Insights about past forest dynamics as a tool for present and future forest management in Switzerland

Authors: Conedera M.[1], Colombaroli D.[2], Tinner W.[2], Krebs P.[1], Whitlock C.[1,2,3]

[1] Swiss Federal Institute for Forest, Snow, and Landscape Research WSL, a Ramél 18, CH-6953 Cadenazzo, Switzerland
[2] Institute of Plant Sciences and Oeschger Centre for Climate Change Research, University of Bern, Altenbergrain 21, CH-3013 Bern, Switzerland
[3] Department of Earth Sciences and Montana Institute on Ecosystems, Montana State University, Bozeman Montana, 59717 USA

Corresponding author:

Marco Conedera
Swiss Federal Institute for Forest, Snow, and Landscape Research WSL
a Ramél 18, CH-6953 Cadenazzo, Switzerland
marco.conedera@wsl.ch

Abstract

Mountain forest ecosystems in central Europe are a product of millennia of land use and climate change, and this historical legacy shapes their vulnerability to projected climate change and related disturbance regimes (e.g. fire, wind throw, insect outbreaks). The transitional and highly dynamic state of present-day forests raises questions about the use of modern ecological observations and modeling approaches to predict their response to future climate change. We draw on records from the different subregions (northern, central and southern Alps and their forelands) in and around the Swiss Alps, which has one of the longest records of human land-use in Europe, to illustrate the importance of paleoecological information for guiding forest management and conservation strategies. The records suggest that past land use had different impacts on the abundance and distribution of woody species, depending on their ecology and economic value. Some species were disadvantaged by intensified burning and browsing (e.g. *Abies alba*, *Ulmus*, *Tilia*, *Fraxinus*, *Pinus cembra* and the evergreen *Ilex aquifolium* and *Hedera helix*); others were selected for food and fiber (e.g. *Castanea sativa*, *Juglans regia*) or increased in abundance as

consequence of their utility (charcoal, acorns, litter and other products) or resistance to disturbance (e.g. *Picea abies*, *Fagus sylvatica*, *Pinus sylvestris* and deciduous *Quercus*). Another group of trees increased in distribution as an indirect result of human-caused disturbance (e.g. *Betula*, *Alnus viridis*, *Juniperus*, and *Pinus mugo*). Knowledge of past species distribution, abundance and responses under a wide range of climate, land use and disturbance conditions is critical for setting silvicultural priorities to maintain healthy forests in the future.

Key words: forest ecology, vegetation history, land use history, fire history, paleoecology, Holocene

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1. Introduction

Present-day Alpine forest ecosystems and their dynamics are fundamentally different from those of the past. In particular, a long human history has had irreversible consequences on Alpine forest ecosystems (e.g. Tinner et al. 2005; Carcaillet et al. 2009; Blarquez et al. 2010; Valsecchi et al. 2010), decoupling natural vegetation-climate relationships in many regions and maintaining plant communities in a non-equilibrium state with climate and disturbance regimes (Svenning et al. 2015). In recent decades, reduced management and abandonment of remote mountain areas have led to expansion of forest cover and loss of high-diversity meadows (Gehrig-Fasel et al. 2007; Loran et al. 2016). The transitional and highly dynamic state of Alpine forests challenges forest managers tasked with assessing the local consequences of climate change on forests and developing adaptive and restorative silvicultural plans to ensure near-to-nature conditions and continued delivery of ecosystem services in the future (Lindner 2000; Schmid et al. 2015). However, the strong human signature on present-day forest composition, structure and dynamics in many regions raises concerns about the use of short-term ecological observations and standard modeling approaches (Iverson and Mckenzie, 2013) to predict forest responses to future climate change (Ibanez et al. 2006; Williams and Jackson 2007; Dawson et al. 2011; Tinner et al. 2013). To understand present-day relationships between climate, humans, vegetation and disturbance requires information on the causes and consequences of ecosystem change in the past. This information is especially critical for forests in the Alpine region of Switzerland, where present-day ecosystem dynamics are conditioned by historical legacies and altered disturbance regimes, and the abundance and distribution of current forest types and taxa are a product of both anthropogenic manipulation and climate change, which are difficult to disentangle.

In this paper, we review and describe the influence of past changes in climate, land use and disturbance on the development of Swiss mountain forest ecosystems and the history of selected woody species. Representative sites with good chronological control (i.e. multiple radiocarbon dates) and taxonomical resolution are selected along a strong north-to-south environmental gradient in the Alps to compare forest history in different settings. The time span of interest is the last ~20,000 years, which covers the period from the end of the last glaciation to the present day. Special focus is on the last 7500 years starting with the onset of the Neolithic period and the progressive human alteration of land cover and forest composition. The specific aim of the paper is to show how knowledge of Alpine forest history can inform management efforts that seek to (1) assess forest sensitivity to future climate change; (2) choose between different management options (e.g. preserving close-to-nature conditions, maintaining cultural landscapes, protecting species of special concern, maximizing biodiversity); and (3) maintain forest capacity to provide important ecosystem goods and services.

We first briefly describe the Holocene climate history of the study area and the main responses of tree species to these changes. Second, we discuss the main human impacts since the onset of the Neolithic period. Finally, we examine the usefulness of this type of paleoecological information as a baseline for making local forest management decisions in the face of global change.

2. Material and methods

2.1 Study area

Three subregions in Switzerland (southern Alps and their forelands, central Alps, and northern Alps and their forelands) constitute a representative environmental transect through central and southern European mountain ecosystems (Fig. 1). The southern Alps and their forelands are the warmest subregion displaying warm-temperate climate conditions in the low-elevation lake area (Insubria). The elevation ranges from 200 m asl (Lago Maggiore Locarno) to 3402 m asl on the Adula Peak in northern Ticino, and about half of the southern subregion lies above 1500 m asl, where mean annual temperature is correspondingly low (e.g. 3.9°C in San Bernardino at 1639 m asl.). Average (1981-2010) annual temperature for the subregion is ~12-13°C (e.g. Swiss

Meteorological Station Locarno-Monti) and annual precipitation ranges from 1300 mm in the west (e.g. meteorological station Acquarossa) to 1900 mm in the east (Locarno-Monti). In winter, the climate is dry and mild and summers are humid (June-September 800 to 1200 mm of precipitation), with thunderstorm events alternating with periods of drought. Present-day forests are organized by elevational belts (Fig. 2). *Castanea sativa* (sweet chestnut) dominates low-elevation forests (up to 900-1000 m asl). These closed forests, which occur in other regions of southern Europe (e.g. Apennines, Pyrenees, the Balkans), occasionally support other thermophilous broadleaved species, such as *Tilia cordata* (small-leaved linden), *Quercus petraea* (sessile oak), *Q. robur* (common oak), and (*Q. pubescens* (downy oak), *Alnus glutinosa* (common alder), *Prunus avium* (sweet cherry), *Acer* spp. (maple), and *Fraxinus* spp. (ash). At middle elevations (900-1400 m asl), forests consist of mostly pure stands of *Fagus sylvatica* (European beech), and at higher elevations, forests are dominated by *Picea abies* (Norway spruce) and at upper treeline by *Larix decidua* (European larch). On south-facing slopes, beech forest is sometimes absent, and *Abies alba* (silver fir) is present in small patches on north-facing slopes in the central part of the subregion. *Pinus sylvestris* (Scots pine) grows on dry south-facing slopes, and *P. cembra* (stone pine) occurs in the most continental settings at high elevations (Ceschi 2014).

The central Alps subregion, including the Valais and Engadine, displays a markedly continental climate characterized by low annual precipitation (e.g. 603 mm in Sion at 482 m asl, 639 mm in Zermatt at 1638 m asl, 713 mm in Samedan at 1703 m asl), cold winters, high insolation and extreme annual and daily temperature excursions. The temperature range is correspondingly large with mean annual temperatures of ~10°C on valley bottoms (e.g. 10.1°C in Sion at 482 m asl), 2.0°C at in Samedan at 1703 m asl, and ~0°C at upper treeline (e.g. -0.6°C in Col du Grand St-Bernard at 2472 m asl). The present distribution of forest types in the central Alps reflects this topographic and climatic gradient (Fig. 2). Termophilous deciduous broadleaves forests support by downy oak in continental sub-mediterranean settings, and sessile oak and common oak in the sub-oceanic lowlands (~400-800 m asl). At medium elevations (~800-1400 m asl), stands of Scots pine and spruce are present, and beech and fir are confined to the most mesic settings. Spruce forest grows at high elevations (~1400-2100 m asl) and is replaced by larch and stone pine forests at upper treeline (Werlen 1994) and mountain pine forests (*Pinus mugo* spp. *uncinata*) on dolomitic soils in the eastern Alps (Gobet et al. 2003; Stähli et al. 2006, Ellenberg 2009).

The northern Alps subregion, which includes the northern Alps and their forelands, displays a cool temperate central European climate, with mild summers (18°C July average), cool winters (−1°C January mean) and annual precipitation ranging from ~1000 mm at low elevations (1196 mm in Interlaken at 577 m asl) to ~1500 mm at higher elevations (1338 mm in Adelboden at 1327 asl). Today's vegetation consists of highly fragmented relict forest patches. As in the southern region, vegetation is organized in belts (Fig. 2), from mixed oak-beech forests (including other deciduous trees such as linden, elm, maple, and ash) at the lowest elevations (<600 m asl), mixed beech-fir forests in the mountain belt (600-1500 m) to spruce forest in the subalpine belt (1500-2000 m; Ellenberg 2009). Stands of larch and/or stone pine are present in the northern Alps above the spruce belt in proximity to the continental central Alps.

2.2 Information from paleorecords

Paleoecological information comes largely from the fossils preserved in the sediments of lakes and wetlands (Smol et al. 2001). Plant macrofossils and microfossils (e.g. pollen, spores, stomata) are commonly used to reconstruct vegetation at local and regional scales (Birks and Birks, 1980). The chronology for these studies comes from the development of age-depth models based on a sequence of radiocarbon dates obtained from terrestrial organic matter in sediment cores. The site-specific chronology provides a timeline for understanding changes in vegetation and other aspects of the environment, often at decadal to century-scale resolution, and allows comparison across sites and with independent evidence of climate and land use.

Climate reconstructions come from proxy records that are sensitive to climate variability on different time scales and from paleoclimate modeling studies that describe the influence of large-scale climate drivers on regional conditions. Biological paleoclimate proxies in sediment cores include diatoms (photosynthesizing algae), chrysophytes (golden algae), cladocera (water fleas), and chironomids (nonbiting midges); these proxies have been used to reconstruct past changes in temperature, nutrient levels, chemistry and pH, lake level, and salinity. Non-biotic proxies, such as stable oxygen isotopes and the geochemical characteristics of the sediments, are also used to infer past climate and stages of landscape evolution (see Smol et al. 2001 for more information).

Human activity is identified in pollen or plant macrofossil records by the presence of remains of crops, fruit tree cultivars, non-native species, and past shifts in vegetation composition associated with particular land use (e.g. Rey et al. 2013). Direct proxies of human activities include cultivated taxa introduced to the area for agricultural purposes (adventive agriopythes), such as cereals (*Avena* t, (t=type), *Triticum* t. and *Hordeum* t, usually grouped as *Cerealia* t or *Secale cerealia*), and other crop species, such as *Fagopyrum tataricum, Cannabis sativa* t or *Linum usitatissimum*. Accidentally introduced species, such as *Plantago lanceolata* t which first appeared in Switzerland in the Late Mesolithic (Behre, 1981, 1988; Tinner et al. 2007) and *Ambrosia* and other pollen types that appeared in modern times, are also unequivocal evidence of land use and anthropogenic disturbance. Past pastoral activity and herbivore density are inferred from pollen (e.g. Cichorioideae, Asteroideae), spores of dung-specialized (coprophilous) fungi, including *Sporormiella* spp., *Podospora* spp., *Ustulina deusta* (van Geel et al. 2003; Graf and Chmura 2006), and particular ferns (e.g. *Botrychium lunaria*). Plants that are altered indirectly by human impact are called apophytes (present in the native flora but favored by land use) and include *Urtica, Artemisia, Rumex acetosella* t, *Succisa, Campanula, Fallopia,* and Brassicaceae (Behre 1981; Lang 1994). Charcoal particles in sediment cores provide direct evidence of past fires, with high charcoal accumulation rates (particles cm^{-2} yr^{-1}) indicating periods of high fire activity (Whitlock and Larsen

2001; Conedera et al. 2009). Not considered here are disturbances, such as pest outbreaks or pathogens, that lack sedimentary proxies.

In this review, we focus on well-dated sedimentary records that have good pollen, plant macrofossil and charcoal data to reconstruct past vegetation, fire, and human impact. We consider nine sites from the northern subregion, seven from the central subregion and seven from the southern subregion (Fig. 1). For details on the reference sites, see Appendix 1.

3. The climate and vegetation history of the Alps

3.1 Past climate variations in the Alps

The end of the last glaciation (~20,000-11,700 cal yr BP = before 1950 AD) is a key period for understanding early landscape development in the Alps, because it experienced major climate variations on a broad geographic scale (from Greenland to Central Europe; von Grafenstein 1998, 1999; Ammann et al. 2000, 2013; Tinner et al. 2003). For example, the onset of the Bølling Interstadial (warm) period at ~14,650 cal yr BP (Ammann et al., 2000) featured a 5-6°C rise in temperature over the time span of a century (the highest rate of increase, 4.6°C, occurred within a 50 year period) (Fig. 3). This warming was followed by an abrupt cooling during the Younger Dryas Cold Period (12,700-11,700 cal yr BP), and then rapid warming at the beginning of the Holocene (11,700 cal yr BP, Ammann et al. 2000). A brief cold reversal occurred at 8200 cal yr BP (Wick and Tinner 1997; Alley and Agustsdottir 2005; Heiri et al. 2014).

A period of sustained warming characterized the early Holocene (11,700-5000 cal yr BP). In Europe, summer temperatures were higher than present by 1–2° C towards the end of the early Holocene and the subsequent mid Holocene. The climate of the late Holocene, the last ~5000 years, was governed by declining summer insolation and rising winter insolation, and this gradual trend, in turn, led to cooler summers and warmer winters in Europe than before. The late Holocene is sometimes referred to as the Neoglaciation, because it experienced century-long periods of colder climate and a renewed glaciation (Holzhauser et al. 2005). However, century-long temperature oscillations also occurred during the early and mid Holocene (Heiri et al. 2004), causing upslope and downslope movements of forests (Wick and Tinner 1997; Haas et al. 1998, Tinner and Theurillat 2003). Recent climatic oscillations included the Roman Warm period (-2250-1600 cal yr BP, corresponding to ~250 BC-400 AD), the Medieval Climate Anomaly (~1200-800 cal yr BP, corresponding to ~800-1200 AD), and the Little Ice Age (550-100 cal yr BP, corresponding to ~1400-1850 AD) (Fig. 3) (Wanner et al. 2008).

3.2 Response of tree species to past climate variations

To understand how Alpine forests developed in response to past climate change, we target three climate periods that occurred before significant human presence (Heiri et al. 2014): the abrupt warming period of Bølling Interstadial (~14,600 cal yr BP), the early-Holocene warming period (11,700-5000 cal yr BP), and the cold reversal at 8200 cal yr BP. In the lowland and mountain areas of the northern subregion (400-1600 m asl) and in the mountain areas of the southern subregion (900-1600 m asl), pollen, macrofossil and stomata records show that the Bølling Interstadial Warming led to a replacement of tundra vegetation by shrubs and light-demanding trees, such as larch, birch, Scots pine and stone pine (Vescovi et al. 2007; Ammann et al. 2013).

Differences in the ecological characteristics of the tree species also accounted for variations in the pattern of treeline development in the early Holocene in the Alps. Larch, Scot pine, and birch were particularly advantaged by high insolation and continentality, low moisture availability and shallow soils, whereas Stone pine expanded later (~10,500-8000 cal BP) when summer-drought stress was reduced, temperatures were higher than before and soils were better developed (Tinner and Kaltenrieder 2005; Gobet et al. 2005; Schwörer et al. 2014b; 2015; Table 1). Subsequently (~9000 cal BP), silver fir expanded into stone pine forests, forming timberline communities that are now nearly extinct in the Alps (Wick et al. 2003, Gobet et al. 2010).

During the early Holocene, thermophilous broadleaved deciduous (e.g. deciduous *Quercus, Acer, Ulmus, Tilia, Fraxinus, Alnus*) and shrubs (e.g. *Corylus avellana,* hazel) became increasingly important at low elevations in all subregions (e.g. Lotter et al. 1992) and expanded their ranges to higher elevations (e.g. Zoller 1960; Zoller and Kleiber 1971; Welten 1982; Vescovi et al. 2006; Rey et al. 2013: Schwörer et al. 2014a; Thöle et al 2016). The progressive build-up of flammable fuel (e.g. pines) and summer warmer-than-present conditions were associated with more fires at high elevations and in the dry central subregion (Wick and Tinner 1997; Gobet et al. 2003; Tinner and Kaltenrieder 2005; Valsecchi and Tinner 2010; Blarquez and Carcaillet 2010; Stähli et al. 2006; Schwörer et al. 2014a; Colombaroli et al. 2010). Increased fire activity probably allowed early-successional mountain pine (*Pinus mugo* spp. *uncinata*) to expand in the driest (eastern) part of the central Alps where infertile dolomite soils are present (Stähli et al. 2006). In the Alpine forelands, early-Holocene fire activity also gradually increased and was associated with an expansion of fire-adapted *Pteridium aquilinum* in the southern subregion at ~10,500 cal BP (Tinner et al. 1999; 2005).

Forest composition experienced a dramatic change as a consequence of the cooling event at 8200 cal yr BP when warm dry summers were abruptly replaced by cool moist conditions (Dansgaard et al. 1993; Heiri et al. 2014). This event was a tipping point for the vegetation and enabled the expansion of moist-tolerant beech and silver fir in the northern subregion at the expense of less mesophilous forest species. Interestingly, the subsequent return to warm conditions at 8000 cal yr BP did not allow more drought-adapted taxa to regain their previous abundance, and moist conditions maintained silver fir-beech forests (Tinner and Lotter 2001; 2006). Unlike in the northern subregion and in contrast to silver fir, beech did not become abundant in the dry continental settings of the central Alps and in the warm-temperate setting of the southern subregion following the 8200 cal yr BP event (Welten 1982, Tinner et al. 1999). Probably the species was limited by its low tolerance to drought and/or competition with previously established silver fir (Tinner et al. 2013). Scots pine and mountain pine in the central Alps and spruce in Engadine grew at high elevations, while mixed oak forests with abundant Scots pine were present at low elevations. In the central Alps, silver fir was important (15-50% of pollen) across all vegetation belts (Welten 1982; Tinner et al. 1996; van der Knaap et al. 2005; Gobet et al. 2003; Colombaroli et al. 2013). The relative sensitivity of different tree taxa to environmental factors (drought, solar radiation, climatic continentality and seasonality, soil development) are summarized in Table 1 based on our understanding and interpretation of their response to past climate changes.

3.3 Human presence and impact in the Alpine region

Hunting and gathering activities in the Alpine lowlands are evidenced during the Late Mesolithic period (~6700-5500 BC, Tinner et al. 2007). With the onset of the Neolithic period (~5500 BC), pastoral (mainly imported goats and sheep) and arable farming is evidenced by the increase of coprophilous fungi and pasture indicators (e.g. Asteroideae, Cichorioideae, *Urtica*, *Plantago lanceolata*, *Rumex* t) in pollen and plant macrofossil records from the reference sites (Wick and Tinner 1997; Colombaroli et al. 2010; Rey et al. 2013; Schwörer et al. 2014a, 2014b, 2015). Fire activity also increased, and although generally attributed to anthropogenic burning, fire occurrence was likely facilitated by warm-dry conditions at this time (Tinner et al. 1999). Fire frequency was locally variable, but charcoal records show clear subregional differences with high fire activity in the south and less fires in the north (Fig. 4). These differences likely reflect the temperature and dry-season gradient that exists across the Alps (Tinner et al. 2005). Increased charcoal abundance and presence of pollen types indicative of open environments, pastures and disturbance (e.g. *Plantago* spp., *Rumex acetosella*, Cichorioideae, Chenopodiaceae, *Apium* spp., *Pteridium aquilinum*) attest to high levels of land use and burning in Neolithic time (Tinner et al. 1999; Rey et al. 2013; Colombaroli et al. 2013), leading to a general habitat diversification with the development of highly diverse grasslands at the expense of forest (Colombaroli et al., 2013, Colombaroli and Tinner 2013). For example, synchronous increases in anthropogenic pollen indicators and charcoal levels occurred with the beginning of the Neolithic period (7500 cal yr BP = 5500 BC) at our three sites, and pollen abundance of disfavored woody taxa dropped significantly (Fig. 4).

Vegetation and fire reconstructions at low and middle elevations (e.g. Tinner et al. 2005; Rey et al. 2013) and at high elevations (e.g. Schwörer et al. 2014a, 2014b) suggest the use of fire to clear forests for farming in the valleys and for pastoralism on mountain slopes. The use of alpine meadows in traditional vertical transhumance (shifting and estivation of the livestock at high elevation) probably started early in mid-Neolithic time (Schwörer et al. 2014b) and extended to the whole Alpine region towards the Neolithic/Bronze Age transition (4200 cal yr BP = 2200 BC) as new meadows were created through deliberate burning (Tinner et al. 1996; Heiri et al. 2006; Colombaroli et al. 2010).

Human-set fires, deforestation and agriculture increased significantly during the Bronze Age across the Alps, and summer farming lowered the upper forest position by ca. 200-400 m elevation (e.g. Welten 1982; Tinner et al. 1996; 1999, 2003; Tinner and Theurillat 2003; Lotter et al. 2006; Hofstetter et al. 2006; Rey et al. 2013;Schwörer et al. 2014a). During the Iron Age (~850 BC – 15 BC), anthropogenic burning reached a maximum (Tinner et al. 2005) and direct anthropogenic proxies of arable agriculture, such as *Cerealia* t., further increased (e.g. Tinner et al. 1999; Colombaroli et al. 2013; Rey et al. 2013; Fig. 4). During the Roman period (15 BC – 476 AD), systematic cultivation of tree species, such as walnut (*Juglans regia*) and sweet chestnut, was undertaken to provide wood and non-fiber products (Conedera et al. 2004). This fundamental change towards commodity-based forest management ended the use of fire as main tool for forest clearance and field maintenance. The Roman period marks the start of forest resource management in the Alpine region, and anthropogenic activity was no longer closely coupled to fire (Conedera and Tinner 2000; Tinner et al. 2005; Morales-Molino et al. 2015).

Historical records, traditional knowledge and written documents, such as the local Medieval bylaws (Stuber and Bürgi 2001, 2002; Bürgi and Stuber 2003, 2013; Bertogliati 2014; Krebs et al. 2015), describe extensive land use, forest management and population increases from the Middle Ages to the end of the 1800s. Forests were managed for non-timber purposes including for infrastructure and settlement protection (*Bannwald*), forage and cattle fodder (wood hay, branches of pollarded broadleaved), cattle and human bedding (collected litter), fuel (collected cones and bark), as well as for very specialized uses (bark collection for leather tanning, resin collection for fumigations, herb collection for medicine). During this time, fires were regulated and mainly used for pasture clearance and maintenance (Conedera et al. 2007).

With industrialization in the 19th century, demand increased for wood for charcoal production and later for timber in the Alps (e.g. Krebs and Bertogliati 2015). The intensity of land use in Alpine forests was unprecedented in the 1800s. In addition to the expansion of meadows and grasslands, this period is also characterized by the extinction in Switzerland of large carnivores, such as the brown bear (*Ursus arctos*), wolf (*Canis lupus*), and Eurasian lynx (*Lynx lynx*), all of which were considered a threat to livestock and game hunting (Breitenmoser 1998). In the late 19th century, depleted and overexploited forests reduced slope stability and hydrological regulation, which in turn increased flood frequency. Forest protection legislation was adopted in most Alpine countries and forest management shifted towards reforestation (Bertogliati 2015; Loran et al. 2016; Bebi et al., this issue). Forest expansion greatly accelerated after the second World War with the abandonment of marginal agricultural and pasture lands (Gehrig-Fasel et al. 2007; Gellrich et al. 2007; Loran et al. 2016).

3.4 Response of tree species to past human impact

Present landscapes in the Alpine region have been significantly shaped by four key cultural periods: (1) the beginning of the Neolithic period (~5500-5000 BC) with onset of agriculture in the lowlands, (2) the Bronze and Iron Ages (~2200-15 BC) that led to a systematic development of alpine pastures, transhumance, and numerous human-set fires; (3) the Roman period until the middle of the 1800s with further intensification of the land use, forest management and population growth (Fig. 4); and (4) the 19th-20th century phase of forest re-establishment. During these periods, tree species responded to anthropogenic land use in different ways as function of their sensitivity to disturbance (e.g. fire, browsing, Table 2) and their economic value.

Increased fire and cattle browsing activity from the Neolithic period to the Iron Age severely reduced forest areas and altered forest composition in the region as evidenced by changes in the pollen and charcoal records (Fig. 4). Some forest taxa were favored in abundance (e.g. beech) but declined in distribution during the past 1500 years, while other taxa declined in the forest but benefited from establishment in plantations (e.g. spruce) or hedges (e.g. hornbeam). Species particularly sensitive to fire and/or browsing (Table 2) were disfavored and declined in abundance and distribution as clearly demonstrated by cross-correlations of charcoal and pollen percentages for selected species (Fig. 5) and dung spores and pollen percentages for the particularly browsing-sensitive fir and browsing-resistant spruce (Fig. 6). In the northern subregion, stone pine and silver fir declined after ~7500 cal yr BP (Wick et al. 2003; Tinner et al. 2005; Rey et al. 2013, Schwörer et al. 2015; Thöle et al. 2016), and in the southern subregion, silver fir became locally extinct in the lowlands (Tinner et al. 1999, 2000, 2005; Hofstetter et al. 2006). Ash, linden, elm, beech, English holly (*Ilex aquifolium*) and ivy (*Hedera helix*) declined with high levels of burning in the Neolithic period and Bronze and Iron Ages in the southern and northern subregions. In contrast, disturbance-adapted species, including fire-adapted green alder (*Alnus viridis*) and browsing-resistant spruce, increased in abundance as a direct consequence of other species reductions (Markgraf 1970; Wick et al. 2003; Gobet et al. 2003; Berthel et al. 2012; Rey et al. 2013; Schwörer et al. 2014b, 2015; Thöle et al. 2016).

Species favored by humans increased in abundance and distribution. As revealed by pollen data, walnut was introduced in the lowlands in the late Iron Age (Tinner et al. 1999; Gobet et al.

2000). Sweet chestnut was first cultivated in Roman time and progressively expanded to all suitable areas of the southern subregion. The history of sweet chestnut is one of the most striking examples of anthropogenic impact on forest composition in the Alps (Zoller 1960; Gobet et al. 2000; Morales-Molino et al. 2014; Thöle et al. 2016) and elsewhere in Europe (Conedera et al. 2004). In the lowlands in and around the Alps, its cultivation was associated with extensive removal of native trees (e.g. linden, elm, ash, and deciduous oaks) that had survived previous periods of high fire use (Tinner et al. 1999).

In the Middle Ages, growing human populations increased the need for ecosystem goods and services, and extensive land use left only remnants of natural vegetation. Some species were indirectly favored by forest and pasture management and expanded in abundance. Beech, for example, was used for charcoal, forage (pollarded branches) and litter (cattle and human bedding) production (Krebs et al. 2015), and selection of beech contributed to further loss of silver fir at middle elevations in the southern (Valsecchi et al. 2010) and northern subregions (Tinner and Amman 2005; Tinner and Lotter 2006). Land use intensified above the upper forest limit, where shrubs, such as green alder, were strongly reduced during the Middle Ages, letting high-diversity alpine meadows expand into the former subalpine belt (e.g. Welten 1982; Tinner et al. 1996; Gobet et al. 2003; Schwörer et al. 2014). From the end of the 18th century, the energy and timber needs of the industrial revolution led to an overexploitation of the forest resources, especially in the Alps (e.g. Ceschi 2014). This trend was reversed at the end of the 19th century, and forest area expanded as a consequence of forest protection measures, planting and sustainable silvicultural management (e.g. Ceschi 2014; Dargavel and Johann 2013). In recent decades, the forestation has accelerated due to secondary forests development on abandoned marginal areas (Loran et al. 2016; Bebi et al., this issue).

4. Discussion

4.1 Species sensitivity to past climate impact

Changes in vegetation composition and dynamics before significant human activity were clearly driven by climate. For example, the three subregions responded similarly to rapid high-amplitude warming trends in the late-glacial period (e.g. the Bølling Interstadial) and at the beginning of the Holocene. Ecosystem reorganization entailed changes from cold-adapted open tundra to shrubland, then subalpine conifer forest and finally to forests dominated by thermophilous and mesophilous species. In many cases, our understanding of the present ecological behavior of Alpine tree species is consistent with their response to past environmental change, providing evidence that the environmental niches of these species are well understood. For example, the pioneering characteristics of juniper, birch, and to some extent also larch, including their ability to colonize poorly developed soils is evidenced after present-day glacial retreat and avalanche activity in the Alps (Ellenberg 2009; Garbarino et al., 2010). Similarly, they were able to colonize deglaciated landscapes soon after ice retreat during the late-glacial period. Differences in present-day moisture requirements between larch, stone pine, beech, and pedunculate oak (*Quercus robur*) are also well reflected in their Holocene history (Tinner and Lotter, 2001; Tinner and Kaltenrieder 2003; Ellenberg 2009). In agreement with the ecology of silver fir, paleoecological records show that silver fir was generally less demanding of moisture conditions than either spruce or beech in the past (Henne et al. 2011).

Paleoecological records prior to the onset of the Neolithic period show that tree species were able to respond rapidly to climate changes and establish a dynamic equilibrium with the environmental conditions in the absence of significant human activity (Schwörer et al. 2014a). For example, establishment of thermophilous tree species, such as deciduous oaks, elm, ash, maple, and linden, at low to middle elevations in the southern and northern Alpine forelands, occurred within a century of warming at ~ 11,500 cal yr BP (Ammann et al. 2000). Similarly, major reorganizations of plant communities in the northern Alpine forelands took place within decades of the cool-moist event at 8200 cal yr BP (Tinner and Lotter, 2001). Although few records have high enough spatial and temporal resolution to detect the influence of other natural disturbances (e.g. fire, browsing by wild ungulates, insect outbreaks, windthrow, erosion), there is no evidence that single or closely spaced disturbance events shifted the vegetation to a new stable state in the absence of humans (e.g. Colombaroli et al. 2010).

4.2 Species sensitivity to human impact

Land use and related disturbances, including fire, browsing, cultivation, and forest management, began with the Neolithic period and became progressively more important in shaping vegetation composition and distribution in recent millennia. At latest by the Iron Age, humans increasingly were the primary driver of forest and vegetation change in the Alps (Tinner et al. 1999, Colombaroli et al. 2010; Rey et al. 2013; Schwörer et al. 2015). Pollen evidence suggests that past land use had different impacts on the abundance and distribution of tree species, depending on their ecology and economic value (Table 3). Species that were sensitive to fire and browsing had little value for food and timber (e.g. silver fir, elm, lime, ash, stone pine and the evergreen English holly and ivy). These species were progressively reduced or even locally eradicated, and we refer to them as “disfavored”. In contrast, species used for food and fiber (e.g. chestnut, walnut) were introduced into new areas, thus increasing their distribution and abundance (so-called “directly favored” species). Other taxa (e.g. spruce, beech, hazel, deciduous oaks, as well as Scots pine in the lowlands of the central Alps and spruce since the onset of the timber industry in the last centuries) increased in abundance as indirect consequences of (1) their economic importance for timber, charcoal, acorns, litter and other products; (2) their resistance to fire and browsing; and (3) their response to the elimination of competitors. These taxa are classified as “indirectly favored in abundance”. Finally, some woody species were “indirectly favored in distribution” because they expanded into suitable habitat as a result of disturbance. Among them are the pioneer birch, disturbance-adapted green alder, juniper, mountain pine; and – during the Neolithic period - browse-resistant spruce.

The ubiquitous and long-term influence of people on ecosystem dynamics and species distributions and abundance points to the importance of considering both climate and human effects as drivers in ecosystem modeling (Birks and Tinner 2016). Models should incorporate long-term information in developing relationships between species distribution and abundance and their environment, by including (1) species distributions under a range of climate conditions and disturbance levels in the past; (2) past ecological consequences of adding or removing species or changing species abundance; and (3) the effects of altered natural disturbance regimes in the past (see discussion in e.g. Henne et al. 2011; Tinner et al. 2013). In reality, however, most species distribution models (SDM), often also called bioclimatic or niche models, are based on present-day distributions in relation to a suite of modern climate variables. Because present distributions are not in equilibrium with climate, models results often under- or overestimate present and potential future ranges for many critical species (Elkin et al. 2013; García-Valdéz et al. 2013; Schwörer et al. 2014b; Ruosch et al. 2016). Estimates in the Alpine region would be improved if SDMs considered early to mid-Holocene vegetation-climate relationships prior to the time when the species ranges and abundance were highly modified by humans (i.e. before the middle to end Neolithic period). Well-resolved paleoclimatic data, specifically in regard to precipitation, sensitivity studies or climatic scenarios can thus be used to assess such issues (Heiri et al. 2006). Dynamic and ecophysiology-based vegetation models, such as LandClim are less affected by this problem, because they consider species-specific traits and the fundamental niche of species (Bugmann 2001; Bugmann and Solomon 2000; Ruosch et al. 2016). Moreover, landscape, disturbance and biochemical feedbacks are also integrated to better assess the interactions of species with their biotic and non-biotic environment. Recent dynamic vegetation models that incorporate the influence of past land use on species distributions also hold considerable promise for recognizing the anthropogenic signal (Kaplan et al. 2010; Schwörer et al. 2014b).

4.3 Using the past to inform future silvicultural approaches

The next decades of land use and climate change will be key for forest management in the Alpine region. Since the Second World War, land abandonment in marginal mountain settings has led to forest encroachment into former high-elevation meadows, increased tree density in forests, and growing levels of fuel biomass (Bebi et al., this issue). Although afforestation threatens often-diverse cultural landscapes, it creates an opportunity to restore more natural conditions to forests by re-establishing key species and processes that have been lost as a consequence of excessive human disturbance. Because present-day forests in the Alpine region have been highly altered by humans over the last 7500 years, species composition, distribution and dynamics are not fully in equilibrium with climate. The starting point for this recovery will vary depending on the extent to which ecosystems have already been altered and the social, economic and cultural objectives that motivate conservation and silvicultural actions.

Knowledge of past species distributions and abundance can help ecologists and forest managers evaluate current and potential distributions in the near future. Divergence between the realized and potential ecological niche of woody species highlights the need for paleo-informed management strategies that consider the impact of long-term land use and human-mediated disturbance on present distributions. Information on species responses to past land-use disturbance can help guide decisions about where to direct efforts for conservation, where disturbances should be introduced or suppressed, and how best to implement “close-to-nature” management strategies that maintain forest dynamics and protect important ecosystem goods and services with reduced interference and investment (Whitlock et al. subm.).

A major challenge for managers going forward will be to incorporate information from the past into an evolving framework of land-use and climate change. Species that have been artificially favored in the absence of their main competitors (e.g. spruce in many Alpine areas) will likely suffer disproportionally from management reduction and post-cultural natural restoration (Schwörer et al. 2014b). Other species, such as sweet chestnut, that are highly prized for their cultural significance, may be maintained despite their anthropogenic dominance in the forest. Silver fir, linden, maples and other trees have the capacity to occupy a more prominent role in the forest if protected from excessive fire and/or grazing (Tinner et al. 2013; Henne et al. 2015).

Present changes in land use and climate have also created new types of disturbances that may affect the future resilience of the concerned forest ecosystems. Wild ungulate populations are growing in the absence of former pastoral activities, large predators and effective hunting regulations. These native herbivores interfere with the ability of some tree species to regenerate (e.g. silver fir) and represent a new type of disturbance for forests (Heuze et al. 2005; Didion et al. 2011; Häsler and Senn 2012; Kupferschmid et al. 2014). Cessation of systematic litter collection, and forest closure and encroachment have caused an accumulation of dead biomass, which has altered fuel loads and over time may create inhibitory and toxic effects of extracellular self-DNA in the soil (Mazzoleni et al. 2015).

Projected climate trends pose direct threats, as evidenced by drought-induced leaf whitening, which caused significant chestnut mortality during the hot and dry summer 2003 in the southern subregion (Conedera et al. 2010). Similarly, recent dieback of Scots pine in dry areas of the Rhone valley of the western central Alps is also related to extreme summer drought and will likely continue in the future (Bigler et al. 2006; Rebetez and Dobbertin 2006; Rigling et al. 2013; Vacchiano et al. 2013). Warming and related increases in drought frequency and severity (Rebetez 1999) and associated fire risk (Reinhard et al. 2005; Wastl et al. 2013; Valese et al. 2014) will alter interactions among woody species (Moser et al. 2010; Maringer et al. 2016) and with pests and diseases (Battisti 2008; Netherer et al. 2010; Marini et al. 2012). In addition, newly introduced exotic species (e.g. *Robinia pseudooacacia*, *Ailanthus altissima*, *Pawlonia* spp.) have become invasive and highly competitive in low- to mid-elevation forest ecosystems and strongly interfere with fire regimes, silvicultural management practices (Grund et al. 2005; Maringer et al. 2012; Radtke et al. 2014; Knüsel et al. 2015), pests (Wermelinger 2014; Roques et al. 2016) and disease (Kowaski and Holdenrieder 2009; Pautasso et al. 2013; Sieber 2014) as well as their possible interactions (e.g. Meyer et al. 2016). Thus, information on species and forest community responses to novel climates and disturbance regimes in the past can help guide management strategies in the future (Williams and Jackson, 2007).

5. Conclusions

Paleoecological information offers critical baseline information for managing and conserving current and future forest ecosystems in the Alpine region. The enormous changes that have occurred in central European forests through time as well as the role of climate and land use on past vegetation and disturbance regimes offer guidelines for assessing current and potential forest composition, distribution, and dynamics. To be useful, paleoecological information must be detailed enough in terms of taxonomic, geographic and temporal precision to describe species histories through time and their response to local human and non-human drivers. A thorough assessment at the regional level would however require additional pollen-independent climate reconstructions and quantitative examinations of species-climate relationships, as well as more data-model comparisons between paleoecology, archaeology and dynamic vegetation modeling. Such information may shed light on the direct effects of ongoing climate change as well as the vulnerabilities inherent in recent forest transitions, including the imbalances in native herbivores, the introduction of non-native species, and drought-mediated diseases. As such, paleoecology offers an important and unique context for close-to-nature silviculture.

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Abbreviations

Cal yr BP (years before present) = years before 1950; BC = before Christ; AD = Anno Domini.

References

Alley, R.B., Agustsdottir, A.M., 2005. The 8k event: cause and consequences of a major Holocene abrupt climate change. Quaternary Science Reviews 24, 1123-1149.
Ammann, B., 1989. Late-Quaternary palynology at Lobsigensee. Regional vegetation history and local lake development. Dissertationes Botanicae 137, 1-157.
Ammann, B., Birks, H.J.B., Brooks, S.J., Eicher, U., von Grafenstein, U., Hofmann, W., Lemdahl, G., Schwander, J., Tobolski, K., Wick, L., 2000. Quantification of biotic responses to rapid climatic changes around the Younger Dryas - a synthesis. Palaeogeography Palaeoclimatology Palaeoecology 159, 313-347.
Ammann, B., van Leeuwen, J.F.N., van der Knaap, W.O., Lischke, H., Heiri, O., Tinner, W., 2013. Vegetation responses to rapid warming and to minor climatic fluctuations during the Late-Glacial Interstadial (GI-1) at Gerzensee (Switzerland). Palaeogeography Palaeoclimatology Palaeoecology 391, 40-59.
Battisti, A., 2008. Forests and climate change - lessons from insects. Iforest-Biogeosciences and Forestry 1, 1-5.
Bebi, P., Seidl, R., Motta, R., Fuhr, M., Krumm, F., Conedera, M., Ginzler, C., Wohlgemuth, T., Kulakowski, D., 2016. Changes in forest cover and disturbance regimes in the mountain forest of the Alps. Forest Ecology and Management (this issue).
Behre, K.-E., 1981. The interpretation of anthropogenic indicators in pollen diagrams. Pollen et Spores 23,.
Behre, K.-E., 1988. The role of man in European vegetation history. In: Huntley, B.W., Webb, I., T., (Eds.), Vegetation History. Kluwer, Dordrecht, pp. 633–672.
Berthel, N., Schwoerer, C., Tinner, W., 2012. Impact of Holocene climate changes on alpine and treeline vegetation at Sanetsch Pass, Bernese Alps, Switzerland. Review of Palaeobotany and Palynology 174, 91-100.
Bertogliati, M., 2014. Dai boschi protetti alle foreste di protezione. Comunità locali e risorse forestali nella Svizzera italiana (1700-1950). Bellinzona, Casagrande.
Bertogliati, M., 2016. Forest Transition - der Wald kehrt zurück. In: Mathieu, J., Backhaus, N., Hürlimann, K., Bürgi, M. (Eds.), Geschichte der Landschaft in der Schweiz. Von der Eiszeit bis zur Gegenwart. Orell Füssli Verlag, Zürich, pp. 267-280.
Bigler, C., Braker, O.U., Bugmann, H., Dobbertin, M., Rigling, A., 2006. Drought as an inciting mortality factor in Scots pine stands of the Valais, Switzerland. Ecosystems 9, 330-343.
Birks, H.J.B., Birks, H.H., 1980. Quaternary Paleoecology. University Park Press, Balitmore.
Birks, H.J.B., Tinner, W., 2016. Past forests of Europe. In: San-Miguel-Ayanz, J., de Rigo, D., Caudullo, G., Houston Durrant, T., Mauri, A. (eds.): European Atlas of Forest Tree Species. Luxembourg: Publication Office of the European Union, pp. 36-39.
Blarquez, O., Carcaillet, C., 2010. Fire, Fuel Composition and Resilience Threshold in Subalpine Ecosystem. Plos One 5, 8.
Blarquez, O., Carcaillet, C., Bremond, L., Mourier, B., Radakovitch, O., 2010. Trees in the subalpine belt since 11 700 cal. BP: origin, expansion and alteration of the modern forest. Holocene 20, 139-146.
Breitenmoser, U., 1998. Large predators in the Alps: The fall and rise of man's competitors. Biological Conservation 83, 279-289.
Bugmann, H.K.M., 2001. A review of forest gap models. Climatic Change 51, 259-305.
Bugmann, H.K.M., Solomon, A.M., 2000. Explaining forest composition and biomass across multiple biogeographical regions. Ecological Applications 10, 95-114.
Bürgi, M., Stuber, M., 2003. Agrarische Waldnutzungen in der Schweiz 1800-1950. Waldfeldbau, Waldfrüchte und Harz Schweiz. Z. Forstwes. 154, 360-375.

Bürgi, M., Stuber, M., 2013. What, How, and Why? Collecting Traditional Knowledge on Forest Uses in Switzerland. . In: Rotherham, I.D. (Ed.), Cultural severance and the environment. The ending of traditional and customary practice on commons and landscapes managed in common. Springer, Dordrecht Heidelberg, pp. 123-132.

Carcaillet, C., Ali, A.A., Blarquez, O., Genries, A., Mourier, B., Bremond, L., 2009. Spatial variability of fire history in subalpine forests: From natural to cultural regimes. Ecoscience 16, 1-12.

Ceschi, I., 2014. Il bosco del canton Ticino. Dipartimento del territorio; Armando Dadò Editore, Locarno.

Colombaroli, D., Henne, P.D., Kaltenrieder, P., Gobet, E., Tinner, W., 2010. Species responses to fire, climate and human impact at tree line in the Alps as evidenced by palaeo-environmental records and a dynamic simulation model. Journal of Ecology 98, 1346-1357.

Colombaroli, D., Tinner, W., 2013. Determining the long-term changes in biodiversity and provisioning services along a transsect from Central Europe to the Mediterranean. The Holocene 23:1477-1486.

Colombaroli, D., Beckmann, M., van der Knaap, W.O., Curdy, P., Tinner, W., 2013. Changes in biodiversity and vegetation composition in the central Swiss Alps during the transition from pristine forest to first farming. Diversity and Distributions 19, 157-170.

Conedera, M., Tinner, W., 2000. The interaction between forest fires and human activity in southern Switzerland.

Conedera, M., Krebs, P., Tinner, W., Pradella, M., Torriani, D., 2004. The cultivation of Castanea sativa (Mill.) in Europe, from its origin to its diffusion on a continental scale. Vegetation History and Archaeobotany 13, 161-179.

Conedera, M., Vassere, S., Neff, C., Meurer, M., Krebs, P., 2007. Using toponymy to reconstruct past land use: a case study of 'brusada' (burn) in southern Switzerland. Journal of Historical Geography 33, 729-748.

Conedera, M., Tinner, W., Neff, C., Meurer, M., Dickens, A.F., Krebs, P., 2009. Reconstructing past fire regimes: methods, applications, and relevance to fire management and conservation. Quaternary Science Reviews 28, 555-576.

Conedera, M., Barthold, F., Torriani, D., Pezzatti, G.B., 2010. Drought Sensitivity of Castanea sativa: Case Study of Summer 2003 in the Southern Alps. Acta Horticolturae 866, 297-302.

Dansgaard, W., Johnsen, S.J., Clausen, H.B., Dahljensen, D., Gundestrup, N.S., Hammer, C.U., Hvidberg, C.S., Steffensen, J.P., Sveinbjornsdottir, A.E., Jouzel, J., Bond, G., 1993. Evidence for general instability of past climate from a 250-kyr ice-core record. Nature 364, 218-220.

Dargavel, J., Johann, E., 2013. Science and hope: A forest history. White Horse press, Cambridge.

Dawson, T.P., Jackson, S.T., House, J.I., Prentice, I.C., Mace, G.M., 2011. Beyond Predictions: Biodiversity Conservation in a Changing Climate. Science 332, 53-58.

Didion, M., Kupferschmid, A.D., Wolf, A., Bugmann, H., 2011. Ungulate herbivory modifies the effects of climate change on mountain forests. Climatic Change 109, 647-669.

Elias, S.A., 2013. Encyclopedia of Quaternary Science. Elsevier.

Elkin, C., Gutierrez, A.G., Leuzinger, S., Manusch, C., Temperli, C., Rasche, L., Bugmann, H., 2013. A 2 degrees C warmer world is not safe for ecosystem services in the European Alps. Global Change Biology 19, 1827-1840.

Ellenberg, H., 2009. Vegetation Ecology of Central Europe. 4th ed., Cambridge University Press, Cambridge.

Ellenberg, H., Leuschner, C., 2010. Vegetation Mitteleuropas mit den Alpen. In öklogischer, dynamischer und historischer Sicht. . Ulmer, Stuttgart.

Garbarino, M., Lingua, E., Nagel, T.A., Godone, D., Motta, R., 2010. Patterns of larch establishment following deglaciation of Ventina glacier, central Italian Alps. Forest Ecology and Management 259, 583-590.

Garcia-Valdes, R., Zavala, M.A., Araujo, M.B., Purves, D.W., 2013. Chasing a moving target: projecting climate change-induced shifts in non-equilibrial tree species distributions. Journal of Ecology 101, 441-453.

Gehrig-Fasel, J., Guisan, A., Zimmermann, N.E., 2007. Tree line shifts in the Swiss Alps: Climate change or land abandonment? Journal of Vegetation Science 18, 571-582.

Gellrich, M., Baur, P., Koch, B., Zimmermann, N.E., 2007. Agricultural land abandonment and natural forest re-growth in the Swiss mountains: A spatially explicit economic analysis. Agriculture Ecosystems & Environment 118, 93-108.

Gobet, E., Tinner, W., Hubschmid, P., Jansen, I., Wehrli, M., Ammann, B., Wick, L., 2000. Influence of human impact and bedrock differences on the vegetational history of the Insubrian Southern Alps. Vegetation History and Archaeobotany 9, 175-187.

Gobet, E., Tinner, W., Hochuli, P.A., van Leeuwen, J.F.N., Ammann, B., 2003. Middle to Late Holocene vegetation history of the Upper Engadine (Swiss Alps): the role of man and fire. Vegetation History and Archaeobotany 12, 143-163.

Gobet, E., Tinner, W., Bigler, C., Hochuli, P.A., Ammann, B., 2005. Early-Holocene afforestation processes in the lower subalpine belt of the Central Swiss Alps as inferred from macrofossil and pollen records. Holocene 15, 672-686.

Gobet, E., Vescovi, E., Tinner, W., 2010. A paleoecological contribution to assess the natural vegetation of Switzerland. Botanica Helvetica 120, 105-115.

Graf, M.-T., Chmura, G.L., 2006. Development of modem analogues for natural, mowed and grazed grasslands using pollen assemblages and coprophilous fungi. Review of Palaeobotany and Palynology 141, 139-149.

Grund, K., Conedera, M., Schroder, H., Walther, G.R., 2005. The role of fire in the invasion process of evergreen broad-leaved species. Basic and Applied Ecology 6, 47-56.

Haas, J.N., Richoz, I., Tinner, W., Wick, L., 1998. Synchronous Holocene climatic oscillations recorded on the Swiss Plateau and at timberline in the Alps. Holocene 8, 301-309.

Häsler, H., Senn, J., 2012. Ungulate browsing on European silver fir Abies alba: the role of occasions, food shortage and diet preferences. Wildlife Biology 18, 67-74.

Heiri, C., Bugmann, H., Tinner, W., Heiri, O., Lischke, H., 2006. A model-based reconstruction of Holocene treeline dynamics in the Central Swiss Alps. Journal of Ecology 94, 206-216.

Heiri, O., Brooks, S.J., Renssen, H., Bedford, A., Hazekamp, M., Ilyashuk, B., Jeffers, E.S., Lang, B., Kirilova, E., Kuiper, S., Millet, L., Samartin, S., Toth, M., Verbruggen, F., Watson, J.E., van Asch, N., Lammertsma, E., Amon, L., Birks, H.H., Birks, H.J.B., Mortensen, M.F., Hoek, W.Z., Magyari, E., Sobrino, C.M., Seppa, H., Tinner, W., Tonkov, S., Veski, S., Lotter, A.F., 2014. Validation of climate model-inferred regional temperature change for late-glacial Europe. Nature Communications 5.

Henne, P.D., Elkin, C.M., Reineking, B., Bugmann, H., Tinner, W., 2011. Did soil development limit spruce (Picea abies) expansion in the Central Alps during the Holocene? Testing a palaeobotanical hypothesis with a dynamic landscape model. Journal of Biogeography 38, 933-949.

Henne, P.D., Elkin, C., Franke, J., Colombaroli, D., Calo, C., La Mantia, T., Pasta, S., Conedera, M., Dermody, O., Tinner, W., 2015. Reviving extinct Mediterranean forest communities may improve ecosystem potential in a warmer future. Frontiers in Ecology and the Environment 13, 356-362.

Heuze, P., Schnitzler, A., Klein, F., 2005. Is browsing the major factor of silver fir decline in the Vosges Mountains of France? Forest Ecology and Management 217, 219-228.

Hofstetter, S., Tinner, W., Valsecchi, V., Carraro, G., Conedera, M., 2006. Lateglacial and Holocene vegetation history in the Insubrian Southern Alps - New indications from a small-scale site. Vegetation History and Archaeobotany 15, 87-98.

Holzhauser, H., Magny, M., Zumbuhl, H.J., 2005. Glacier and lake-level variations in west-central Europe over the last 3500 years. Holocene 15, 789-801.

Ibanez, I., Clark, J.S., Dietze, M.C., Feeley, K., Hersh, M., LaDeau, S., McBride, A., Welch, N.E., Wolosin, M.S., 2006. Predicting biodiversity change: Outside the climate envelope, beyond the species-area curve. Ecology 87, 1896-1906.

Iverson, L.R., McKenzie, D., 2013. Tree-species range shifts in a changing climate: detecting, modeling, assisting. Landscape Ecology 28, 879-889.
Kaltenrieder, P., Tinner, W., Ammann, B., 2005. Long-term vegetation history at timberline in the Swiss Alps (Alpe d'Essertse, VS). Botanica Helvetica 115, 137-154.
Kaplan, J.O., Krumhardt, K.M., Zimmermann, N., 2009. The prehistoric and preindustrial deforestation of Europe. Quaternary Science Reviews 28, 3016-3034.
Keller, F., Lischke, H., Mathis, T., Mohl, A., Wick, L., Ammann, B., Kienast, F., 2002. Effects of climate, fire, and humans on forest dynamics: forest simulations compared to the palaeological record. Ecological Modelling 152, 109-127.
Knüsel, S., Conedera, M., Rigling, A., Fonti, P., Wunder, J., 2015. A tree-ring perspective on the invasion of Ailanthus altissima in protection forests. Forest Ecology and Management 354, 334-343.
Kowalski, T., Holdenrieder, O., 2009. Pathogenicity of Chalara fraxinea. Forest Pathology 39, 1-7.
Krebs, P., Bertogliati, M., 2015. Indagini sulle piazze dei carbonai. In: Ferrari, C., Donati, B., Zanini, M. (Eds.), Profumi di boschi e pascoli. Vicende umane, natura e Riserva forestale in Valle di Lodano. Patriziato di Lodano, Lodano, pp. 214-241.
Krebs, P., Bertogliati, M., Donati, B., Zoppi, D., Donati, A., 2015. Il libro dei patti e ordini di Broglio del 1595-1626 : consuetudini antiche, organizzazione socio-economica e concezione degli statuti di un comune della Val Lavizzara. Fondazione Ticino Nostro / Armando Dadò Editore, Locarno.
Kupferschmid, A.D., Wasem, U., Bugmann, H., 2014. Light availability and ungulate browsing determine growth, height and mortality of Abies alba saplings. Forest Ecology and Management 318, 359-369.
Lang, G., 1994. Quartäre Vegetationsgeschichte Europas. Methoden und Ergebnisse. G. Fischer, Jena.
Lindner, M., 2000. Developing adaptive forest management strategies to cope with climate change. Tree Physiology 20, 299-307.
Loran, C., Ginzler, C., Bürgi, M., 2016. Evaluating forest transition based on a multi-scale approach: forest area dynamics in Switzerland 1850-2000. Reg. Environ. Change online first, 12 p.
Lotter, A.F., Kienast, F., 1990. Validation of a forest succession model by means of annually laminated sediments. Geological Survey of Finland, 14 (Special Paper), 25-31.
Lotter, A.F., Eicher, U., Siegenthaler, U., Birks, H.J.B., 1992. Late-glacial climatic oscillations as recorded in Swiss lake sediments. Journal of Quaternary Science 7, 187-204.
Lotter, A.F., Heiri, O., Hofmann, W., van der Knaap, W.O., van Leeuwen, J.F.N., Walker, I.R., Wick, L., 2006. Holocene timber-line dynamics at Bachalpsee, a lake at 2265 m a.s.l. in the northern Swiss Alps. Vegetation History and Archaeobotany 15, 295-307.
Maringer, J., Wohlgemuth, T., Neff, C., Pezzatti, G.B., Conedera, M., 2012. Post-fire spread of alien plant species in a mixed broad-leaved forest of the Insubric region. Flora 207, 19-29.
Maringer, J., Ascoli, D., Kueffer, N., Schmidtlein, S., Conedera, M., 2016. What drives European beech (Fagus sylvatica L.) mortality after forest fires of varying severity? Forest Ecology and Management 368, 81-93.
Marini, L., Ayres, M.P., Battisti, A., Faccoli, M., 2012. Climate affects severity and altitudinal distribution of outbreaks in an eruptive bark beetle. Climatic Change 115, 327-341.
Markgraf, V., 1970. Palaeohistory of the Spruce in Switzerland. Nature 228, 249-251.
Mazzoleni, S., Bonanomi, G., Incerti, G., Chiusano, M.L., Termolino, P., Mingo, A., Senatore, M., Giannino, F., Carteni, F., Rietkerk, M., Lanzotti, V., 2015. Inhibitory and toxic effects of extracellular self-DNA in litter: a mechanism for negative plant-soil feedbacks? New Phytologist 205, 1195-1210.
Meyer, J.B., Gallien, L., Prospero, S., 2015. Interaction between two invasive organisms on the European chestnut: does the chestnut blight fungus benefit from the presence of the gall wasp? Fems Microbiology Ecology 91.
Morales-Molino, C., Vescovi, E., Krebs, P., Carlevaro, E., Kaltenrieder, P., Conedera, M., Tinner, W., Colombaroli, D., 2015. The role of human-induced fire and sweet chestnut (Castanea sativa Mill.) cultivation on the long-term landscape dynamics of the southern Swiss Alps. Holocene 25, 482-494.

Moser, B., Temperli, C., Schneiter, G., Wohlgemuth, T., 2010. Potential shift in tree species composition after interaction of fire and drought in the Central Alps. European Journal of Forest Research 129, 625-633.

Netherer, S., Schopf, A., 2010. Potential effects of climate change on insect herbivores in European forests-General aspects and the pine processionary moth as specific example. Forest Ecology and Management 259, 831-838.

Pautasso, M., Aas, G., Queloz, V., Holdenrieder, O., 2013. European ash (Fraxinus excelsior) dieback - A conservation biology challenge. Biological Conservation 158, 37-49.

Radtke, A., Ambrass, S., Zerbe, S., Tonon, G., Fontana, V., Ammer, C., 2013. Traditional coppice forest management drives the invasion of Ailanthus altissima and Robinia pseudoacacia into deciduous forests. Forest Ecology and Management 291, 308-317.

Rasmussen, S.O., Andersen, K.K., Svensson, A.M., Steffensen, J.P., Vinther, B.M., Clausen, H.B., Siggaard-Andersen, M.L., Johnsen, S.J., Larsen, L.B., Dahl-Jensen, D., Bigler, M., Rothlisberger, R., Fischer, H., Goto-Azuma, K., Hansson, M.E., Ruth, U., 2006. A new Greenland ice core chronology for the last glacial termination. Journal of Geophysical Research-Atmospheres 111, Rasmussen, S.O., Andersen, K.K., Svensson, A.M., Steffensen, J.P., Vinther, B.M., Clausen, H.B., Siggaard-Andersen, M.L., Johnsen, S.J., Larsen, L.B., Dahl-Jensen, D., Bigler, M., Rothlisberger, R., Fischer, H., Goto-Azuma, K., Hansson, M.E., Ruth, U., 2006. A new Greenland ice core chronology for the last glacial termination. Journal of Geophysical Research-Atmospheres 111.D6, D0610.

Rebetez, M., 1999. Twentieth century trends in droughts in southern Switzerland. Geophysical Research Letters 26, 755-758.

Rebetez, M., Dobbertin, M., 2004. Climate change may already threaten Scots pine stands in the Swiss Alps. Theoretical and Applied Climatology 79, 1-9.

Reinhard, M., Rebetez, M., Schlaepfer, R., 2005. Recent climate change: Rethinking drought in the context of Forest Fire Research in Ticino, South of Switzerland. Theoretical and Applied Climatology 82, 17-25.

Rey, F., Schwoerer, C., Gobet, E., Colombaroli, D., van Leeuwen, J.F.N., Schleiss, S., Tinner, W., 2013. Climatic and human impacts on mountain vegetation at Lauenensee (Bernese Alps, Switzerland) during the last 14,000 years. Holocene 23, 1415-1427.

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

Roques, A., Auger-Rozenberg, M.-A., Blackburn, T.M., Garnas, J., Pysek, P., Rabitsch, W., Richardson, D.M., Wingfield, M.J., Liebhold, A.M., Duncan, R.P., 2016. Temporal and interspecific variation in rates of spread for insect species invading Europe during the last 200 years. Biological Invasions 18, 907-920.

Ruosch, M., Spahni, R., Joos, F., Henne, P.D., Van der Knaap, W.O., Tinner, W., 2016. Past and future evolution of Abies alba forests in Europe - comparison of a dynamic vegetation model with palaeo data and observations. Global Change Biology 22, 727-740.

Schmid, U., Bircher, N., Bugmann, H., 2015. Naturnaher und multifunktionaler Waldbau in Zeiten des Klimawandels – eine Fallstudie. Schweizerische Zeitschrift fur Forstwesen 166, 314-324.

Schwörer, C., Kaltenrieder, P., Glur, L., Berlinger, M., Elbert, J., Frei, S., Gilli, A., Hafner, A., Anselmetti, F.S., Grosjean, M., Tinner, W., 2014a. Holocene climate, fire and vegetation dynamics at the treeline in the Northwestern Swiss Alps. Vegetation History and Archaeobotany 23, 479-496.

Schwörer, C., Henne, P.D., Tinner, W., 2014b. A model-data comparison of Holocene timberline changes in the Swiss Alps reveals past and future drivers of mountain forest dynamics. Global Change Biology 20, 1512-1526.

Schwörer, C., Colombaroli, D., Kaltenrieder, P., Rey, F., Tinner, W., 2015. Early human impact (5000-3000

BC) affects mountain forest dynamics in the Alps. Journal of Ecology 103, 281-295.

Sieber, T.N., 2014. Neomyzeten – eine anhaltende Bedrohung für den Schweizer Wald. Schweizerische Zeitschrift fur Forstwesen 165, 173-182.

Smol, J.P., Birks, H.J.-B., Last, W.M. (Eds.), 2001. Tracking Environmental Change using Lake Sediments. Vol. 3: Terrestrial, Algal, and Siliceous Indicators. Kluwer Academic Publisher, Dordrecht.

Staehli, M., Finsinger, W., Tinner, W., Allgoewer, B., 2006. Wildfire history and fire ecology of the Swiss National Park (Central Alps): new evidence from charcoal, pollen and plant macrofossils. Holocene 16, 805-817.

Stuber, M., Bürgi, M., 2001. Agrarische Waldnutzungen in der Schweiz 1800-1950. Waldweide, Waldheu, Nadel- und Laubfutter. Schweiz. Z. Forstwes. 152, 490-508.

Stuber, M., Bürgi, M., 2002. Agrarische Waldnutzungen in der Schweiz 1800-1950. Nadel- und Laubstreue. Schweiz. Z. Forstwes. 153, 397-410.

Svenning, J.-C., Eiserhardt, W.L., Normand, S., Ordonez, A., Sandel, B., 2015. The Influence of Paleoclimate on Present-Day Patterns in Biodiversitv and Ecosystems. In: Futuyma, D.J. (Ed.), Annual Review of Ecology, Evolution, and Systematics, Vol 46, pp. 551-572.

Thöle, L., Schworer, C., Colombaroli, D., Gobet, E., Kaltenrieder, P., van Leeuwen, J., Tinner, W., 2016. Reconstruction of Holocene vegetation dynamics at Lac de Bretaye, a high-mountain lake in the Swiss Alps. Holocene 26, 380-396.

Tinner, W., Ammann, B., Germann, P., 1996. Treeline fluctuations recorded for 12,500 years by soil profiles, pollen, and plant macrofossils in the Central Swiss Alps. Arctic and Alpine Research 28, 131-147.

Tinner, W., Hubschmid, P., Wehrli, M., Ammann, B., Conedera, M., 1999. Long-term forest fire ecology and dynamics in southern Switzerland. Journal of Ecology 87, 273-289.

Tinner, W., Conedera, M., Gobet, E., Hubschmid, P., Wehrli, M., Ammann, B., 2000. A palaeoecological attempt to classify fire sensitivity of trees in the southern Alps. Holocene 10, 565-574.

Tinner, W., Lotter, A.F., 2001. Central European vegetation response to abrupt climate change at 8.2 ka. Geology 29, 551-554.

Tinner, W., Theurillat, J.P., 2003. Uppermost limit, extent, and fluctuations of the timberline and treeline ecocline in the Swiss Central Alps during the past 11,500 years. Arctic Antarctic and Alpine Research 35, 158-169.

Tinner, W., Lotter, A.F., Ammann, B., Conedera, M., Hubschmid, P., van Leeuwen, J.F.N., Wehrli, M., 2003. Climatic change and contemporaneous land-use phases north and south of the Alps 2300 BC to 800 AD. Quaternary Science Reviews 22, 1447-1460.

Tinner, W., Ammann, B., 2005. Long-term Responses of Mountain Ecosystems to Environmental Changes: Resilience, Adjustment, and Vulnerability. In: Huber, U.M., Bugmann, H.K.M., Reasoner, M.A. (Eds.), Global change in mountain regions. Springer, The Netherlands, pp. 133-143.

Tinner, W., Kaltenrieder, P., 2005. Rapid responses of high-mountain vegetation to early Holocene environmental changes in the Swiss Alps. Journal of Ecology 93, 936-947.

Tinner, W., Conedera, M., Ammann, B., Lotter, A.F., 2005. Fire ecology north and south of the Alps since the last ice age. Holocene 15, 1214-1226.

Tinner, W., Lotter, A.F., 2006. Holocene expansions of Fagus silvatica and Abies alba in Central Europe: where are we after eight decades of debate? Quaternary Science Reviews 25, 526-549.

Tinner, W., Nielsen, E.H., Lotter, A.F., 2007. Mesolithic agriculture in Switzerland? A critical review of the evidence. Quaternary Science Reviews 26, 1416-1431.

Tinner, W., Colombaroli, D., Heiri, O., Henne, P.D., Steinacher, M., Untenecker, J., Vescovi, E., Allen, J.R.M., Carraro, G., Conedera, M., Joos, F., Lotter, A.F., Luterbacher, J., Samartin, S., Valsecchi, V., 2013. The past ecology of Abies alba provides new perspectives on future responses of silver fir forests to global warming. Ecological Monographs 83, 419-439.

Vacchiano, G., Motta, R., 2015. An improved species distribution model for Scots pine and downy oak under

future climate change in the NW Italian Alps. Annals of Forest Science 72.
Valese, E., Conedera, M., Held, A.C., Ascoli, D., 2014. Fire, humans and landscape in the European Alpine region during the Holocene. Anthropocene 6, 63-74.
Valsecchi, V., Tinner, W., 2010. Vegetation responses to climatic variability in the Swiss Southern Alps during the Misox event at the early-mid Holocene transition. Journal of Quaternary Science 25, 1248-1258.
Valsecchi, V., Carraro, G., Conedera, M., Tinner, W., 2010. Late-Holocene vegetation and land-use dynamics in the Southern Alps (Switzerland) as a basis for nature protection and forest management. Holocene 20, 483-495.
van der Knaap, W.O., van Leeuwen, J.F.N., Finsinger, W., Gobet, E., Pini, R., Schweizer, A., Valsecchi, V., Ammann, B., 2005. Migration and population expansion of Abies, Fagus, Picea, and Quercus since 15000 years in and across the Alps, based on pollen-percentage threshold values. Quaternary Science Reviews 24, 645-680.
van Geel, B., Buurman, J., Brinkkemper, O., Schelvis, J., Aptroot, A., van Reenen, G., Hakbijl, T., 2003. Environmental reconstruction of a Roman Period settlement site in Uitgeest (The Netherlands), with special reference to coprophilous fungi. Journal of Archaeological Science 30, 873-883.
Vescovi, E., Ravazzi, C., Arpenti, E., Finsinger, W., Pini, R., Valsecchi, V., Wick, L., Ammann, B., Tinner, W., 2007. Interactions between climate and vegetation during the Lateglacial period as recorded by lake and mire sediment archives in Northern Italy and Southern Switzerland. Quaternary Science Reviews 26, 1650-1669.
von Grafenstein, U., Erlenkeuser, H., Brauer, A., Jouzel, J., Johnsen, S.J., 1999. A Mid-European decadal isotope-climate record from 15,500 to 5000 years B.P. Science 284, 1654-1557.
von Grafenstein, U., Erlenkeuser, H., Müller, J., Jouzel, J., Johnsen, S., 1998. The cold event 8200 years ago documented in oxygen isotope records of precipitation in Europe and Greenland. Clim. Dyn. 14, 73-81.
Wanner, H., Beer, J., Buetikofer, J., Crowley, T.J., Cubasch, U., Flueckiger, J., Goosse, H., Grosjean, M., Joos, F., Kaplan, J.O., Kuettel, M., Mueller, S.A., Prentice, I.C., Solomina, O., Stocker, T.F., Tarasov, P., Wagner, M., Widmann, M., 2008. Mid- to Late Holocene climate change: an overview. Quaternary Science Reviews 27, 1791-1828.
Wastl, C., Schunk, C., Lupke, M., Cocca, G., Conedera, M., Valese, E., Menzel, A., 2013. Large-scale weather types, forest fire danger, and wildfire occurrence in the Alps. Agric. For. Meteorol. 168, 15-25.
Wehrli, M., Tinner, W., Ammann, B., 2007. 16 000 years of vegetation and settlement history from Egelsee (Menzingen, central Switzerland). Holocene 17, 747-761.
Welten, M., 1982. Vegetationsgeschichtliche Untersuchungen in den westlichen Schweizer Alpen: Bern-Wallis. Denkschriften Schweizerische Naturforschende Gesellschaft 95, 1-104.
Werlen, C., 1994. Werlen C. 1994. Elaboration de la carte de végétation forestière du Valais. Schweiz. Z. Forstwes. 145, 607-617.
Wermelinger, B., 2014. Invasive Gehölzinsekten: Bedrohung für den Schweizer Wald? Schweizerische Zeitschrift fur Forstwesen 165, 166-172.
Whitlock, C., Larsen, C., 2001. Charcoal as a fire proxy. In: Smol, J.P., H.J.B., B., Last, W.M., Bradley, R.S., Alverson, K. (Eds.), Tracking environmental change using lake sediments. Volume 3: Terrestrial, algal and siliceous indicators. Kluwer Academic Publishers, pp. 75-97.
Whitlock, C., Colombaroli, D., Conedera, M., Tinner, W., (subm). Land-use history as a guide for forest management and conservation. Conservation biology.
Wick, L., Tinner, W., 1997. Vegetation changes and timberline fluctuations in the central alps as indicators of Holocene climatic oscillations. Arctic and Alpine Research 29, 445-458.

Wick, L., van Leeuwen, J.F.N., van der Knaap, W.O., Lotter, A.F., 2003. Holocene vegetation development in the catchment of Sagistalsee (1935 m asl), a small lake in the Swiss Alps. Journal of Paleolimnology 30, 261-272.

Williams, J.W., Jackson, S.T., 2007. Novel climates, no-analog communities, and ecological surprises. Frontiers in Ecology and the Environment 5, 475-482.

Zoller, H., 1960. Pollenanalytische Untersuchungen zur Vegetationsgeschichte der insubrischen Schweiz. Denkschriften Schweizerische Naturforschende Gesellschaft 83, 45-156.

Zoller, H., Kleiber, H., 1971. Vegetationsgeschichtliche Untersuchungen in der montanen und subalpinen Stufe der Tessintäler. Verhandlungen der Naturforschenden Gesellschaft Basel 81, 90-154.

Figures

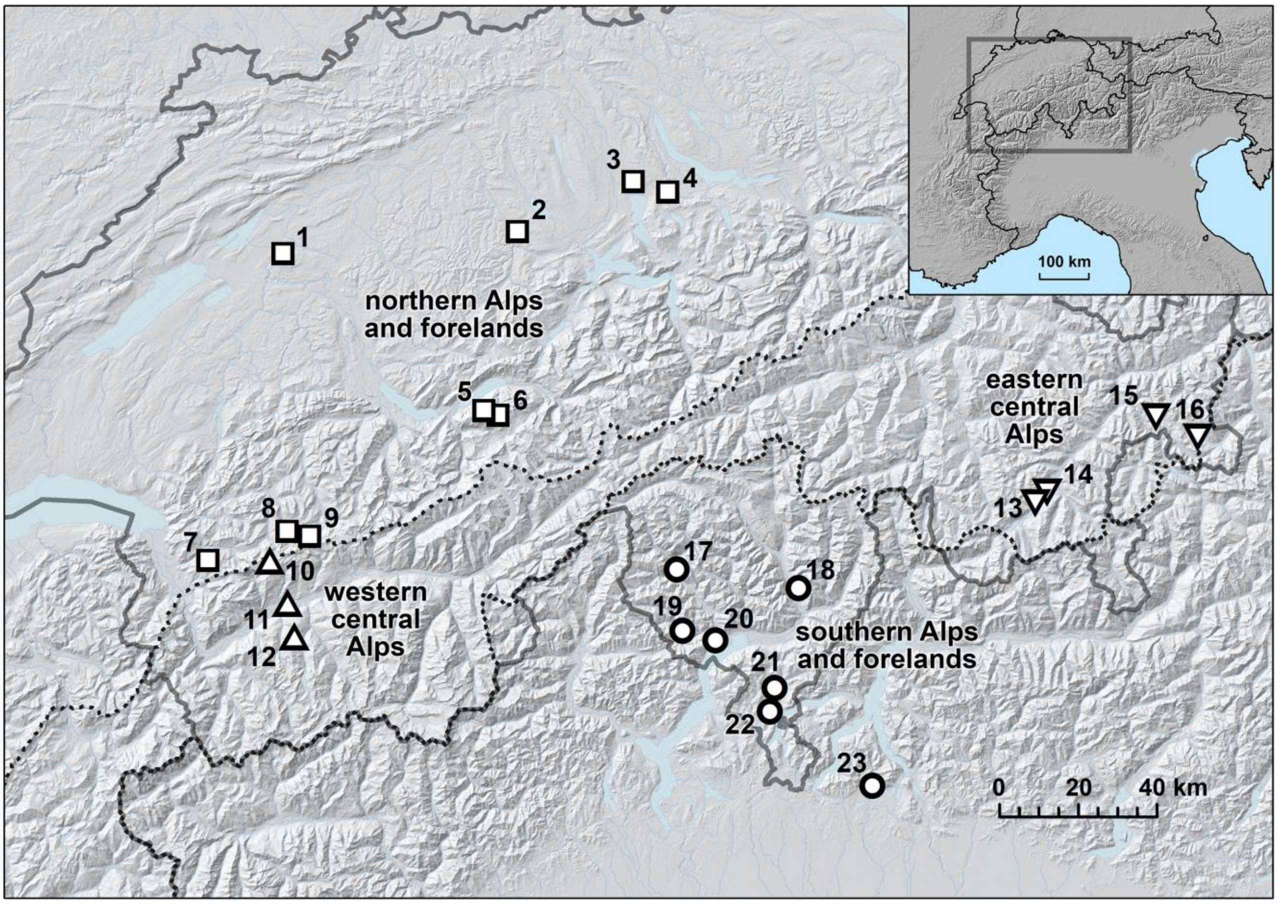

Fig. 1. Study area with detailed location of subregions and study sites
Northern Alps and forelands (1. Lobsigensee, 2. Soppensee, 3. Bibersee, 4. Egelsee, 5. Sägistalsee, 6. Bachalpsee, 7. Lac de Bretaye, 8. Lauenensee, 9. Iffigsee); Central Alps (western part: 10. Sanetsch, 11. Lac du Mont d'Orge, 12. Gouillé Rion; eastern part: 13. Lej da Champfér, 14. Lej da San Murezan, 15. Il Fuorn, 16. Fuldra/Palü Lunga), Southern Aps and forelands (17. Piano, 18. Guér , 19. Segna, 20. Balladrum, 21. Origlio, 22. Muzzano, 23.Segrino).

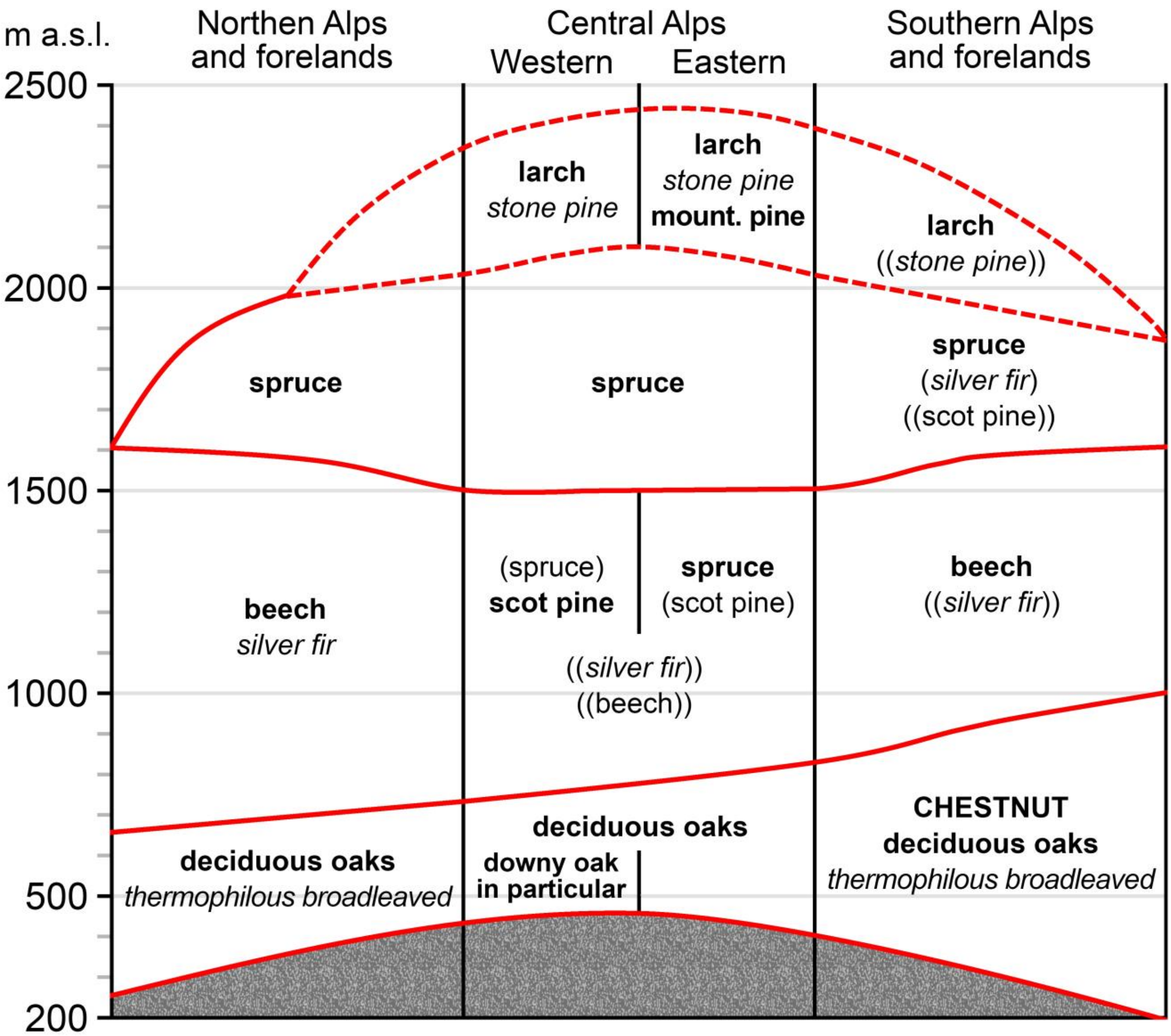

Fig. 2. Schematic representation of the present forest tree species distribution in the study area (species) = locally present only; ((species)) sporadic present only; *italic* = disfavored species according to Table 3; **bold** = indirectly favored species according to Table 3; **CAPITAL_BOLD** = directly favored species according to Table 3; --- = no sharp limits Thermophilous broadleaved: *Ulmus* spp., *Tilia* spp., *Acer* spp, *Fraxinus* spp., *Ostrya carpinifolia*, see also Table 2.

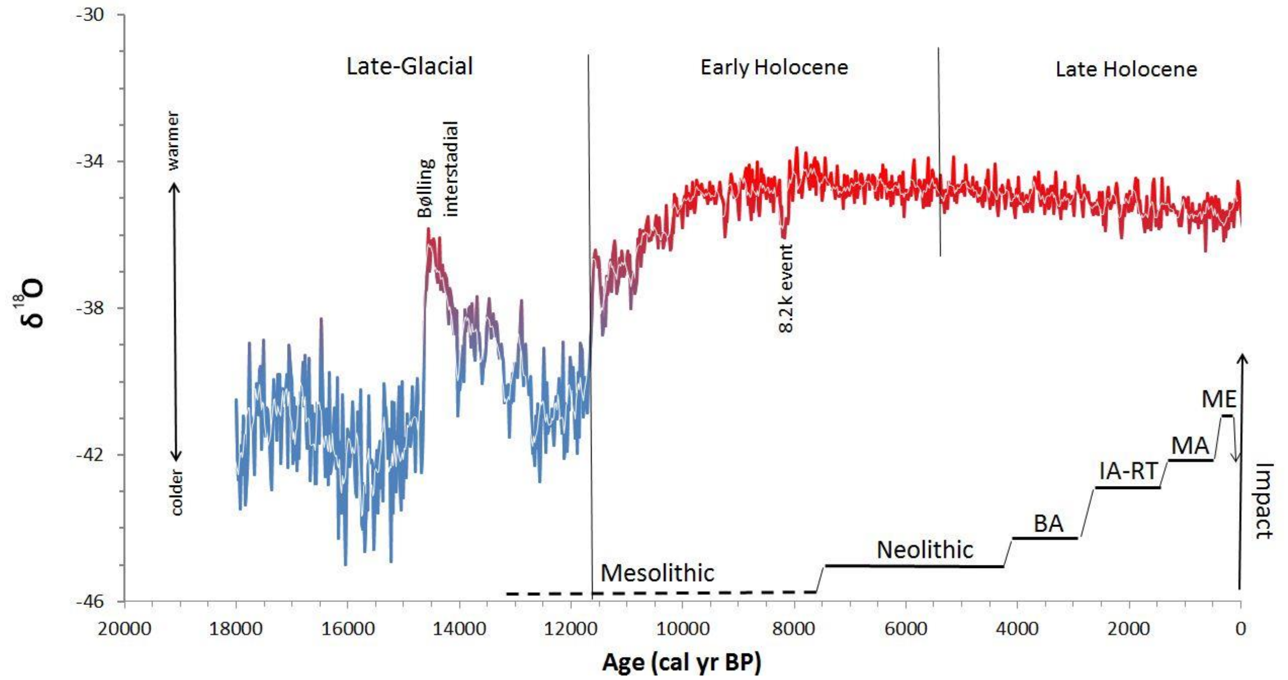

Fig. 3. Evolution of the temperature during the last 20,000 cal years in Greenland as reconstructed from NGRIP δ18O values on GICC05 time scale (modified from Ramussen et al. 2006). Age scale has been changed to show cal BP 1950 (original is BP 2000).

Human impact periods: Mesolithic (13,000-7500 cal yr BP); Neolithic (7500-4200 cal yr BP); BA - Bronze Age (4200-2850 cal yr BP); IA - Iron Age (2850 cal yr BP-15 BC); RT - Roman Times (15 BC-476 AD); MA - Middle Ages (476-1492 AD); ME - Modern Epoch (1492 AD to present).

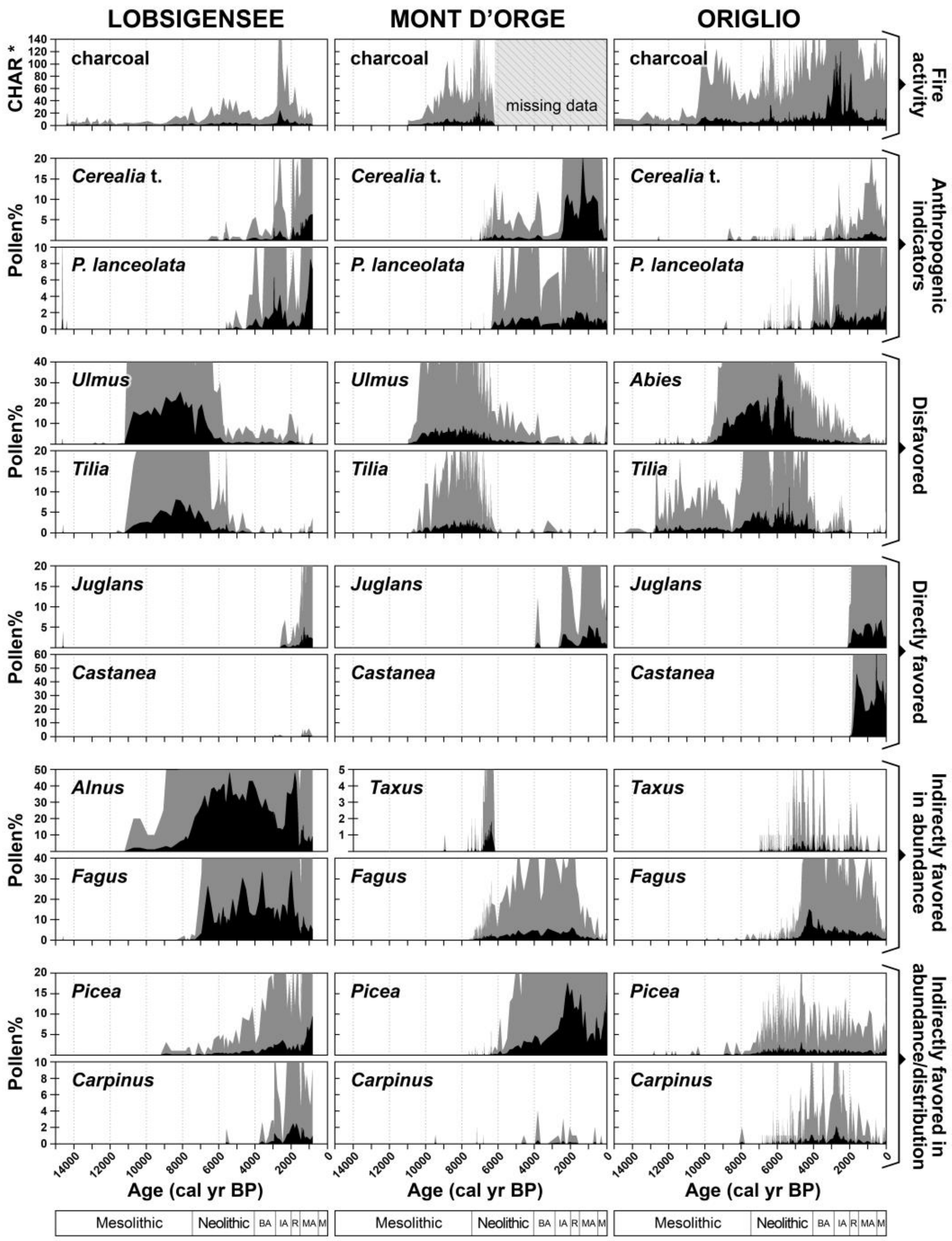

Fig. 4. Charcoal influx (CHAR) and pollen percentage diagrams (Pollen %) of selected taxa over last 15,000 years at representative low elevation sites in the northern (Lobsigensee), central (Mont d'Orge) and southern (Lago di Origlio) subregions.

Grey curves represent the 10x exaggeration of the Y-axis.

* CHAR units are expressed in $mm^2.cm^{-2}.yr^{-1}$ for Lobsigensee and Lago di Origlio and in $particles.cm^{-2}.yr^{-1}$ for Mont d'Orge.

Human impact periods: Mesolithic (13,000-7500 cal yr BP); Neolithic (7500-4200 cal yr BP); BA - Bronze Age (4200-2850 cal yr BP); IA - Iron Age (2850 cal yr BP-15 BC); R - Roman Times (15 BC-476 AD); MA - Middle Ages (476-1492 AD); M - Modern Epoch (1492 AD to present).

Source: modified from Welten (1982); Ammann (1985); Tinner et al. (2005); Tinner et al. (1999); Colombaroli et al. (2013).

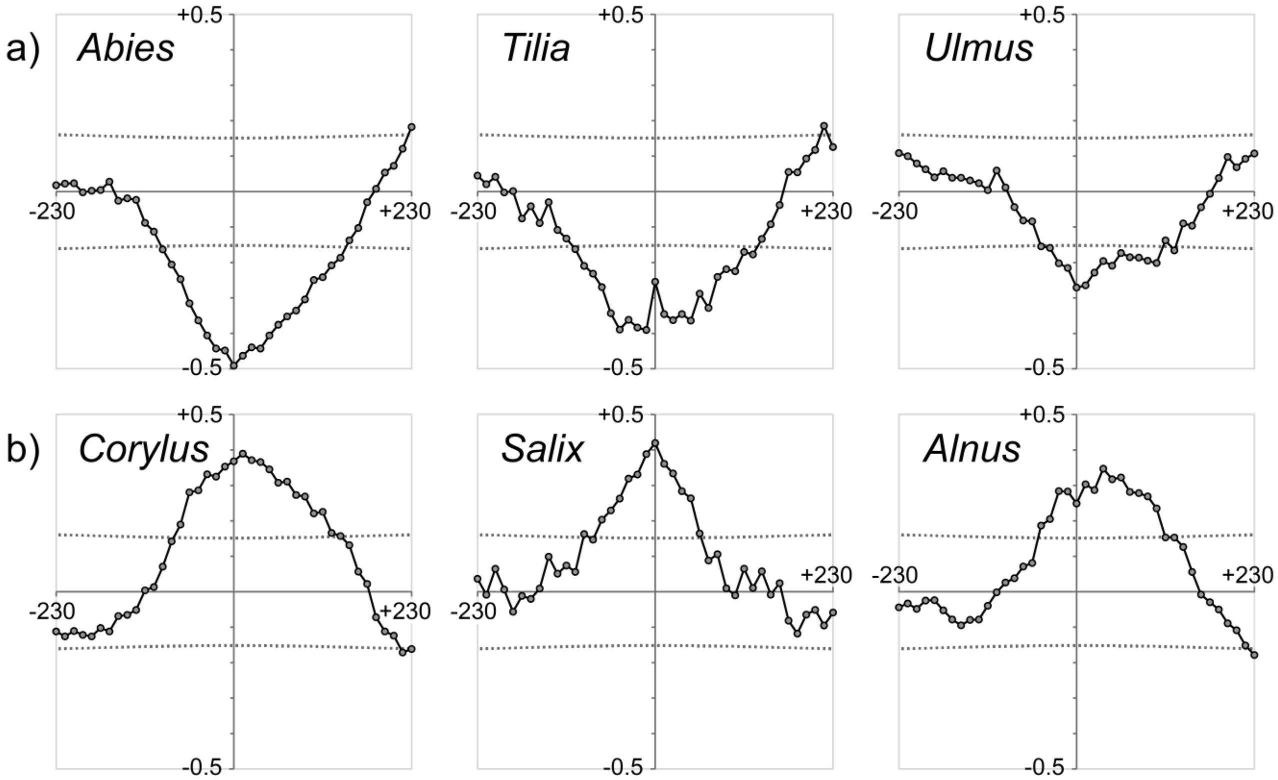

Fig. 5 Cross correlations of charcoal accumulation rates (CHAR) *vs* pollen percentages of selected taxa at Lago di Origlio (southern subregion) for the period 5100-3100 BC.
a) fire-sensitive (or fire-disfavored) taxa: *Abies* (extremely sensitive according to Table 2), *Tilia* (highly sensitive) and *Ulmus* (highly sensitive); b) fire-resistant and fire-favored taxa: *Corylus* (highly resistant according to Table 2), *Alnus* (highly resistant) and *Salix* (extremely resistant).
Dots on the horizontal axis represent a time lag of ~11.5 years with respect to the fire peak. Vertical axis represent the correlation coefficients. Dots outside the significance interval (dashed lines) are significantly positively or negatively correlated at $p < 0.05$.
Source: modified from Tinner et al. (1999).

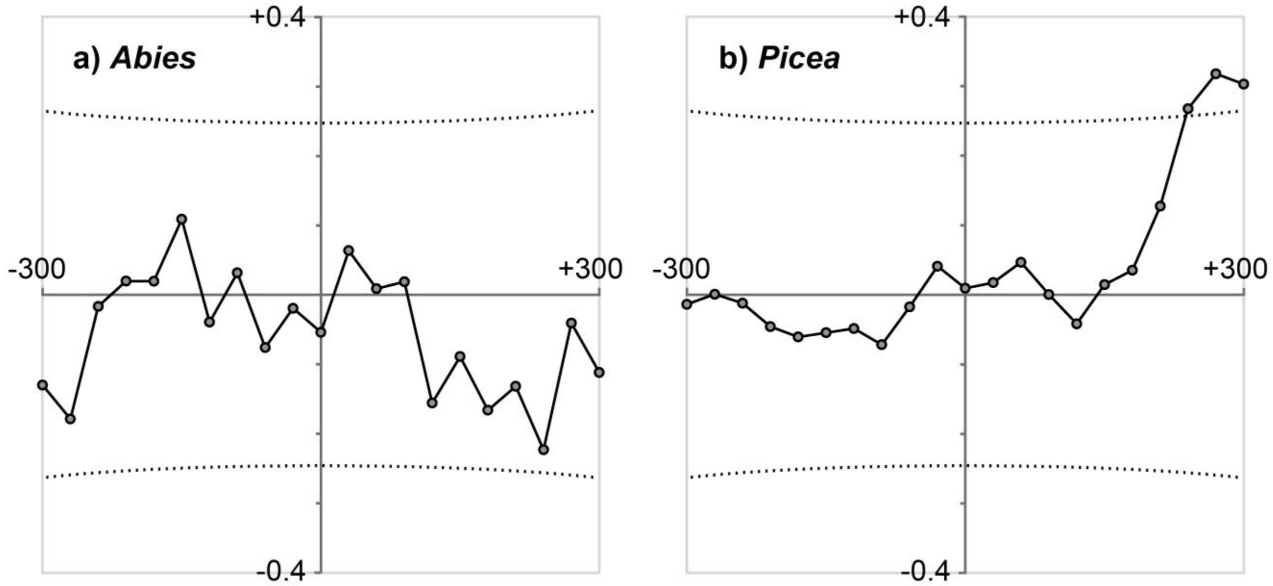

Fig. 6 Cross correlations of dung spores (*Sporormiella* spp.) influx vs pollen percentages of selected taxa at Iffigsee for the period 4960-3160 BC.

a) browsing-sensitive (or browsing-disfavored) silver fir; b) browsing-resistant (or browsing-favored) spruce.

Steps on the horizontal axis represent a time lag of ~30 years with respect to the browsing peak. Vertical axis represent the correlation coefficients. Dots outside the significance interval (dashed lines) are significantly positively or negatively correlated at $p < 0.05$. First signs of negative effects of browsing occur at lag +4 that is 120 years after the browsing peak, which probably corresponds to the surviving span of mature silver fir before the lack of regeneration (as registered in pollen). Similarly, but in the opposite sense, spruce significantly increases to become dominant after more than 240 year (8 lags) under intense browsing activity.

Source: modified from Schwörer et al. (2014b).

Tables

Table 1: Response of selected woody species to environmental conditions in the Alps according to pollen, stomata and macrofossil records

species	Environmental conditions				subregions	reference
	Drought	Solar radiation	Continentality / seasonality	Soil development		
Abies alba	--	-	--	++	Northern Alps and Forelands; Central Alps; Southern Forelands	Welten 1982; Tinner and Lotter 2001; 2006; Tinner and Kaltenrieder 2005; Lotter et al. 2006; Vescovi et al. 2006
Acer spp.	-	+	+	+	Northern Forelands; Central Alps	Welten 1982; Tinner and Lotter 2001; 2006
Alnus viridis	---	--	--	--	Southern Alps; Central Alps	Wick and Tinner 1997; Gobet et al. 2003
Betula (tree)	+++	+++	++	---	Central Alps ; Northern Forelands	Ammann et al. 2013 ; Schwörer et al. 2014a
Corylus avellana	++	+++	++	-		
Fagus sylvatica	---	--	--	++	Northern Forelands; Central Alps	Welten 1982; Tinner and Lotter 2001; 2006
Fraxinus excelsior	-	+	+	+	Northern Forelands; Central Alps	Welten 1982; Tinner and Lotter 2001; 2006
Juniperus communis ssp. *nana*	---+++	+++	++	---	Central Alps ; Northern Alps and Forelands	Lotter et al. 2006 ; Rey et al. 2013 ; Ammann et al. 2013 ; Schwörer et al. 2014a
Larix decidua	+++	+++	+++	---	Central Alps	Lotter et al. 2006 ; Tinner and Kaltenrieder 2005
Quercus (Deciduous)	++	+	+	+	Northern Forelands; Central Alps	Welten 1982; Tinner and Lotter 2001; 2006
Picea abies	---	-	-	++	Central Alps ; Northern Alps	Lotter et al. 2006 ; Rey et al. 2013
Pinus cembra	+	-	++	-	Central Alps	Lotter et al. 2006 ; Schwörer et al. 2014b ; Thöle et al. 2016
Pinus sylvestris	++	++	++	---	Central Alps, Northern and Southern Forelands	Welten 1982; Tinner and Lotter 2001; 2006, Vescovi et al. 2006
Tilia spp.	+	+	+	+	Northern Forelands; Central Alps	Welten 1982; Tinner and Lotter 2001; 2006
Ulmus spp.	+	+	++	+	Northern Forelands; Central Alps	Welten 1982; Tinner and Lotter 2001; 2006

Symbols to the environmental conditions: --- = extremely sensitive; -- = highly sensitive, - = sensitive; + = resistant/requiring; ++ = highly resistant/requiring, +++ = extremely resistant/requiring

Table 2: Disturbance sensitivity of the main woody species of the Alps according to paleorecords

Species	**Sensitivity**		**Remarks**
	fire	**browsing**	
Abies alba	+++	+++	see also Figures 5 and 6
Alnus spp.	--	--	see also Figure 5
Alnus viridis	---	--	
Betula spp.	-	---	
Castanea sativa	---	?	
Corylus avellana	--	--	see also Figure 5
Fagus sylvatica	+	-	
Fraxinus ornus	++	?	
Hedera helix	+++	+	
Ilex aquifolium	+++	?	
Juniperus spp.	?	---	
Juglans regia	?	?	
Larix decidua	-	--	
Picea abies	+	---	see also Figure 6
Pinus cembra	++	++	
Pinus mugo	---	---	
Pinus sylvestris	--	--	
Quercus (deciduous)	--	--	*Q. robur*, *Q. petraea*, *Q. pubescens*, and *Q. cerris* in the southern forelands
Salix spp.	--	--	see also Figure 5
Thermophilous broadleaveds	++	?	*Ulmus* spp., *Tilia* spp., *Acer* spp, *Fraxinus* spp., *Ostrya carpinifolia*, see also Figure 5

Sensitivity: +++ = extremely sensitive; ++ = highly sensitive; + = sensitive; - = resistant; -- = highly resistant; --- = extremely resistant; ? = not applicable from paleorecords

Source: Ammann (1989), Wick and Tinner (1997); Tinner et al. (1999); Gobet et al. (2000); Wick et al. (2003); Gobet et al. (2003); Tinner et al. (2005); Tinner and Kaltenrieder (2005); Tinner and Lotter (2006); Hofstetter et al. (2006); Lotter et al. (2006); Stähli et al. (2006); Wehrli et al. 2007; Colombaroli et al. (2010); Valsecchi et al. (2010); Rey et al. (2013); Berthel et al. (2013); Colombaroli et al. (2013); Schwörer et al. (2014a); Schwörer et al. (2015); Morales-Molino et al. (2015); Thöle et al. (2016).

Table 3. Species response to human-induced disturbance and land use change in the Alps and their forelands

Response	Drivers	Species	Remarks
Disfavored	Reduced by human-induced disturbance (e.g. fire, browsing), little economic value	*Abies alba*	see also figures 2, 4, 5, and 6
		Acer spp.	see also figure 2
		Fraxinus excelsior	see also figure 2 and 4
		Hedera helix	
		Ilex aquifolium	
		Pinus cembra	
		Tilia spp.	see also figures 2, 4 and 5
		Ulmus spp.	see also figures 2, 4 and 5
Directly favored	Benefited from deliberate introduction, maintained through plantation and cultivation; high economic value	*Castanea sativa*	not on limestone, see also figure 2 and 4
		Juglans regia	on lime-stone in particular, see also figure 2 and 4
Indirectly favored in abundance	Benefited from relative resistance to disturbances, some utility for humans	*Alnus* spp.	*A. glutinosa*, *A. incana*, see also figure 5
		Corylus avellana	see also figure 5
		Fraxinus ornus	on lime-stone
		Fagus sylvatica	see also figure 2 and 4
		Larix decidua	see also figure 2
		Picea abies	at mid to high-elevation since Neolithic, see also figures 2, 4, and 6
		Quercus (deciduous)	*Q. robur*, *Q. petraea*, *Q. pubescens*, and *Q. cerris* in the southern forelands, see also figure 2
		Salix spp.	see also figure 5
		Taxus baccata	especially in the early Neolithic, see also figure 4
Indirectly favored in distribution and abundance	Benefited from disturbance-induced suitable ecological conditions and by reduction of competitors	*Alnus viridis*	
		Betula pendula	
		Carpinus betulus	see also figure 4
		Juniperus spp.	*J. nana* and *J. communis*
		Ostrya carpinifolia	on limestone
		Picea abies	at low elevations especially since modern times
		Pinus mugo	eastern central Alps, on limestone and dolomite, see figure 2

Source: Ammann (1989), Wick and Tinner (1997); Tinner et al. (1999); Gobet et al. (2000); Wick et al. (2003); Gobet et al. (2003); Tinner et al. (2005); Tinner and Kaltenrieder (2005); Tinner and Lotter (2006); Hofstetter et al. (2006); Lotter et al. (2006); Stähli et al. (2006); Wehrli et al. 2007; Colombaroli et al. (2010); Valsecchi et al. (2010); Rey et al. (2013); Berthel et al. (2013); Colombaroli et al. (2013); Schwörer et al. (2014a); Schwörer et al. (2015); Morales-Molino et al. (2015); Thöle et al. (2016).