

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

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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

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

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

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48 **1. Introduction**

49 Present-day Alpine forest ecosystems and their dynamics are fundamentally different from
50 those of the past. In particular, a long human history has had irreversible consequences on Alpine
51 forest ecosystems (e.g. Tinner et al. 2005; Carcaillet et al. 2009; Blarquez et al. 2010; Valsecchi et
52 al. 2010), decoupling natural vegetation-climate relationships in many regions and maintaining
53 plant communities in a non-equilibrium state with climate and disturbance regimes (Svenning et al.
54 2015). In recent decades, reduced management and abandonment of remote mountain areas have
55 led to expansion of forest cover and loss of high-diversity meadows (Gehrig-Fasel et al. 2007;
56 Loran et al. 2016). The transitional and highly dynamic state of Alpine forests challenges forest
57 managers tasked with assessing the local consequences of climate change on forests and developing
58 adaptive and restorative silvicultural plans to ensure near-to-nature conditions and continued
59 delivery of ecosystem services in the future (Lindner 2000; Schmid et al. 2015). However, the
60 strong human signature on present-day forest composition, structure and dynamics in many regions
61 raises concerns about the use of short-term ecological observations and standard modeling
62 approaches (Iverson and Mckenzie, 2013) to predict forest responses to future climate change
63 (Ibanez et al. 2006; Williams and Jackson 2007; Dawson et al. 2011; Tinner et al. 2013). To
64 understand present-day relationships between climate, humans, vegetation and disturbance requires
65 information on the causes and consequences of ecosystem change in the past. This information is
66 especially critical for forests in the Alpine region of Switzerland, where present-day ecosystem
67 dynamics are conditioned by historical legacies and altered disturbance regimes, and the abundance
68 and distribution of current forest types and taxa are a product of both anthropogenic manipulation
69 and climate change, which are difficult to disentangle.

70 In this paper, we review and describe the influence of past changes in climate, land use and
71 disturbance on the development of Swiss mountain forest ecosystems and the history of selected

72 woody species. Representative sites with good chronological control (i.e. multiple radiocarbon
 73 dates) and taxonomical resolution are selected along a strong north-to-south environmental gradient
 74 in the Alps to compare forest history in different settings. The time span of interest is the last
 75 ~20,000 years, which covers the period from the end of the last glaciation to the present day.
 76 Special focus is on the last 7500 years starting with the onset of the Neolithic period and the
 77 progressive human alteration of land cover and forest composition. The specific aim of the paper is
 78 to show how knowledge of Alpine forest history can inform management efforts that seek to (1)
 79 assess forest sensitivity to future climate change; (2) choose between different management options
 80 (e.g. preserving close-to-nature conditions, maintaining cultural landscapes, protecting species of
 81 special concern, maximizing biodiversity); and (3) maintain forest capacity to provide important
 82 ecosystem goods and services.

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

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88 **2. Material and methods**

89 *2.1 Study area*

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

98 Meteorological Station Locarno-Monti) and annual precipitation ranges from 1300 mm in the west
 99 (e.g. meteorological station Acquarossa) to 1900 mm in the east (Locarno-Monti). In winter, the
 100 climate is dry and mild and summers are humid (June-September 800 to 1200 mm of precipitation),
 101 with thunderstorm events alternating with periods of drought. Present-day forests are organized by
 102 elevational belts (Fig. 2). *Castanea sativa* (sweet chestnut) dominates low-elevation forests (up to
 103 900-1000 m asl). These closed forests, which occur in other regions of southern Europe (e.g.
 104 Apennines, Pyrenees, the Balkans), occasionally support other thermophilous broadleaved species,
 105 such as *Tilia cordata* (small-leaved linden), *Quercus petraea* (sessile oak), *Q. robur* (common oak),
 106 and (*Q. pubescens* (downy oak), *Alnus glutinosa* (common alder), *Prunus avium* (sweet cherry),
 107 *Acer* spp. (maple), and *Fraxinus* spp. (ash). At middle elevations (900-1400 m asl), forests consist
 108 of mostly pure stands of *Fagus sylvatica* (European beech), and at higher elevations, forests are
 109 dominated by *Picea abies* (Norway spruce) and at upper treeline by *Larix decidua* (European larch).
 110 On south-facing slopes, beech forest is sometimes absent, and *Abies alba* (silver fir) is present in
 111 small patches on north-facing slopes in the central part of the subregion. *Pinus sylvestris* (Scots
 112 pine) grows on dry south-facing slopes, and *P. cembra* (stone pine) occurs in the most continental
 113 settings at high elevations (Ceschi 2014).

114 The central Alps subregion, including the Valais and Engadine, displays a markedly
 115 continental climate characterized by low annual precipitation (e.g. 603 mm in Sion at 482 m asl,
 116 639 mm in Zermatt at 1638 m asl, 713 mm in Samedan at 1703 m asl), cold winters, high insolation
 117 and extreme annual and daily temperature excursions. The temperature range is correspondingly
 118 large with mean annual temperatures of ~10°C on valley bottoms (e.g. 10.1°C in Sion at 482 m asl),
 119 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-
 120 Bernard at 2472 m asl). The present distribution of forest types in the central Alps reflects this
 121 topographic and climatic gradient (Fig. 2). Thermophilous deciduous broadleaves forests support by
 122 downy oak in continental sub-mediterranean settings, and sessile oak and common oak in the sub-
 123 oceanic lowlands (~400-800 m asl). At medium elevations (~800-1400 m asl), stands of Scots pine

124 and spruce are present, and beech and fir are confined to the most mesic settings. Spruce forest
 125 grows at high elevations (~1400-2100 m asl) and is replaced by larch and stone pine forests at upper
 126 treeline (Werlen 1994) and mountain pine forests (*Pinus mugo* spp. *uncinata*) on dolomitic soils in
 127 the eastern Alps (Gobet et al. 2003; Stähli et al. 2006, Ellenberg 2009).

128 The northern Alps subregion, which includes the northern Alps and their forelands, displays a
 129 cool temperate central European climate, with mild summers (18°C July average), cool winters
 130 (−1°C January mean) and annual precipitation ranging from ~1000 mm at low elevations (1196 mm
 131 in Interlaken at 577 m asl) to ~1500 mm at higher elevations (1338 mm in Adelboden at 1327 asl).
 132 Today's vegetation consists of highly fragmented relict forest patches. As in the southern region,
 133 vegetation is organized in belts (Fig. 2), from mixed oak-beech forests (including other deciduous
 134 trees such as linden, elm, maple, and ash) at the lowest elevations (<600 m asl), mixed beech-fir
 135 forests in the mountain belt (600-1500 m) to spruce forest in the subalpine belt (1500-2000 m;
 136 Ellenberg 2009). Stands of larch and/or stone pine are present in the northern Alps above the spruce
 137 belt in proximity to the continental central Alps.

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139 2.2 Information from paleorecords

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

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

156 Human activity is identified in pollen or plant macrofossil records by the presence of remains
 157 of crops, fruit tree cultivars, non-native species, and past shifts in vegetation composition associated
 158 with particular land use (e.g. Rey et al. 2013). Direct proxies of human activities include cultivated
 159 taxa introduced to the area for agricultural purposes (adventive agriophytes), such as cereals (*Avena*
 160 *t*, (*t*=type), *Triticum t*. and *Hordeum t*, usually grouped as *Cerealia t* or *Secale cerealia*), and other
 161 crop species, such as *Fagopyrum tataricum*, *Cannabis sativa t* or *Linum usitatissimum*. Accidentally
 162 introduced species, such as *Plantago lanceolata t* which first appeared in Switzerland in the Late
 163 Mesolithic (Behre, 1981, 1988; Tinner et al. 2007) and *Ambrosia* and other pollen types that
 164 appeared in modern times, are also unequivocal evidence of land use and anthropogenic
 165 disturbance. Past pastoral activity and herbivore density are inferred from pollen (e.g.
 166 Cichorioideae, Asteroideae), spores of dung-specialized (coprophilous) fungi, including
 167 *Sporormiella* spp., *Podospora* spp., *Ustilina deusta* (van Geel et al. 2003; Graf and Chmura 2006),
 168 and particular ferns (e.g. *Botrychium lunaria*). Plants that are altered indirectly by human impact are
 169 called apophytes (present in the native flora but favored by land use) and include *Urtica*, *Artemisia*,
 170 *Rumex acetosella t*, *Succisa*, *Campanula*, *Fallopia*, and Brassicaceae (Behre 1981; Lang 1994).
 171 Charcoal particles in sediment cores provide direct evidence of past fires, with high charcoal
 172 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).

225 During the early Holocene, thermophilous broadleaved deciduous (e.g. deciduous *Quercus*,
 226 *Acer*, *Ulmus*, *Tilia*, *Fraxinus*, *Alnus*) and shrubs (e.g. *Corylus avellana*, hazel) became increasingly
 227 important at low elevations in all subregions (e.g. Lotter et al. 1992) and expanded their ranges to
 228 higher elevations (e.g. Zoller 1960; Zoller and Kleiber 1971; Welten 1982; Vescovi et al. 2006; Rey
 229 et al. 2013; Schwörer et al. 2014a; Thöle et al 2016). The progressive build-up of flammable fuel
 230 (e.g. pines) and summer warmer-than-present conditions were associated with more fires at high
 231 elevations and in the dry central subregion (Wick and Tinner 1997; Gobet et al. 2003; Tinner and
 232 Kaltenrieder 2005; Valsecchi and Tinner 2010; Blarquez and Carcaillet 2010; Stähli et al. 2006;
 233 Schwörer et al. 2014a; Colombaroli et al. 2010). Increased fire activity probably allowed early-
 234 successional mountain pine (*Pinus mugo* spp. *uncinata*) to expand in the driest (eastern) part of the
 235 central Alps where infertile dolomite soils are present (Stähli et al. 2006). In the Alpine forelands,
 236 early-Holocene fire activity also gradually increased and was associated with an expansion of fire-
 237 adapted *Pteridium aquilinum* in the southern subregion at ~10,500 cal BP (Tinner et al. 1999;
 238 2005).

239 Forest composition experienced a dramatic change as a consequence of the cooling event at
 240 8200 cal yr BP when warm dry summers were abruptly replaced by cool moist conditions
 241 (Dansgaard et al. 1993; Heiri et al. 2014). This event was a tipping point for the vegetation and
 242 enabled the expansion of moist-tolerant beech and silver fir in the northern subregion at the expense
 243 of less mesophilous forest species. Interestingly, the subsequent return to warm conditions at 8000
 244 cal yr BP did not allow more drought-adapted taxa to regain their previous abundance, and moist
 245 conditions maintained silver fir-beech forests (Tinner and Lotter 2001; 2006). Unlike in the
 246 northern subregion and in contrast to silver fir, beech did not become abundant in the dry
 247 continental settings of the central Alps and in the warm-temperate setting of the southern subregion
 248 following the 8200 cal yr BP event (Welten 1982, Tinner et al. 1999). Probably the species was
 249 limited by its low tolerance to drought and/or competition with previously established silver fir
 250 (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.

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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).

301 Historical records, traditional knowledge and written documents, such as the local Medieval
 302 bylaws (Stuber and Bürgi 2001, 2002; Bürgi and Stuber 2003, 2013; Bertogliati 2014; Krebs et al.
 303 2015), describe extensive land use, forest management and population increases from the Middle
 304 Ages to the end of the 1800s. Forests were managed for non-timber purposes including for
 305 infrastructure and settlement protection (*Bannwald*), forage and cattle fodder (wood hay, branches
 306 of pollarded broadleaved), cattle and human bedding (collected litter), fuel (collected cones and
 307 bark), as well as for very specialized uses (bark collection for leather tanning, resin collection for
 308 fumigations, herb collection for medicine). During this time, fires were regulated and mainly used
 309 for pasture clearance and maintenance (Conedera et al. 2007).

310 With industrialization in the 19th century, demand increased for wood for charcoal
 311 production and later for timber in the Alps (e.g. Krebs and Bertogliati 2015). The intensity of land
 312 use in Alpine forests was unprecedented in the 1800s. In addition to the expansion of meadows and
 313 grasslands, this period is also characterized by the extinction in Switzerland of large carnivores,
 314 such as the brown bear (*Ursus arctos*), wolf (*Canis lupus*), and Eurasian lynx (*Lynx lynx*), all of
 315 which were considered a threat to livestock and game hunting (Breitenmoser 1998). In the late 19th
 316 century, depleted and overexploited forests reduced slope stability and hydrological regulation,
 317 which in turn increased flood frequency. Forest protection legislation was adopted in most Alpine
 318 countries and forest management shifted towards reforestation (Bertogliati 2015; Loran et al. 2016;
 319 Bebi et al., this issue). Forest expansion greatly accelerated after the second World War with the
 320 abandonment of marginal agricultural and pasture lands (Gehrig-Fasel et al. 2007; Gellrich et al.
 321 2007; Loran et al. 2016).

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324 3.4 Response of tree species to past human impact

325 Present landscapes in the Alpine region have been significantly shaped by four key cultural
 326 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).

376

377 **4. Discussion**

378 *4.1 Species sensitivity to past climate impact*

379 Changes in vegetation composition and dynamics before significant human activity were
 380 clearly driven by climate. For example, the three subregions responded similarly to rapid high-
 381 amplitude warming trends in the late-glacial period (e.g. the Bølling Interstadial) and at the
 382 beginning of the Holocene. Ecosystem reorganization entailed changes from cold-adapted open
 383 tundra to shrubland, then subalpine conifer forest and finally to forests dominated by thermophilous
 384 and mesophilous species. In many cases, our understanding of the present ecological behavior of
 385 Alpine tree species is consistent with their response to past environmental change, providing
 386 evidence that the environmental niches of these species are well understood. For example, the
 387 pioneering characteristics of juniper, birch, and to some extent also larch, including their ability to
 388 colonize poorly developed soils is evidenced after present-day glacial retreat and avalanche activity
 389 in the Alps (Ellenberg 2009; Garbarino et al., 2010). Similarly, they were able to colonize
 390 deglaciaded landscapes soon after ice retreat during the late-glacial period. Differences in present-
 391 day moisture requirements between larch, stone pine, beech, and pedunculate oak (*Quercus robur*)
 392 are also well reflected in their Holocene history (Tinner and Lotter, 2001; Tinner and Kaltenrieder
 393 2003; Ellenberg 2009). In agreement with the ecology of silver fir, paleoecological records show
 394 that silver fir was generally less demanding of moisture conditions than either spruce or beech in the
 395 past (Henne et al. 2011).

396 Paleoecological records prior to the onset of the Neolithic period show that tree species were
 397 able to respond rapidly to climate changes and establish a dynamic equilibrium with the
 398 environmental conditions in the absence of significant human activity (Schwörer et al. 2014a). For
 399 example, establishment of thermophilous tree species, such as deciduous oaks, elm, ash, maple, and
 400 linden, at low to middle elevations in the southern and northern Alpine forelands, occurred within a
 401 century of warming at ~ 11,500 cal yr BP (Ammann et al. 2000). Similarly, major reorganizations
 402 of plant communities in the northern Alpine forelands took place within decades of the cool-moist
 403 event at 8200 cal yr BP (Tinner and Lotter, 2001). Although few records have high enough spatial
 404 and temporal resolution to detect the influence of other natural disturbances (e.g. fire, browsing by

405 wild ungulates, insect outbreaks, windthrow, erosion), there is no evidence that single or closely
 406 spaced disturbance events shifted the vegetation to a new stable state in the absence of humans (e.g.
 407 Colombaroli et al. 2010).

408

409 4.2 *Species sensitivity to human impact*

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

429 The ubiquitous and long-term influence of people on ecosystem dynamics and species
 430 distributions and abundance points to the importance of considering both climate and human effects

431 as drivers in ecosystem modeling (Birks and Tinner 2016). Models should incorporate long-term
 432 information in developing relationships between species distribution and abundance and their
 433 environment, by including (1) species distributions under a range of climate conditions and
 434 disturbance levels in the past; (2) past ecological consequences of adding or removing species or
 435 changing species abundance; and (3) the effects of altered natural disturbance regimes in the past
 436 (see discussion in e.g. Henne et al. 2011; Tinner et al. 2013). In reality, however, most species
 437 distribution models (SDM), often also called bioclimatic or niche models, are based on present-day
 438 distributions in relation to a suite of modern climate variables. Because present distributions are not
 439 in equilibrium with climate, models results often under- or overestimate present and potential future
 440 ranges for many critical species (Elkin et al. 2013; García-Valdéz et al. 2013; Schwörer et al.
 441 2014b; Ruosch et al. 2016). Estimates in the Alpine region would be improved if SDMs considered
 442 early to mid-Holocene vegetation-climate relationships prior to the time when the species ranges
 443 and abundance were highly modified by humans (i.e. before the middle to end Neolithic period).
 444 Well-resolved paleoclimatic data, specifically in regard to precipitation, sensitivity studies or
 445 climatic scenarios can thus be used to assess such issues (Heiri et al. 2006). Dynamic and
 446 ecophysiology-based vegetation models, such as LANDCLIM are less affected by this problem,
 447 because they consider species-specific traits and the fundamental niche of species (Bugmann 2001;
 448 Bugmann and Solomon 2000; Ruosch et al. 2016). Moreover, landscape, disturbance and
 449 biochemical feedbacks are also integrated to better assess the interactions of species with their
 450 biotic and non-biotic environment. Recent dynamic vegetation models that incorporate the influence
 451 of past land use on species distributions also hold considerable promise for recognizing the
 452 anthropogenic signal (Kaplan et al. 2010; Schwörer et al. 2014b).

453

454 4.3 *Using the past to inform future silvicultural approaches*

455 The next decades of land use and climate change will be key for forest management in the
 456 Alpine region. Since the Second World War, land abandonment in marginal mountain settings has

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

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

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

483 Present changes in land use and climate have also created new types of disturbances that may
 484 affect the future resilience of the concerned forest ecosystems. Wild ungulate populations are
 485 growing in the absence of former pastoral activities, large predators and effective hunting
 486 regulations. These native herbivores interfere with the ability of some tree species to regenerate
 487 (e.g. silver fir) and represent a new type of disturbance for forests (Heuze et al. 2005; Didion et al.
 488 2011; Häsler and Senn 2012; Kupferschmid et al. 2014). Cessation of systematic litter collection,
 489 and forest closure and encroachment have caused an accumulation of dead biomass, which has
 490 altered fuel loads and over time may create inhibitory and toxic effects of extracellular self-DNA in
 491 the soil (Mazzoleni et al. 2015).

492 Projected climate trends pose direct threats, as evidenced by drought-induced leaf whitening,
 493 which caused significant chestnut mortality during the hot and dry summer 2003 in the southern
 494 subregion (Conedera et al. 2010). Similarly, recent dieback of Scots pine in dry areas of the Rhone
 495 valley of the western central Alps is also related to extreme summer drought and will likely
 496 continue in the future (Bigler et al. 2006; Rebetez and Dobbertin 2006; Rigling et al. 2013;
 497 Vacchiano et al. 2013). Warming and related increases in drought frequency and severity (Rebetez
 498 1999) and associated fire risk (Reinhard et al. 2005; Wastl et al. 2013; Valese et al. 2014) will alter
 499 interactions among woody species (Moser et al. 2010; Maringer et al. 2016) and with pests and
 500 diseases (Battisti 2008; Netherer et al. 2010; Marini et al. 2012). In addition, newly introduced
 501 exotic species (e.g. *Robinia pseudooacacia*, *Ailanthus altissima*, *Pawlonia* spp.) have become
 502 invasive and highly competitive in low- to mid-elevation forest ecosystems and strongly interfere
 503 with fire regimes, silvicultural management practices (Grund et al. 2005; Maringer et al. 2012;
 504 Radtke et al. 2014; Knüsel et al. 2015), pests (Wermelinger 2014; Roques et al. 2016) and disease
 505 (Kowaski and Holdenrieder 2009; Pautasso et al. 2013; Sieber 2014) as well as their possible
 506 interactions (e.g. Meyer et al. 2016). Thus, information on species and forest community responses
 507 to novel climates and disturbance regimes in the past can help guide management strategies in the
 508 future (Williams and Jackson, 2007).

509

510 **5. Conclusions**

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

525

526

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532

533 **Abbreviations**

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

535

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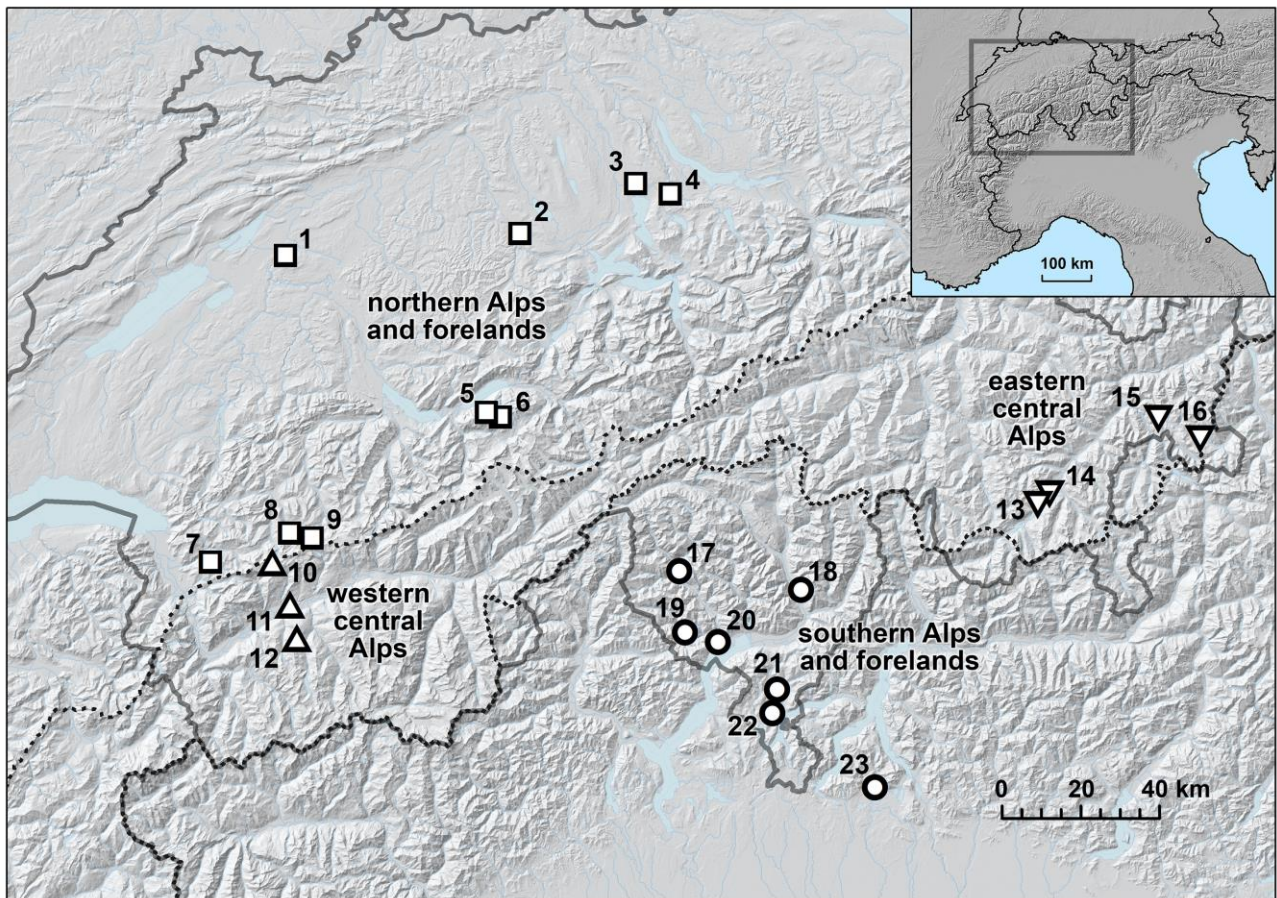
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884 **Figures**

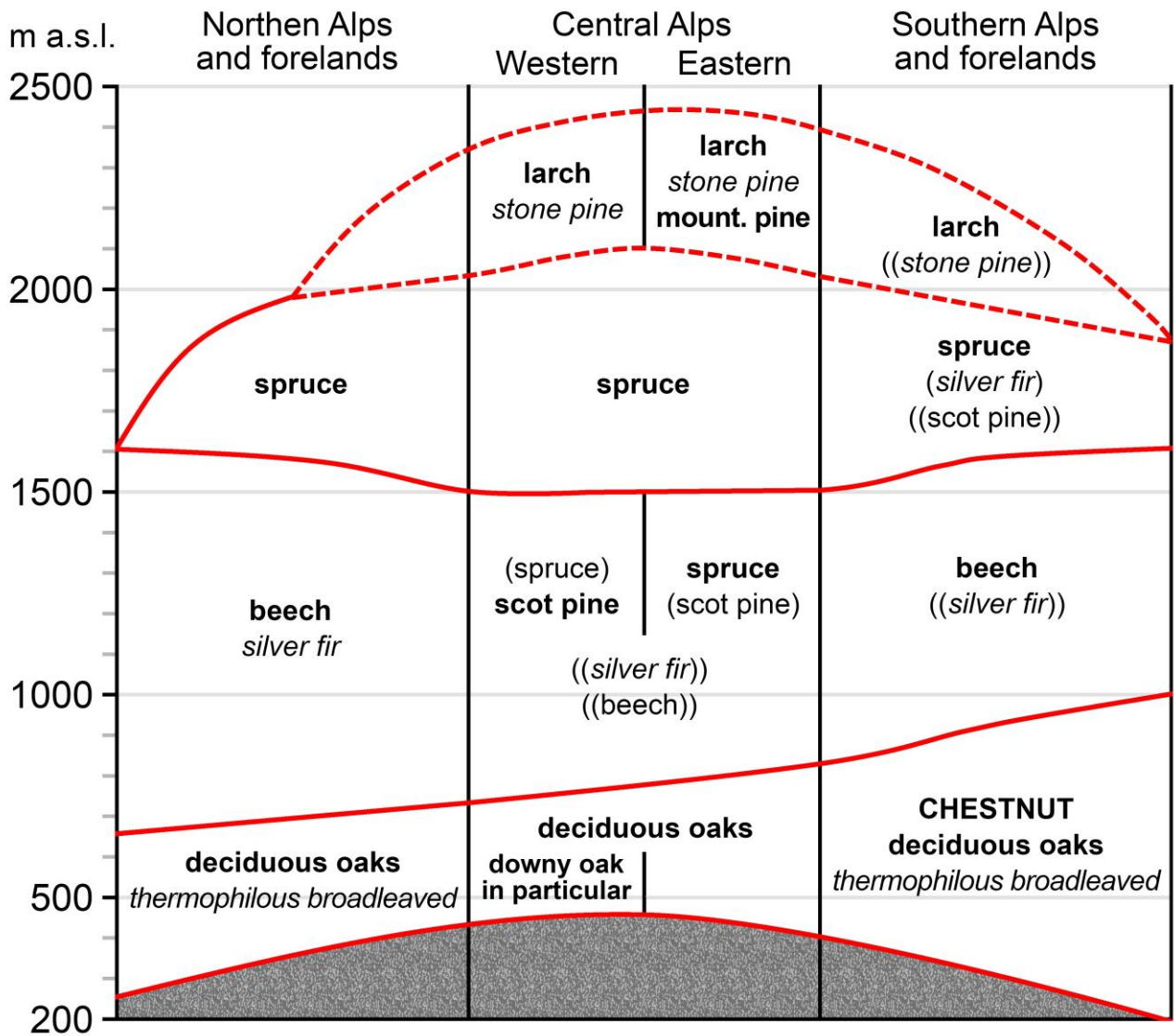


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886 Fig. 1. Study area with detailed location of subregions and study sites

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

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894

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

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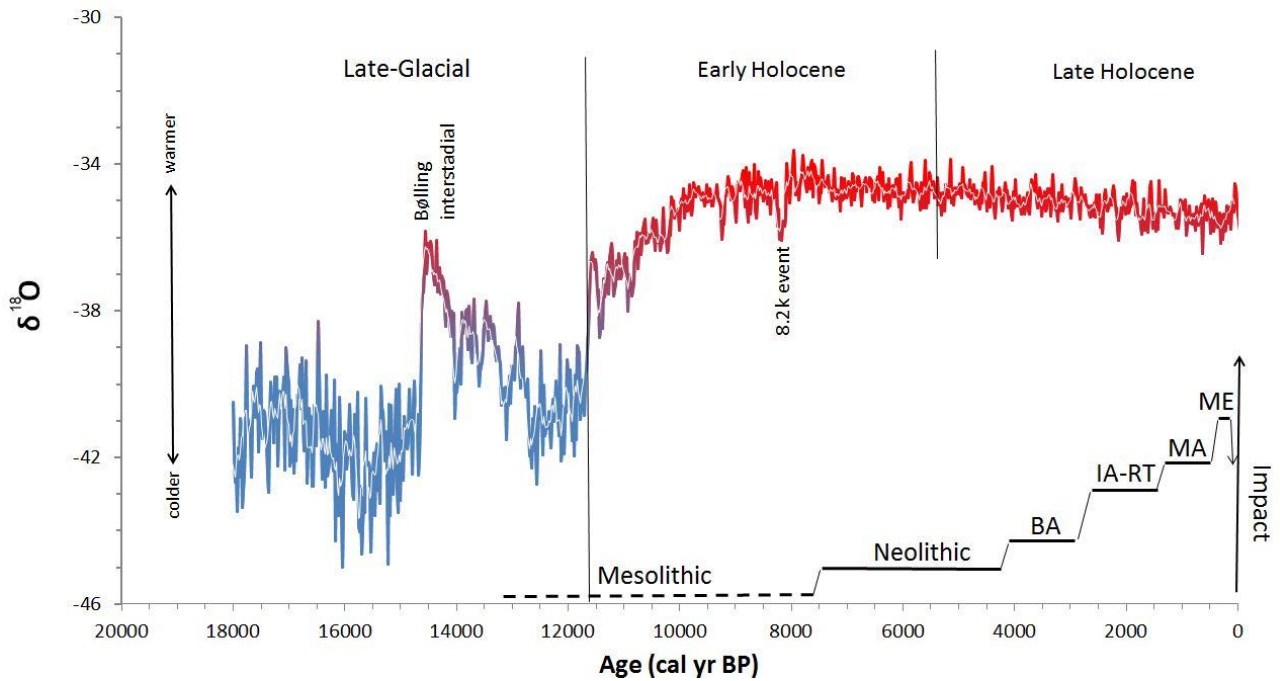


Fig. 3. Evolution of the temperature during the last 20,000 cal years in Greenland as reconstructed from NGRIP $\delta^{18}\text{O}$ values on GICC05 time scale (modified from Ramussen et al. 2006). Age scale has been changed to show cal BP 1950 (original is BP 2000).

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).

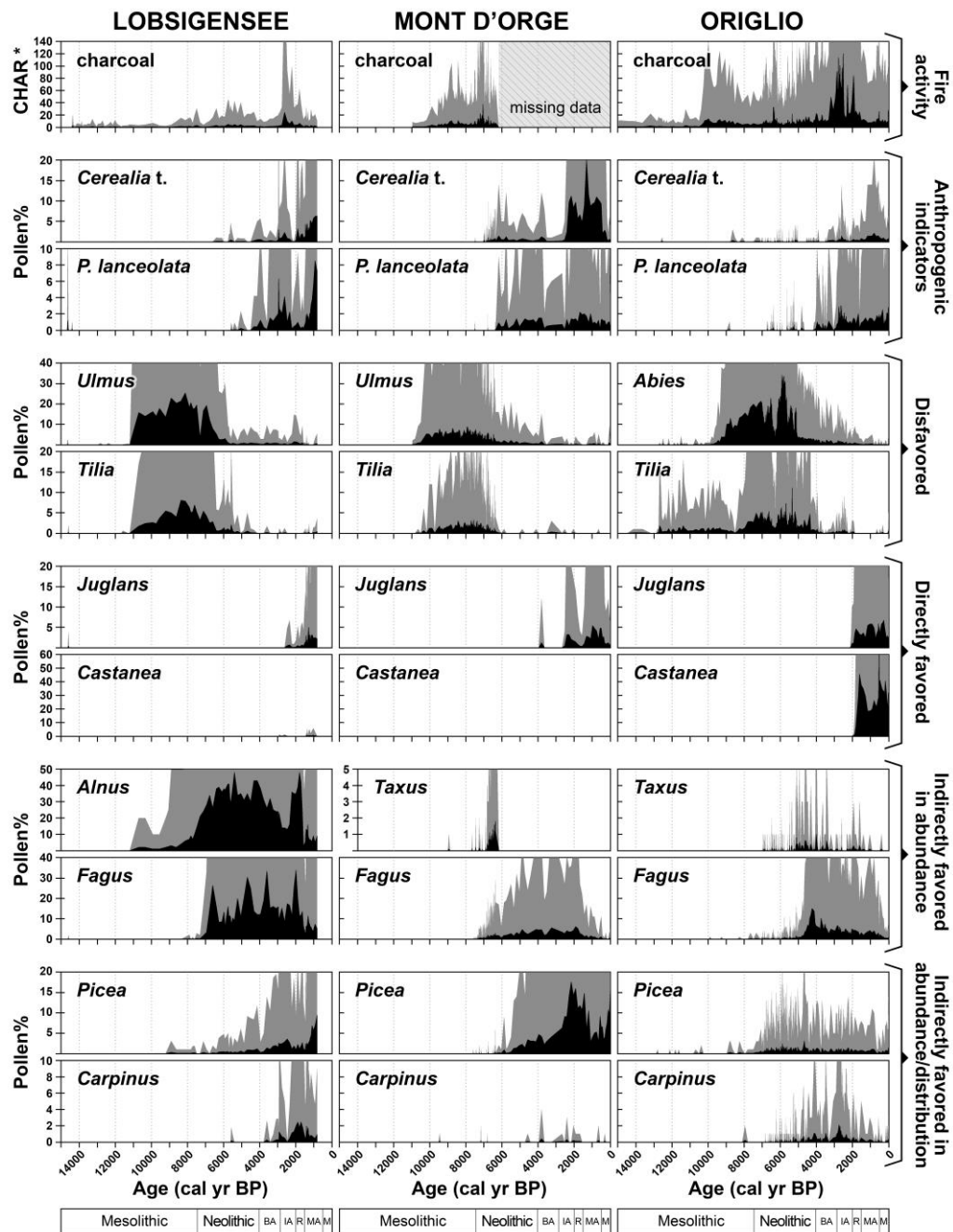


Fig. 4. Charcoal influx (CHAR) and pollen percentage diagrams (Pollen %) of selected taxa over last 15,000 years at representative low elevation sites in the northern (Lobsigensee), central (Mont d'Orge) and southern (Lago di Origlio) subregions.

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

* CHAR units are expressed in $\text{mm}^2 \cdot \text{cm}^{-2} \cdot \text{yr}^{-1}$ for Lobsigensee and Lago di Origlio and in $\text{particles} \cdot \text{cm}^{-2} \cdot \text{yr}^{-1}$ 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).

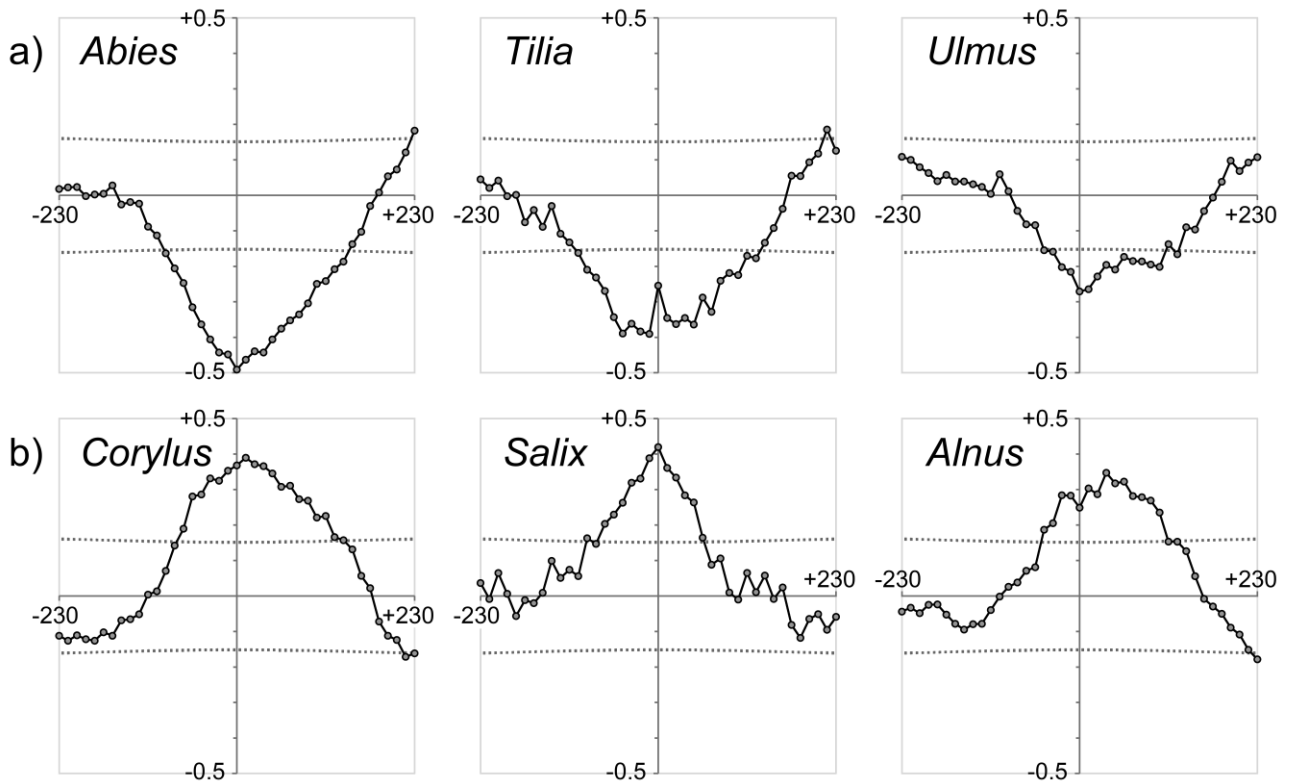


Fig. 5 Cross correlations of charcoal accumulation rates (CHAR) vs pollen percentages of selected taxa at Lago di Origlio (southern subregion) for the period 5100-3100 BC. a) fire-sensitive (or fire-disfavored) taxa: *Abies* (extremely sensitive according to Table 2), *Tilia* (highly sensitive) and *Ulmus* (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).

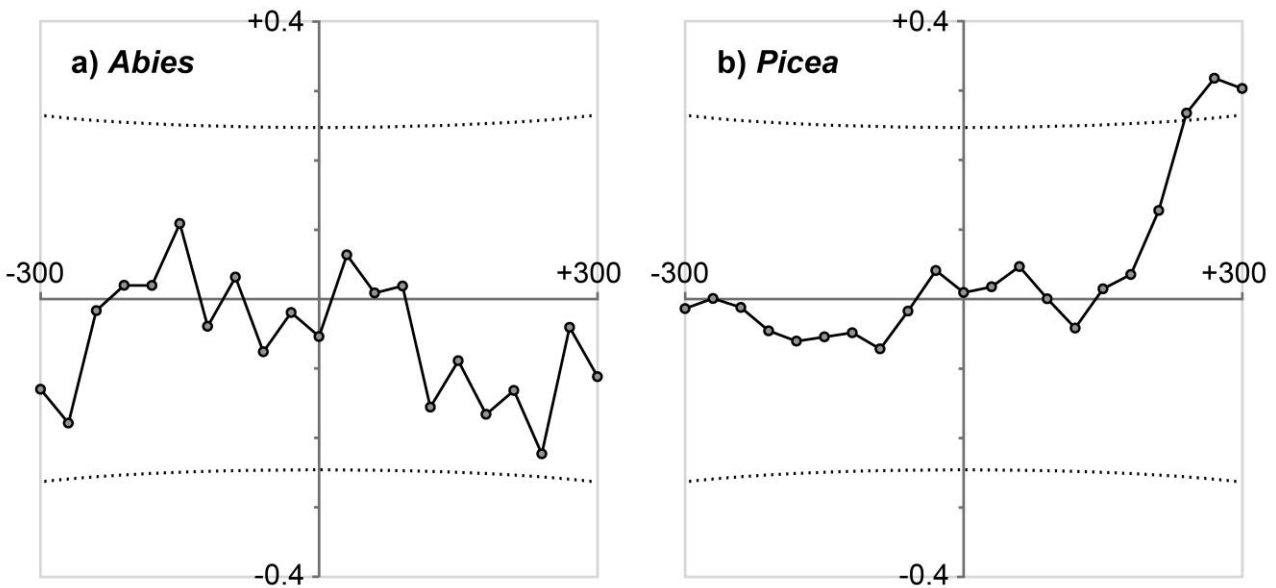


Fig. 6 Cross correlations of dung spores (*Sporormiella* spp.) influx vs pollen percentages of selected taxa at Iffigsee for the period 4960-3160 BC.
 a) browsing-sensitive (or browsing-disfavored) silver fir; b) browsing-resistant (or browsing-favored) spruce.
 Steps on the horizontal axis represent 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).

953 **Tables**

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

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

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

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

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

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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).

970 Table 3. Species response to human-induced disturbance and land use change in the Alps and their
 971 forelands
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Response	Drivers	Species	Remarks
Disfavored	Reduced by human-induced disturbance (e.g. fire, browsing), little economic value	<i>Abies alba</i>	see also figures 2, 4, 5, and 6
		<i>Acer</i> spp.	see also figure 2
		<i>Fraxinus excelsior</i>	see also figure 2 and 4
		<i>Hedera helix</i>	
		<i>Ilex aquifolium</i>	
		<i>Pinus cembra</i>	
		<i>Tilia</i> spp.	see also figures 2, 4 and 5
		<i>Ulmus</i> spp.	see also figures 2, 4 and 5
Directly favored	Benefited from deliberate introduction, maintained through plantation and cultivation; high economic value	<i>Castanea sativa</i>	not on limestone, see also figure 2 and 4
		<i>Juglans regia</i>	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	<i>Alnus</i> spp.	<i>A. glutinosa</i> , <i>A. incana</i> , see also figure 5
		<i>Corylus avellana</i>	see also figure 5
		<i>Fraxinus ornus</i>	on lime-stone
		<i>Fagus sylvatica</i>	see also figure 2 and 4
		<i>Larix decidua</i>	see also figure 2
		<i>Picea abies</i>	at mid to high-elevation since Neolithic, see also figures 2, 4, and 6
		<i>Quercus</i> (deciduous)	<i>Q. robur</i> , <i>Q. petraea</i> , <i>Q. pubescens</i> , and <i>Q. cerris</i> in the southern forelands, see also figure 2
		<i>Salix</i> spp.	see also figure 5
		<i>Taxus baccata</i>	especially in the early Neolithic, see also figure 4
		<i>Alnus viridis</i>	
Indirectly favored in distribution and abundance	Benefited from disturbance-induced suitable ecological conditions and by reduction of competitors	<i>Betula pendula</i>	
		<i>Carpinus betulus</i>	see also figure 4
		<i>Juniperus</i> spp.	<i>J. nana</i> and <i>J. communis</i>
		<i>Ostrya carpinifolia</i>	on limestone
		<i>Picea abies</i>	at low elevations especially since modern times
		<i>Pinus mugo</i>	eastern central Alps, on limestone and dolomite, see figure 2

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