1 **Insights about past forest dynamics as a tool for present and future forest management in** 2 **Switzerland**

4 **1. Introduction**

5 Present-day Alpine forest ecosystems and their dynamics are fundamentally different from
6 those of the past. In particular, a long human history has had irreversible consequences on Alpine
7 forest ecosystems (e.g. Tinner et al. 2005; Carcaillet et al. 2009; Blarquez et al. 2010; Valsecchi et
8 al. 2010), decoupling natural vegetation-climate relationships in many regions and maintaining
9 plant communities in a non-equilibrium state with climate and disturbance regimes (Svenning et al.
10 2015). In recent decades, reduced management and abandonment of remote mountain areas have
11 led to expansion of forest cover and loss of high-diversity meadows (Gehrig-Fasel et al. 2007;
12 Loran et al. 2016). The transitional and highly dynamic state of Alpine forests challenges forest
13 managers tasked with assessing the local consequences of climate change on forests and developing
14 adaptive and restorative silvicultural plans to ensure near-to-nature conditions and continued
15 delivery of ecosystem services in the future (Lindner 2000; Schmid et al. 2015). However, the
16 strong human signature on present-day forest composition, structure and dynamics in many regions
17 raises concerns about the use of short-term ecological observations and standard modeling
18 approaches (Iverson and McKenzie, 2013) to predict forest responses to future climate change
19 (Ibanez et al. 2006; Williams and Jackson 2007; Dawson et al. 2011; Tinner et al. 2013). To
20 understand present-day relationships between climate, humans, vegetation and disturbance requires
21 information on the causes and consequences of ecosystem change in the past. This information is
22 especially critical for forests in the Alpine region of Switzerland, where present-day ecosystem
23 dynamics are conditioned by historical legacies and altered disturbance regimes, and the abundance
24 and distribution of current forest types and taxa are a product of both anthropogenic manipulation
25 and climate change, which are difficult to disentangle.

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

28 woody species. Representative sites with good chronological control (i.e. multiple radiocarbon
29 dates) and taxonomical resolution are selected along a strong north-to-south environmental gradient
30 in the Alps to compare forest history in different settings. The time span of interest is the last
31 ~20,000 years, which covers the period from the end of the last glaciation to the present day.
32 Special focus is on the last 7500 years starting with the onset of the Neolithic period and the
33 progressive human alteration of land cover and forest composition. The specific aim of the paper is
34 to show how knowledge of Alpine forest history can inform management efforts that seek to (1)
35 assess forest sensitivity to future climate change; (2) choose between different management options
36 (e.g. preserving close-to-nature conditions, maintaining cultural landscapes, protecting species of
37 special concern, maximizing biodiversity); and (3) maintain forest capacity to provide important
38 ecosystem goods and services.

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

43

44 **2. Material and methods**

45 *2.1 Study area*

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

54 Meteorological Station Locarno-Monti) and annual precipitation ranges from 1300 mm in the west
55 (e.g. meteorological station Acquarossa) to 1900 mm in the east (Locarno-Monti). In winter, the
56 climate is dry and mild and summers are humid (June-September 800 to 1200 mm of precipitation),
57 with thunderstorm events alternating with periods of drought. Present-day forests are organized by
58 elevational belts (Fig. 2). *Castanea sativa* (sweet chestnut) dominates low-elevation forests (up to
59 900-1000 m asl). These closed forests, which occur in other regions of southern Europe (e.g.
60 Apennines, Pyrenees, the Balkans), occasionally support other thermophilous broadleaved species,
61 such as *Tilia cordata* (small-leaved linden), *Quercus petraea* (sessile oak), *Q. robur* (common oak),
62 and (*Q. pubescens* (downy oak), *Alnus glutinosa* (common alder), *Prunus avium* (sweet cherry),
63 *Acer* spp. (maple), and *Fraxinus* spp. (ash). At middle elevations (900-1400 m asl), forests consist
64 of mostly pure stands of *Fagus sylvatica* (European beech), and at higher elevations, forests are
65 dominated by *Picea abies* (Norway spruce) and at upper treeline by *Larix decidua* (European larch).
66 On south-facing slopes, beech forest is sometimes absent, and *Abies alba* (silver fir) is present in
67 small patches on north-facing slopes in the central part of the subregion. *Pinus sylvestris* (Scots
68 pine) grows on dry south-facing slopes, and *P. cembra* (stone pine) occurs in the most continental
69 settings at high elevations (Ceschi 2014).

70 The central Alps subregion, including the Valais and Engadine, displays a markedly
71 continental climate characterized by low annual precipitation (e.g. 603 mm in Sion at 482 m asl,
72 639 mm in Zermatt at 1638 m asl, 713 mm in Samedan at 1703 m asl), cold winters, high insolation
73 and extreme annual and daily temperature excursions. The temperature range is correspondingly
74 large with mean annual temperatures of ~10°C on valley bottoms (e.g. 10.1°C in Sion at 482 m asl),
75 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-
76 Bernard at 2472 m asl). The present distribution of forest types in the central Alps reflects this
77 topographic and climatic gradient (Fig. 2). Thermophilous deciduous broadleaves forests support by
78 downy oak in continental sub-mediterranean settings, and sessile oak and common oak in the sub-
79 oceanic lowlands (~400-800 m asl). At medium elevations (~800-1400 m asl), stands of Scots pine

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

84 The northern Alps subregion, which includes the northern Alps and their forelands, displays a
85 cool temperate central European climate, with mild summers (18°C July average), cool winters
86 (−1°C January mean) and annual precipitation ranging from ~1000 mm at low elevations (1196 mm
87 in Interlaken at 577 m asl) to ~1500 mm at higher elevations (1338 mm in Adelboden at 1327 asl).
88 Today's vegetation consists of highly fragmented relict forest patches. As in the southern region,
89 vegetation is organized in belts (Fig. 2), from mixed oak-beech forests (including other deciduous
90 trees such as linden, elm, maple, and ash) at the lowest elevations (<600 m asl), mixed beech-fir
91 forests in the mountain belt (600-1500 m) to spruce forest in the subalpine belt (1500-2000 m;
92 Ellenberg 2009). Stands of larch and/or stone pine are present in the northern Alps above the spruce
93 belt in proximity to the continental central Alps.

94

95 2.2 Information from paleorecords

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

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

112 Human activity is identified in pollen or plant macrofossil records by the presence of remains
113 of crops, fruit tree cultivars, non-native species, and past shifts in vegetation composition associated
114 with particular land use (e.g. Rey et al. 2013). Direct proxies of human activities include cultivated
115 taxa introduced to the area for agricultural purposes (adventive agriophytes), such as cereals (*Avena*
116 *t*, (*t*=type), *Triticum t*. and *Hordeum t*, usually grouped as *Cerealia t* or *Secale cerealia*), and other
117 crop species, such as *Fagopyrum tataricum*, *Cannabis sativa t* or *Linum usitatissimum*. Accidentally
118 introduced species, such as *Plantago lanceolata t* which first appeared in Switzerland in the Late
119 Mesolithic (Behre, 1981, 1988; Tinner et al. 2007) and *Ambrosia* and other pollen types that
120 appeared in modern times, are also unequivocal evidence of land use and anthropogenic
121 disturbance. Past pastoral activity and herbivore density are inferred from pollen (e.g.
122 Cichorioideae, Asteroideae), spores of dung-specialized (coprophilous) fungi, including
123 *Sporormiella* spp., *Podospora* spp., *Ustilina deusta* (van Geel et al. 2003; Graf and Chmura 2006),
124 and particular ferns (e.g. *Botrychium lunaria*). Plants that are altered indirectly by human impact are
125 called apophytes (present in the native flora but favored by land use) and include *Urtica*, *Artemisia*,
126 *Rumex acetosella t*, *Succisa*, *Campanula*, *Fallopia*, and Brassicaceae (Behre 1981; Lang 1994).
127 Charcoal particles in sediment cores provide direct evidence of past fires, with high charcoal
128 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

155 sometimes referred to as the Neoglaciation, because it experienced century-long periods of colder
156 climate and a renewed glaciation (Holzhauser et al. 2005). However, century-long temperature
157 oscillations also occurred during the early and mid Holocene (Heiri et al. 2004), causing upslope
158 and downslope movements of forests (Wick and Tinner 1997; Haas et al. 1998, Tinner and
159 Theurillat 2003). Recent climatic oscillations included the Roman Warm period (-2250-1600 cal yr
160 BP, corresponding to ~250 BC-400 AD), the Medieval Climate Anomaly (~1200-800 cal yr BP,
161 corresponding to ~800-1200 AD), and the Little Ice Age (550-100 cal yr BP, corresponding to
162 ~1400-1850 AD) (Fig. 3) (Wanner et al. 2008).

163

164 *3.2 Response of tree species to past climate variations*

165 To understand how Alpine forests developed in response to past climate change, we target three
166 climate periods that occurred before significant human presence (Heiri et al. 2014): the abrupt
167 warming period of Bølling Interstadial (~14,600 cal yr BP), the early-Holocene warming period
168 (11,700-5000 cal yr BP), and the cold reversal at 8200 cal yr BP. In the lowland and mountain areas
169 of the northern subregion (400-1600 m asl) and in the mountain areas of the southern subregion
170 (900-1600 m asl), pollen, macrofossil and stomata records show that the Bølling Interstadial
171 Warming led to a replacement of tundra vegetation by shrubs and light-demanding trees, such as
172 larch, birch, Scots pine and stone pine (Vescovi et al. 2007; Ammann et al. 2013).

173 Differences in the ecological characteristics of the tree species also accounted for variations
174 in the pattern of treeline development in the early Holocene in the Alps. Larch, Scot pine, and birch
175 were particularly advantaged by high insolation and continentality, low moisture availability and
176 shallow soils, whereas Stone pine expanded later (~10,500-8000 cal BP) when summer-drought
177 stress was reduced, temperatures were higher than before and soils were better developed (Tinner
178 and Kaltenrieder 2005; Gobet et al. 2005; Schwörer et al. 2014b; 2015; Table 1). Subsequently
179 (~9000 cal BP), silver fir expanded into stone pine forests, forming timberline communities that are
180 now nearly extinct in the Alps (Wick et al. 2003, Gobet et al. 2010).

181 During the early Holocene, thermophilous broadleaved deciduous (e.g. deciduous *Quercus*,
182 *Acer*, *Ulmus*, *Tilia*, *Fraxinus*, *Alnus*) and shrubs (e.g. *Corylus avellana*, hazel) became increasingly
183 important at low elevations in all subregions (e.g. Lotter et al. 1992) and expanded their ranges to
184 higher elevations (e.g. Zoller 1960; Zoller and Kleiber 1971; Welten 1982; Vescovi et al. 2006; Rey
185 et al. 2013; Schwörer et al. 2014a; Thöle et al 2016). The progressive build-up of flammable fuel
186 (e.g. pines) and summer warmer-than-present conditions were associated with more fires at high
187 elevations and in the dry central subregion (Wick and Tinner 1997; Gobet et al. 2003; Tinner and
188 Kaltenrieder 2005; Valsecchi and Tinner 2010; Blarquez and Carcaillet 2010; Stähli et al. 2006;
189 Schwörer et al. 2014a; Colombaroli et al. 2010). Increased fire activity probably allowed early-
190 successional mountain pine (*Pinus mugo* spp. *uncinata*) to expand in the driest (eastern) part of the
191 central Alps where infertile dolomite soils are present (Stähli et al. 2006). In the Alpine forelands,
192 early-Holocene fire activity also gradually increased and was associated with an expansion of fire-
193 adapted *Pteridium aquilinum* in the southern subregion at ~10,500 cal BP (Tinner et al. 1999;
194 2005).

195 Forest composition experienced a dramatic change as a consequence of the cooling event at
196 8200 cal yr BP when warm dry summers were abruptly replaced by cool moist conditions
197 (Dansgaard et al. 1993; Heiri et al. 2014). This event was a tipping point for the vegetation and
198 enabled the expansion of moist-tolerant beech and silver fir in the northern subregion at the expense
199 of less mesophilous forest species. Interestingly, the subsequent return to warm conditions at 8000
200 cal yr BP did not allow more drought-adapted taxa to regain their previous abundance, and moist
201 conditions maintained silver fir-beech forests (Tinner and Lotter 2001; 2006). Unlike in the
202 northern subregion and in contrast to silver fir, beech did not become abundant in the dry
203 continental settings of the central Alps and in the warm-temperate setting of the southern subregion
204 following the 8200 cal yr BP event (Welten 1982, Tinner et al. 1999). Probably the species was
205 limited by its low tolerance to drought and/or competition with previously established silver fir
206 (Tinner et al. 2013). Scots pine and mountain pine in the central Alps and spruce in Engadine grew

207 at high elevations, while mixed oak forests with abundant Scots pine were present at low elevations.
208 In the central Alps, silver fir was important (15-50% of pollen) across all vegetation belts (Welten
209 1982; Tinner et al. 1996; van der Knaap et al. 2005; Gobet et al. 2003; Colombaroli et al. 2013).
210 The relative sensitivity of different tree taxa to environmental factors (drought, solar radiation,
211 climatic continentality and seasonality, soil development) are summarized in Table 1 based on our
212 understanding and interpretation of their response to past climate changes.

213

214

215 3.3 Human presence and impact in the Alpine region

216 Hunting and gathering activities in the Alpine lowlands are evidenced during the Late
217 Mesolithic period (~6700-5500 BC, Tinner et al. 2007). With the onset of the Neolithic period
218 (~5500 BC), pastoral (mainly imported goats and sheep) and arable farming is evidenced by the
219 increase of coprophilous fungi and pasture indicators (e.g. Asteroideae, Cichorioideae, *Urtica*,
220 *Plantago lanceolata*, *Rumex* t) in pollen and plant macrofossil records from the reference sites
221 (Wick and Tinner 1997; Colombaroli et al. 2010; Rey et al. 2013; Schwörer et al. 2014a, 2014b,
222 2015). Fire activity also increased, and although generally attributed to anthropogenic burning, fire
223 occurrence was likely facilitated by warm-dry conditions at this time (Tinner et al. 1999). Fire
224 frequency was locally variable, but charcoal records show clear subregional differences with high
225 fire activity in the south and less fires in the north (Fig. 4). These differences likely reflect the
226 temperature and dry-season gradient that exists across the Alps (Tinner et al. 2005). Increased
227 charcoal abundance and presence of pollen types indicative of open environments, pastures and
228 disturbance (e.g. *Plantago* spp., *Rumex acetosella*, Cichorioideae, Chenopodiaceae, *Apium* spp.,
229 *Pteridium aquilinum*) attest to high levels of land use and burning in Neolithic time (Tinner et al.
230 1999; Rey et al. 2013; Colombaroli et al. 2013), leading to a general habitat diversification with the
231 development of highly diverse grasslands at the expense of forest (Colombaroli et al., 2013,

232 Colombaroli and Tinner 2013). For example, synchronous increases in anthropogenic pollen
233 indicators and charcoal levels occurred with the beginning of the Neolithic period (7500 cal yr BP =
234 5500 BC) at our three sites, and pollen abundance of disfavored woody taxa dropped significantly
235 (Fig. 4).

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

244 Human-set fires, deforestation and agriculture increased significantly during the Bronze
245 Age across the Alps, and summer farming lowered the upper forest position by ca. 200-400 m
246 elevation (e.g. Welten 1982; Tinner et al. 1996; 1999, 2003; Tinner and Theurillat 2003; Lotter et
247 al. 2006; Hofstetter et al. 2006; Rey et al. 2013; Schwörer et al. 2014a). During the Iron Age (~850
248 BC – 15 BC), anthropogenic burning reached a maximum (Tinner et al. 2005) and direct
249 anthropogenic proxies of arable agriculture, such as *Cerealia* t., further increased (e.g. Tinner et al.
250 1999; Colombaroli et al. 2013; Rey et al. 2013; Fig. 4). During the Roman period (15 BC – 476
251 AD), systematic cultivation of tree species, such as walnut (*Juglans regia*) and sweet chestnut, was
252 undertaken to provide wood and non-fiber products (Conedera et al. 2004). This fundamental
253 change towards commodity-based forest management ended the use of fire as main tool for forest
254 clearance and field maintenance. The Roman period marks the start of forest resource management
255 in the Alpine region, and anthropogenic activity was no longer closely coupled to fire (Conedera
256 and Tinner 2000; Tinner et al. 2005; Morales-Molino et al. 2015).

257 Historical records, traditional knowledge and written documents, such as the local Medieval
258 bylaws (Stuber and Bürgi 2001, 2002; Bürgi and Stuber 2003, 2013; Bertogliati 2014; Krebs et al.
259 2015), describe extensive land use, forest management and population increases from the Middle
260 Ages to the end of the 1800s. Forests were managed for non-timber purposes including for
261 infrastructure and settlement protection (*Bannwald*), forage and cattle fodder (wood hay, branches
262 of pollarded broadleaved), cattle and human bedding (collected litter), fuel (collected cones and
263 bark), as well as for very specialized uses (bark collection for leather tanning, resin collection for
264 fumigations, herb collection for medicine). During this time, fires were regulated and mainly used
265 for pasture clearance and maintenance (Conedera et al. 2007).

266 With industrialization in the 19th century, demand increased for wood for charcoal
267 production and later for timber in the Alps (e.g. Krebs and Bertogliati 2015). The intensity of land
268 use in Alpine forests was unprecedented in the 1800s. In addition to the expansion of meadows and
269 grasslands, this period is also characterized by the extinction in Switzerland of large carnivores,
270 such as the brown bear (*Ursus arctos*), wolf (*Canis lupus*), and Eurasian lynx (*Lynx lynx*), all of
271 which were considered a threat to livestock and game hunting (Breitenmoser 1998). In the late 19th
272 century, depleted and overexploited forests reduced slope stability and hydrological regulation,
273 which in turn increased flood frequency. Forest protection legislation was adopted in most Alpine
274 countries and forest management shifted towards reforestation (Bertogliati 2015; Loran et al. 2016;
275 Bebi et al., this issue). Forest expansion greatly accelerated after the second World War with the
276 abandonment of marginal agricultural and pasture lands (Gehrig-Fasel et al. 2007; Gellrich et al.
277 2007; Loran et al. 2016).

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279

280 3.4 Response of tree species to past human impact

281 Present landscapes in the Alpine region have been significantly shaped by four key cultural
282 periods: (1) the beginning of the Neolithic period (~5500-5000 BC) with onset of agriculture in the

283 lowlands, (2) the Bronze and Iron Ages (~2200-15 BC) that led to a systematic development of
284 alpine pastures, transhumance, and numerous human-set fires; (3) the Roman period until the
285 middle of the 1800s with further intensification of the land use, forest management and population
286 growth (Fig. 4); and (4) the 19th-20th century phase of forest re-establishment. During these periods,
287 tree species responded to anthropogenic land use in different ways as function of their sensitivity to
288 disturbance (e.g. fire, browsing, Table 2) and their economic value.

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

307 Species favored by humans increased in abundance and distribution. As revealed by pollen
308 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).

332

4. Discussion

4.1 Species sensitivity to past climate impact

335 Changes in vegetation composition and dynamics before significant human activity were
336 clearly driven by climate. For example, the three subregions responded similarly to rapid high-
337 amplitude warming trends in the late-glacial period (e.g. the Bølling Interstadial) and at the
338 beginning of the Holocene. Ecosystem reorganization entailed changes from cold-adapted open
339 tundra to shrubland, then subalpine conifer forest and finally to forests dominated by thermophilous
340 and mesophilous species. In many cases, our understanding of the present ecological behavior of
341 Alpine tree species is consistent with their response to past environmental change, providing
342 evidence that the environmental niches of these species are well understood. For example, the
343 pioneering characteristics of juniper, birch, and to some extent also larch, including their ability to
344 colonize poorly developed soils is evidenced after present-day glacial retreat and avalanche activity
345 in the Alps (Ellenberg 2009; Garbarino et al., 2010). Similarly, they were able to colonize
346 deglaciaded landscapes soon after ice retreat during the late-glacial period. Differences in present-
347 day moisture requirements between larch, stone pine, beech, and pedunculate oak (*Quercus robur*)
348 are also well reflected in their Holocene history (Tinner and Lotter, 2001; Tinner and Kaltenrieder
349 2003; Ellenberg 2009). In agreement with the ecology of silver fir, paleoecological records show
350 that silver fir was generally less demanding of moisture conditions than either spruce or beech in the
351 past (Henne et al. 2011).

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

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

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365 4.2 *Species sensitivity to human impact*

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

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

387 as drivers in ecosystem modeling (Birks and Tinner 2016). Models should incorporate long-term
388 information in developing relationships between species distribution and abundance and their
389 environment, by including (1) species distributions under a range of climate conditions and
390 disturbance levels in the past; (2) past ecological consequences of adding or removing species or
391 changing species abundance; and (3) the effects of altered natural disturbance regimes in the past
392 (see discussion in e.g. Henne et al. 2011; Tinner et al. 2013). In reality, however, most species
393 distribution models (SDM), often also called bioclimatic or niche models, are based on present-day
394 distributions in relation to a suite of modern climate variables. Because present distributions are not
395 in equilibrium with climate, models results often under- or overestimate present and potential future
396 ranges for many critical species (Elkin et al. 2013; García-Valdéz et al. 2013; Schwörer et al.
397 2014b; Ruosch et al. 2016). Estimates in the Alpine region would be improved if SDMs considered
398 early to mid-Holocene vegetation-climate relationships prior to the time when the species ranges
399 and abundance were highly modified by humans (i.e. before the middle to end Neolithic period).
400 Well-resolved paleoclimatic data, specifically in regard to precipitation, sensitivity studies or
401 climatic scenarios can thus be used to assess such issues (Heiri et al. 2006). Dynamic and
402 ecophysiology-based vegetation models, such as LANDCLIM are less affected by this problem,
403 because they consider species-specific traits and the fundamental niche of species (Bugmann 2001;
404 Bugmann and Solomon 2000; Ruosch et al. 2016). Moreover, landscape, disturbance and
405 biochemical feedbacks are also integrated to better assess the interactions of species with their
406 biotic and non-biotic environment. Recent dynamic vegetation models that incorporate the influence
407 of past land use on species distributions also hold considerable promise for recognizing the
408 anthropogenic signal (Kaplan et al. 2010; Schwörer et al. 2014b).

409

410 4.3 *Using the past to inform future silvicultural approaches*

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

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

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

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

439 Present changes in land use and climate have also created new types of disturbances that may
440 affect the future resilience of the concerned forest ecosystems. Wild ungulate populations are
441 growing in the absence of former pastoral activities, large predators and effective hunting
442 regulations. These native herbivores interfere with the ability of some tree species to regenerate
443 (e.g. silver fir) and represent a new type of disturbance for forests (Heuze et al. 2005; Didion et al.
444 2011; Häsler and Senn 2012; Kupferschmid et al. 2014). Cessation of systematic litter collection,
445 and forest closure and encroachment have caused an accumulation of dead biomass, which has
446 altered fuel loads and over time may create inhibitory and toxic effects of extracellular self-DNA in
447 the soil (Mazzoleni et al. 2015).

448 Projected climate trends pose direct threats, as evidenced by drought-induced leaf whitening,
449 which caused significant chestnut mortality during the hot and dry summer 2003 in the southern
450 subregion (Conedera et al. 2010). Similarly, recent dieback of Scots pine in dry areas of the Rhone
451 valley of the western central Alps is also related to extreme summer drought and will likely
452 continue in the future (Bigler et al. 2006; Rebetez and Dobbertin 2006; Rigling et al. 2013;
453 Vacchiano et al. 2013). Warming and related increases in drought frequency and severity (Rebetez
454 1999) and associated fire risk (Reinhard et al. 2005; Wastl et al. 2013; Valese et al. 2014) will alter
455 interactions among woody species (Moser et al. 2010; Maringer et al. 2016) and with pests and
456 diseases (Battisti 2008; Netherer et al. 2010; Marini et al. 2012). In addition, newly introduced
457 exotic species (e.g. *Robinia pseudooacacia*, *Ailanthus altissima*, *Pawlonia* spp.) have become
458 invasive and highly competitive in low- to mid-elevation forest ecosystems and strongly interfere
459 with fire regimes, silvicultural management practices (Grund et al. 2005; Maringer et al. 2012;
460 Radtke et al. 2014; Knüsel et al. 2015), pests (Wermelinger 2014; Roques et al. 2016) and disease
461 (Kowaski and Holdenrieder 2009; Pautasso et al. 2013; Sieber 2014) as well as their possible
462 interactions (e.g. Meyer et al. 2016). Thus, information on species and forest community responses
463 to novel climates and disturbance regimes in the past can help guide management strategies in the
464 future (Williams and Jackson, 2007).

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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

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

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840

841 **Figure legends**

842

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

850

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

857

858 Fig. 3. Evolution of the temperature during the last 20,000 cal years in Greenland as reconstructed
859 from NGRIP $\delta^{18}\text{O}$ values on GICC05 time scale (modified from Ramussen et al. 2006).
860 Age scale has been changed to show cal BP 1950 (original is BP 2000).
861
862 Human impact periods: Mesolithic (13,000-7500 cal yr BP); Neolithic (7500-4200 cal yr
863 BP); BA - Bronze Age (4200-2850 cal yr BP); IA - Iron Age (2850 cal yr BP-15 BC); RT -
864 Roman Times (15 BC-476 AD); MA - Middle Ages (476-1492 AD); ME - Modern Epoch
865 (1492 AD to present).

866

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

870 grey curves represent the 10x exaggeration of the Y-axis.

871 * CHAR units are expressed in $\text{mm}^2 \cdot \text{cm}^{-2} \cdot \text{yr}^{-1}$ for Lobsigensee and Lago di Origlio and
872 in $\text{particles} \cdot \text{cm}^{-2} \cdot \text{yr}^{-1}$ for Mont d’Orge.

873 Human impact periods: Mesolithic (13,000-7500 cal yr BP); Neolithic (7500-4200 cal
874 yr BP); BA - Bronze Age (4200-2850 cal yr BP); IA - Iron Age (2850 cal yr
875 BP-15 BC); R - Roman Times (15 BC-476 AD); MA - Middle Ages (476-
876 1492 AD); M - Modern Epoch (1492 AD to present).

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

879

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

890

891 Fig. 6 Cross correlations of dung spores (*Sporormiella* spp.) influx vs pollen percentages of
892 selected taxa at Iffigsee for the period 4960-3160 BC.
893 a) browsing-sensitive (or browsing-disfavored) silver fir; b) browsing-resistant (or
894 browsing-favored) spruce.
895 Steps on the horizontal axis represent a time lag of ~30 years with respect to the browsing
896 peak. Vertical axis represent the correlation coefficients. Dots outside the significance
897 interval (dashed lines) are significantly positively or negatively correlated at $p < 0.05$.
898 First signs of negative effects of browsing occur at lag +4 that is 120 years after the
899 browsing peak, which probably corresponds to the surviving span of mature silver fir
900 before the lack of regeneration (as registered in pollen). Similarly, but in the opposite
901 sense, spruce significantly increases to become dominant after more than 240 year (8 lags)
902 under intense browsing activity.
903 Source: modified from Schwörer et al. (2014b).

LOBSIGENSEE

MONT D'ORGE

ORIGLIO

1 Table 1: Response of selected woody species to environmental conditions in the Alps according to pollen,
2 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

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

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

2

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

3

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

6

7 Source: Ammann (1989), Wick and Tinner (1997); Tinner et al. (1999); Gobet et al. (2000); Wick et al. (2003); Gobet
8 et al. (2003); Tinner et al. (2005); Tinner and Kaltenrieder (2005); Tinner and Lotter (2006); Hofstetter et al. (2006);
9 Lotter et al. (2006); Stähli et al. (2006); Wehrli et al. 2007; Colombaroli et al. (2010); Valsecchi et al. (2010); Rey et al.
10 (2013); Berthel et al. (2013); Colombaroli et al. (2013); Schwörer et al. (2014a); Schwörer et al. (2015); Morales-
11 Molino et al. (2015); Thöle et al. (2016).

1 Table 3. Species response to human-induced disturbance and land use change in the Alps and their
2 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
Indirectly favored in distribution and abundance	Benefited from disturbance-induced suitable ecological conditions and by reduction of competitors	<i>Alnus viridis</i>	
		<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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5 Source: Ammann (1989), Wick and Tinner (1997); Tinner et al. (1999); Gobet et al. (2000); Wick et al. (2003); Gobet
6 et al. (2003); Tinner et al. (2005); Tinner and Kaltenrieder (2005); Tinner and Lotter (2006); Hofstetter et al. (2006);
7 Lotter et al. (2006); Stähli et al. (2006); Wehrli et al. 2007; Colombaroli et al. (2010); Valsecchi et al. (2010); Rey et al.
8 (2013); Berthel et al. (2013); Colombaroli et al. (2013); Schwörer et al. (2014a); Schwörer et al. (2015); Morales-
9 Molino et al. (2015); Thöle et al. (2016).