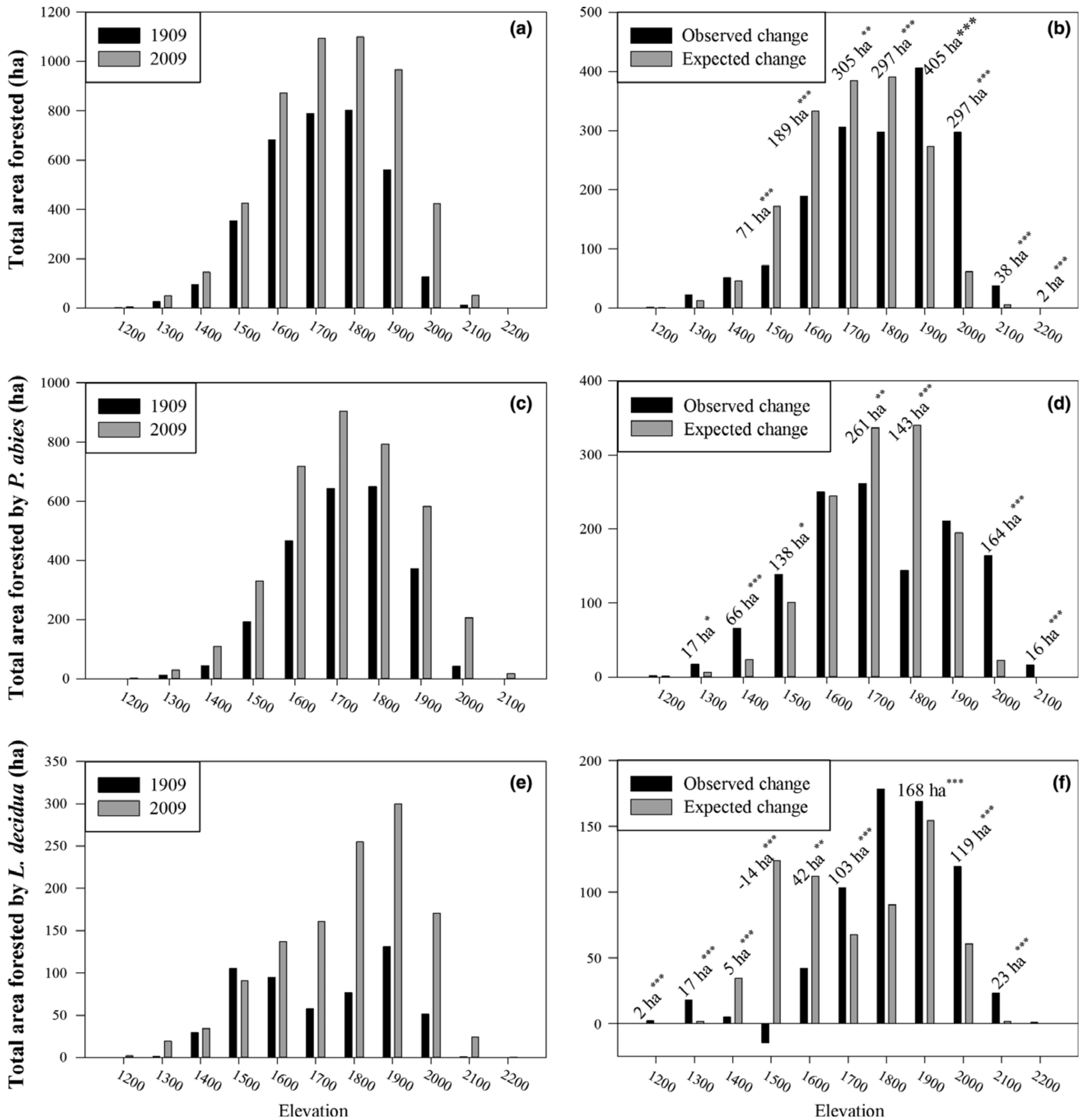

Fig. 4. Forest cover (ha) cumulative expansion in terms of elevation (**a**) and the observed and expected forest cover per elevation (**b**). Forest cover (ha) cumulative expansion in terms of elevation of Picea abies (**c**) and the observed and expected forest cover per elevation (**d**). Forest cover (ha) cumulative expansion in terms of elevation of Larix decudia (**e**) and the observed and expected forest cover per elevation (**f**). Values above the bars indicate total observed forest change in hectares. Asterisks indicate significant differences (*P = 0.05; **P = 0.01;***P < 0.001) based on 1000 Monte Carlo simulations and subsequent *t*-tests.

suggests that the position of tree line did not increase everywhere in the landscape and may be overestimated by the analysis of historical maps alone, possible due to uncertain criteria for definitions of forest. We suggest that while the use of either historical maps or repeat photographs may lead to an incomplete, or even misleading, view of ecological change, the combination of these approaches provides a more comprehensive, robust, and reliable representation.

Both methods applied in this study confirm a long-term increase in landscape homogeneity. Over the past century, the number of unique forest patches has decreased and

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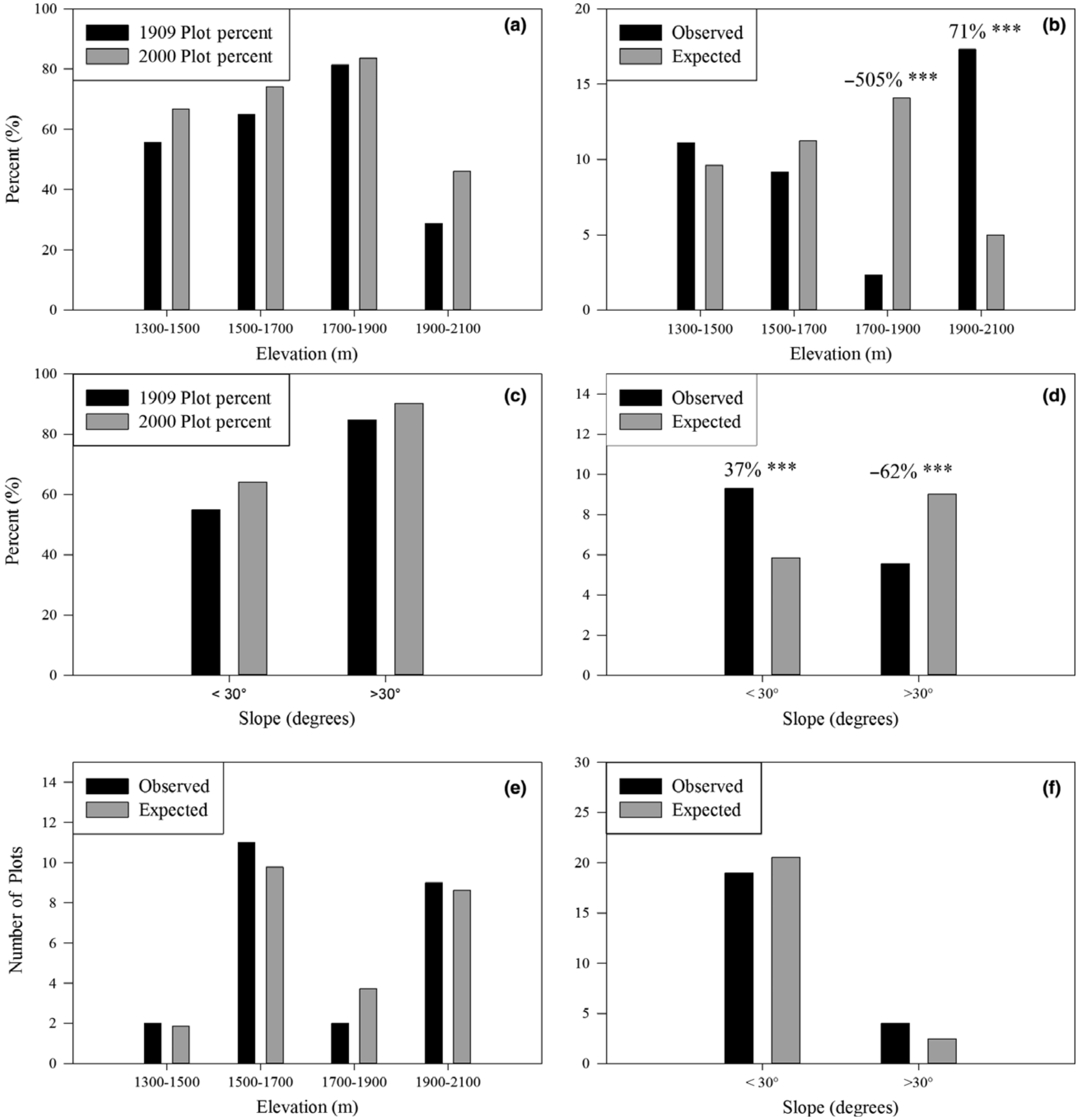

Fig. 5. Amount forested stratified by elevation (**a**) and slope (**c**) per plot for 1909 and 2009 based on terrestrial repeat photography. Percentages above bars indicate departure from the expected per plot percent stratified by elevation (**b**) and slope (**d**). Observed versus expected total forested area across the number of plots stratified by elevation (**e**) and slope (**f**). Asterisks indicate significant differences (*$P = 0.05$; **$P = 0.01$;***$P < 0.001$) based on 1000 Monte Carlo simulations and subsequent *t*-tests.

patch size has increased (Table 1). Because of differences in data sources and their minimum mapping units, our results are not directly comparable to previous analyses of changes in landscape homogeneity in this region (Kulakowski et al. 2011). However, we note that as with changes in overall forest extent, increases in landscape homogeneity are more pronounced than those reported over the past 50 yr, suggesting that the processes that drive landscape homogenization have been at play at least for the past century. Changes in stand structure and landscape homogeneity are likely to affect biodiversity, disturbance regimes and other key ecological process. A less fragmented forest facilitates the movement of certain fauna species (Thomas 2000) as well as the spread of forest

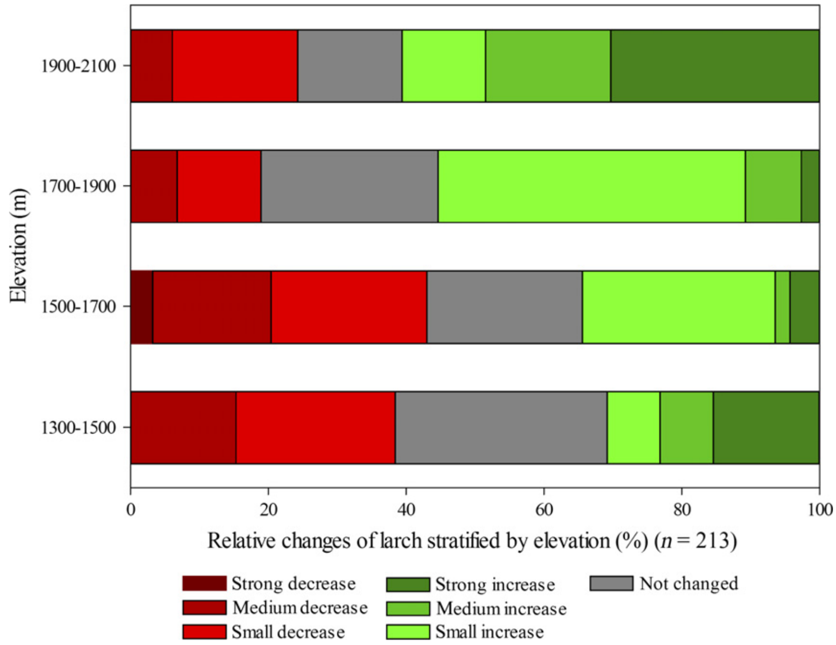

Fig. 6. Relative changes in larch density stratified by elevation plot from 1909 and 2009 based on terrestrial repeat photography. [Colour figure can be viewed at wileyonlinelibrary.com]

disturbances such as fire (Veblen et al. 1994) and insect outbreaks (Raffa et al. 2008). For example, higher fuel continuity in less fragmented landscapes can facilitate fire spread, as compared to more fragmented landscapes in which fragmentation can inhibit fire spread. Thus, reduced forest fragmentation and increased forest density over the past 100 yr may have increased the risk of more extensive fires in the Davos region as well as in other regions that have been affected by similar processes.

In addition to important changes in landscape homogeneity, over the past century the position of tree line has increased on all slopes, elevations and aspects (Figs 3a,c, 4a). The position of tree line in the study area has been historically driven by climate, land use and natural disturbances. Intensive land use since about the 13th century depressed tree line, at least in some parts of the study area. Furthermore, avalanche disturbances also depress tree line in some areas and can interact with land use. Since the end of the 19th century grazing pressure has been reduced in some regions, which has led to increased tree growth in tree line ecotones where tree line may have been depressed. The most notable changes of forest cover in our study region were in locations close to tree line (e.g. high elevations >1900 m a.s.l) and on western aspects, where temperature may have been particularly limiting and where land-use change has been most pronounced. This is consistent with previous work in the central Alps that has shown temperature to be limiting on cooler (northern) aspects and moisture to be limiting on warmer (southern) aspects (Brang 1998). Limited moisture on southern aspects is likely to continue to limit *Pi. abies* seedling establishment (Brang 1998). However, southern slopes (more often than northern slopes) still are used for cattle grazing above tree line, which likely interacts with moisture limitations on these aspects to determine tree establishment and growth (Bebi et al. 2017). In some parts of the study area that are still intensively grazed or where frequent avalanche disturbances are the dominant factor, tree line has not changed detectably (Bebi et al. 2009, 2017)

The long-term changes documented in the current study are likely associated with the major changes in land use and climate that begun in the Alps and across Europe in the mid-19th century. However, it is probable the dynamics in this region have been affected by broad trends in land use and climate as well as local circumstances of economic development and land use (Price & Thompson 1997). As a result, the exact rate of change over the same time period would be expected to vary across the Alps and other regions (Mather & Fairbairn 2000).

Regional temperature in the Swiss Alps has increased 1.4 °C over the past century (Begert et al. 2005), contributing to more favourable conditions for plant growth and tree establishment, particularly on sites that are otherwise favourable (i.e. less steep slopes, early snow disappearance in spring, moderate or no competition from other vegetation). Warming in temperature-limited regions has been shown to be one of the main drivers of

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increased tree line and forest expansion (Jurasinski & Kreyling 2007; Kulakowski et al. 2011), increased seedling establishment and increased forest homogeneity (Niedrist et al. 2009). For example, shifts in tree line in southwest Switzerland from 1901 to 2000 have been strongly related to the climatic warming over this period (Leonelli et al. 2011). However, Leonelli et al. (2011) suggested that future increases will be limited by localized processes (e.g. rockslides, landslides, debris flow, etc.) and unstable land forms (e.g. talus slopes, screes, rock faces, etc.), which are located in areas that are not limited by climatic factors.

Changes in tree lines and sub-alpine forests are often primarily associated with warmer temperature during growing season (Körner & Paulsen 2004) and/or during winter (Harsch et al. 2009). However, in the Alps changes in climate (e.g. temperature, precipitation, duration of snowpack, etc.) have been shown to strongly interact with changes in land use and disturbance regimes over the past decades to affect forest structure and cover (Motta et al. 2006; Kulakowski et al. 2011), and it is also likely that such interactions over the past century have shaped forest ecosystems. For centuries, the landscape of the Alps has been shaped by intensive grazing by cattle and goats and other agricultural land use (especially at high elevations above tree line and at low elevation below tree line), deforestation for settlement, fuels and mining, and urbanization (Price & Thompson 1997). These activities generally reduced forest cover and forest density and increased landscape fragmentation. However, industrial expansion and new employment opportunities in tourism and related economic sectors over the past century spurred the migration of peoples towards urban settings, leaving less productive agricultural and grazing fields abandoned. Over the past century, less steep slopes in valley bottoms have been managed, worked and developed for urban and suburban purposes (Walther 1986). In contrast, steeper slopes and higher elevations have become economically unviable as they are more labour intensive and, thus, have largely been abandoned (Gellrich et al. 2007).

Over the past decades even relatively moderate changes in land use have facilitated successful seedling establishment along and above tree line, and have been one of the most important drivers of changes in forest cover and structure in the Davos area (Kulakowski et al. 2011) and in other mountain regions in developed countries (Moen et al. 2004; Gehrig-Fasel et al. 2007; Jurasinski & Kreyling 2007; Garbarino et al. 2010; Krumm et al. 2011). In the current study, reduced grazing intensity, shifts from grazing by goats to cattle and changes in land use away from agricultural pastures and meadows are likely to have been important drivers of not only forest extent, but also of changes in forest composition and forest structure. Low-intensity cattle grazing normally increases exposed bare mineral soil, reduces competition from grasses but results in relatively few seedlings being established (Mast et al. 1997; Garbarino et al. 2010), and can thereby preferentially facilitate regeneration of the shade-intolerant *L. decidua*. In contrast, reduced extent of *L. decidua* at the lowest elevations is likely to have been the result of competitive replacement by the more shade-tolerant but also more frost-intolerant *Pi. abies* (Pretzsch & Schütze 2009).

Changes in the amount and location of forested area over the 20th century that are documented in the current study are so pronounced that there are likely major implications for several ecosystem services (e.g. biodiversity, recreation, protection against natural hazards, tourism, etc.), as well as for above-ground C stocks and climate feedbacks. Protection against natural hazards, which is often seen as the most important ecosystem service in the region, has improved considerably over the past century (Grêt-Regamey et al. 2008; Bebi et al. 2009). However, other ecosystem services may be compromised with increasing forest cover density, decreasing fragmentation and shifts in species compositions. In particular, shifts from open larch-dominated forests, which have been favoured by traditional silvo-pastoral management (Garbarino et al. 2009, 2011) to more spruce-dominated and denser forest structures potentially may decrease tourism values due to changes in aesthetic of these landscapes and habitat for certain species (Garbarino et al. 2011; Bebi et al. 2012).

Conclusion

Over the past century, elevation of tree line and total forest area increased on all aspects and elevations, but most where changes in land use and climate have been favourable to establishment and growth of tree species. Importantly, the magnitude of ecological change in the first part of the 20th century is greater than that reported for the latter half of the 20th century in this region (Kulakowski et al. 2011), suggesting that the on-going major trajectory in forest cover began with key changes in land use and climate in the 19th century.

Assessing long-term changes is critical for better understanding on-going and future ecological changes. In the present study, we used a unique combination of a high-quality historical map, recent remotely sensed data, cutting-edge image classification protocols, as well as geo-referenced monoplotting of repeat terrestrial photographs to precisely quantify different parameters of forest change over the past century. To our knowledge, no previous work has used this combination of approaches to robustly describe long-term ecological change. We suggest integrating multiple sources of historical data to most accurately describe long-term ecological dynamics.

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Supporting Information

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

Appendix S1. Detailed enlargement of the 1909 historical map.

Appendix S2. Examples of the resulting image 1909 historical map classification from the synthetic approach of combining automated techniques with manual correction.

Appendix S3. Examples of the resulting image 2009 aerial imagery classification from the synthetic approach of combining automated techniques with manual correction.

Appendix S4. Total change in lower limit tree line per slope and aspect.

Appendix S5. Total forest cover cumulative expansion for the entire study area, *Picea abies* and *Larix decudia* as a function of aspect.

Appendix S6. Total forest cover cumulative expansion for the entire study area, *Picea abies* and *Larix decudia* as a function of slope.

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