

## Effects of the lack of forest management on spatio-temporal dynamics of a subalpine *Pinus cembra* forest

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Keywords:	Forest dynamics, Spatial patterns, Dendroecology, Growth dominance

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3 1 **Effects of the lack of forest management on spatio-temporal dynamics of a subalpine *Pinus cembra* forest**

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26 12 Keywords: Forest dynamics, Spatial patterns, Dendroecology, Growth dominance  
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31 14 **Abstract**

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33 15 Knowledge about the stand structure and dynamics of subalpine forests is crucial to preserve their  
34 16 multifunctionality. In the present study, we reconstructed the spatio-temporal dynamics of a subalpine *Pinus*  
35 17 *cembra* forest in the eastern Italian Alps in response to natural disturbances and forest management. We  
36 18 adopted a concurrent point pattern, dendroecological and growth dominance analysis. We mapped and  
37 19 measured all trees of *Pinus cembra* and *Larix decidua* in a 1 ha plot. We analyzed intra- and inter-specific  
38 20 spatial patterns and spatial autocorrelation of tree size and age. We explored establishment dynamics and  
39 21 shifts in competition by analyzing growth suppression/release patterns and growth dominance trends. Results  
40 22 showed a clumped, uneven-aged, multi-layered structure where pine was dominant. The synergic action of  
41 23 ecological and human-induced factors is discussed to explain the prevalence of pine over time. Spatial pattern  
42 24 and autocorrelation analyses suggest a different colonization strategy of the two species, in which pine  
43 25 established after small-scale perturbations and experienced a stronger inter- and intra-specific competition.  
44 26 The interruption of tree establishment and shift in growth dominance towards large trees resulting from the  
45 27 lack of forest management is the most important finding of this research. This highlights the importance of an  
46 28 active management to avoid a homogenization of the forest structure that is generally associated with a  
47 29 reduction of biodiversity and protective ability of forests.  
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## 31 Introduction

32 Swiss stone pine (*Pinus cembra* L.) and mixed pine – larch (*Larix decidua* Mill.) forests are typical ecosystems of  
33 the subalpine belt of the Alps, where they often build up the timberline (Risch et al. 2003), establishing with  
34 harsh environmental conditions such as mean annual temperatures ranging from 1°C to 5°C, minimum  
35 temperatures reaching -25°C and snow cover and frozen soil lasting trough the beginning of the growing  
36 season (Tranquillini 1979). These two species have complementary life traits and hence their distribution and  
37 mixture depend on the growth conditions they experience. Larch is a light-demanding, wind-dispersed species,  
38 whose regeneration takes advantage of disturbances that expose mineral soil (Schloeth 1998), and thus can be  
39 considered a pioneer species. By contrast, stone pine is a shade-tolerant species, achieving dominance in mid-  
40 and late-successive subalpine forests (Krüsi and Moser 2000). Its heavy seeds are mainly dispersed by the  
41 European thickbilled nutcracker (*Nucifraga caryocatactes* L.) and regeneration can also take place on soil  
42 covered by litter or grass.

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44 In absence of human influence, the main drivers of species composition and growth of the larch-stone pine  
45 subalpine forests are summer temperatures (Pfeifer et al. 2005; Tinner and Kaltenrieder 2005; Casalegno et al.  
46 2010), snow cover (Frey 1983), microtopography (Schönenberger 1985; Holtmeier 2009) and natural  
47 disturbances. These latter are usually characterized by high-frequency (seasonal to yearly), low- to mid-  
48 severity events, such as avalanches, rockfall, or larch budmoth (*Zeiraphera griseana* Hubner) outbreaks  
49 (Baltensweiler 1964; Nola et al. 2006). The occurrence of major disturbances such as fires or bark beetle  
50 outbreaks (Veblen et al. 1994) has been ascertained, starting from the mid Holocene (Blarquez et al. 2010), but  
51 their role in regulating species composition is uncertain and seemingly variable between sites (Genries et al.  
52 2009). In the past, the influence of climate and natural disturbances have been obfuscated by the human  
53 impact, such as livestock grazing and tree cutting. Starting from the 20<sup>th</sup> century, because of the depopulation  
54 of mountain areas and the adoption of more conservative forestry systems, natural factors have returned to  
55 be the predominant drivers of forest dynamics (Motta and Lingua 2005), especially at higher altitudes (Lingua  
56 et al. 2008).

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58 Currently, forest management at the timberline presents the challenge of preserving long-term ecological  
59 integrity and supplying environmental services (Dorren et al. 2004) in face of the extreme climate, peculiar soil  
60 and geo-morphological conditions and high frequency of disturbances. Therefore, knowledge of the stand  
61 structure and dynamics of high-elevation forests in response to the abovementioned drivers is crucial for their  
62 sustainable management, for instance to maintain their protective function (Brang et al. 2006). However, few  
63 monitoring experiments have been set up in Alpine high-elevation forest ecosystems (Wunder et al. 2008), and  
64 they generally lack sufficient timespan, if compared to the temporal length of these forests dynamics. To this  
65 end, evidence of past dynamics and response to perturbations can be inferred by retrospective analyses.  
66 Among these, dendroecological techniques aimed at dating past increases (releases) and/or decreases  
67 (suppressions) of tree growth (Rubino and McCarthy 2004) can provide important information on the dynamic  
68 response of forests to perturbations (Camarero et al. 2000), especially when this analysis is associated with the

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3 69 study of spatial distribution of trees. In this context, spatial pattern distribution can be seen as the result of the  
4 70 interaction between establishment dynamics, intra- and inter-specific competition, past climate, type of  
5 71 disturbances and forest management (Moeur 1993; Dale 1999; Tonon et al. 2005).  
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9 73 In light of the previous considerations, the aims of the present study were: (1) to analyze the current spatial  
10 74 patterns of trees in a high-elevation Swiss stone pine forest of the Eastern Italian Alps, focusing on inter-  
11 75 specific (larch vs. pine) and inter-size (small vs. large trees) spatial relationships; (2) to reconstruct the process  
12 76 of forest establishment and (3) infer, by a concurrent dendroecological analysis of tree age,  
13 77 release/suppression events and growth dominance, which past natural and anthropogenic drivers brought to  
14 78 the current forest structure.  
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## 19 80 **Materials and methods**

### 20 81 **Study site**

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22 82 The study area is located in the Natura 2000 site IT3120128 "Alta Val di Stava" (TN, Italy) (46°19'79"N,  
23 83 11°32'26"E). The 1775 ha site, at an average elevation of 1840 m a.s.l. (max. 2345 m a.s.l., min. 1249 m a.s.l.),  
24 84 is dominated by coniferous woodlands (52%); subalpine scrub, alpine grasslands, and rocks that cover about  
25 85 15% of total land area. The most common forest habitats are acidophilus Norway spruce (*Picea abies* (L.)  
26 86 Karst.) stands in the mountain belt (15% of total land area), and mixed European larch-Swiss stone pine stands  
27 87 (36%) in the subalpine belt up to the treeline, at about 2200 m a.s.l. (coded 9420 and 9410, respectively, by  
28 88 the EU Habitat Directive 92/43/EEC). The area was a grazed woodland during the 18<sup>th</sup> and 19<sup>th</sup> century (Ridolfi  
29 89 2009). The abandonment of the traditional silvo-pastoral system reportedly occurred at the beginning of 20<sup>th</sup>  
30 90 century, except for the flat highlands that are still presently managed as pastures (Provincia Autonoma di  
31 91 Trento 2013). We selected a patch of European larch-Swiss stone pine forest at an elevation of 1860 m a.s.l.,  
32 92 and in 2009 we established a permanent 100x100 m plot in which we carried out our study. The plot is  
33 93 dominated by Swiss stone pine with a minor presence of European larch and few trees of European rowan  
34 94 (*Sorbus aucuparia* L.) and Norway spruce (*Picea abies* Karst.). The understory is composed by a thick layer of  
35 95 *Rhododendron ferrugineum* L., *Vaccinium myrtillus* L. and *Vaccinium vitis-idaea* L. Average slope angle is 25°  
36 96 with a NNE aspect. Mean temperature is 3.9 °C (mean minimum temperature: -15 °C; mean maximum  
37 97 temperature: 23 °C) and the cumulated mean annual precipitation is 1100 mm (Passo Lavazè meteorological  
38 98 station). The parent material is limestone. Due to its nontrivial slope, it is unsure whether the study area has  
39 99 ever been managed as a pasture. In the Trento province, all public forests have been subject to management  
40 100 plans since 1954 (Ferrari 1988), based on close-to-nature silvicultural criteria (Wolynski et al. 2009). In  
41 101 particular, the forest under scrutiny was managed by selection cutting until 1966, when a mudflow  
42 102 permanently damaged the nearby forest road and active management ceased (Ridolfi 2009).  
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### 53 103 54 104 **Field sampling and tree mapping**

55 105 Within the plot, all living trees were mapped on a Cartesian coordinate system by a total station (Leica, UK),  
56 106 permanently tagged, and measured for species, stem height and stem diameter. The diameter was measured  
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3 107 at 130 cm height for large trees (diameter at breast height [dbh]  $\geq 7.5$ ) and at the root collar (rcd) for small  
4 108 trees (dbh < 7.5 cm). Additionally, two 33x100 m perpendicular transects were delimited (55% of the plot  
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6 109 area), crossing the center of the plot. Within the transects, an increment core was taken at 80 cm height from  
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8 110 both large and small trees, parallel to slope in order to avoid sampling compression wood and obtaining biased  
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10 111 measurements (Cook and Kairiukstis 1990). Coring height was chosen to maximize the accuracy of true age  
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12 112 estimates, while avoiding the most asymmetric part of the basal stem. A total of 229 large trees of pine and 31  
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14 113 large trees of larch were sampled, i.e., 47% and 49% of all the respective large trees in the plot. Concerning  
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16 114 small trees, 55 pines and 10 larches were sampled, corresponding to the 24% and 20% of each species in the  
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18 115 whole plot. In order to compute the mean age difference between stem base and 80 cm height, we cut 10  
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20 116 Swiss stone pine and 10 European larch small trees outside the experimental area. From each felled stem, we  
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22 117 collected a cross-section at the stem base and at 80 cm and counted tree rings. The difference between the  
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24 118 mean ring counts at collar and at 80 cm height were subsequently added to ring counts at coring height, in  
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26 119 order to obtain a corrected estimate of tree age (Motta and Lingua 2005). Given the exploratory nature of the  
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28 120 study and being ~~it~~ a beginning step for advanced studies, the statistical analyses used in this paper are  
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30 121 generally basic if compared to more up to date techniques (Druckenbrod 2005, Ise and Moorcroft 2008,  
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32 122 Renshaw 2010, Shimatani et al. 2011).  
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#### 35 124 **Dendroecological analysis**

36 125 Following tree cores preparation by sanding with increasingly graded sandpaper, tree-ring width and number  
37 126 were measured by means of a LINTAB6 station and TSAP-Win software (Rinntech, Heidelberg). Individual tree-  
38 127 ring series were cross-dated and standardized using a negative exponential curve (Fritts et al. 1969) to remove  
39 128 age-related trends while preserving growth fluctuation related to past disturbances (Fritts 1976; Cook and  
40 129 Kairiukstis 1990). Standardization was performed through the ARSTAN package (Cook 1985). In order to  
41 130 identify past disturbance periods, radial growth release and suppression analysis (Lorimer 1985; Motta et al.  
42 131 1999) was performed on 25 detrended tree-ring series of Swiss stone pine and 25 of European larch, evenly  
43 132 distributed in the two transect areas (Fig. 1). Only the oldest 25 trees available for each species were selected  
44 133 in order to have a broader time span while avoiding a huge unbalance in the size sample before and after the  
45 134 period of major establishment, bias that would have took place if we started to include younger trees. After  
46 135 computing 5-year running median segments starting from the first recorded year for each species (segment  
47 136 1753-1757 for Swiss stone pine; segment 1830-1834 for European larch), we identified a release when the 5-  
48 137 year median growth was  $\geq 50\%$  of the median of the previous five years, and a suppression if it was  $\leq 50\%$ .  
49 138 Median values were chosen instead of simple average as they better represent the non-normality of tree-  
50 139 growth patterns (Rubino and McCarthy 2004). Release and suppression data were expressed as the percentage  
51 140 of trees showing release/suppression among the total number of trees analyzed in each 5-year period.  
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#### 54 142 **Point pattern analysis**

55 143 Several methods have been proposed to describe point pattern spatial patterns (Diggle 1983). The main aim of  
56 144 these methodologies is to assess whether trees have a random, regular or clumped spatial distribution, in

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3 145 order to infer the nature, intensity and duration of processes that may have originated the observed spatial  
4 146 structure (Diggle 1983; Camarero et al. 2000; Tonon et al. 2005). For this purpose, both a second-order  
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6 147 analysis based on Ripley's K function (Ripley 1977), which calculates the variance of the distance between all  
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8 148 possible point pairs within a given bi-dimensional space with a radius  $d$  (Duncan 1991), and the refined  
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10 149 nearest-neighbour Diggle's G function (Diggle 1983), which is based on the distance between the event of a  
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12 150 sample and its nearest neighbour, were computed for all the trees of the plot. Ripley's K was linearized by a  
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14 151 square root transformation to  $L(d)$ , that has an expected value of zero under a Poisson distribution (Ripley  
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16 152 1979; Moeur 1993; Haase 1995). Obtained spatial patterns can be described, at any distance, as significantly  
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18 153 clumped, regular or random when  $L(d)$  or  $G(w)$  are respectively higher, lower, or within a given quantile bound  
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20 154 generated by  $n$  randomized iterations of tree positions within the plot. Both univariate analyses were carried  
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22 155 out on all trees pooled, and separately on each species (Swiss stone pine, European larch) and size class (large  
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24 156 and small trees), under the complete spatial randomness (CSR) null hypothesis, by using a Monte Carlo 99%  
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26 157 confidence interval. Bivariate analyses were performed to assess the spatial relationship between large and  
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28 158 small trees of stone pine ( $N = 481$  and  $224$ , respectively) and larch ( $N = 63$  and  $49$ ). We used Ripley's  $K_{12}$   
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30 159 function (Lotwick and Silverman 1982; Diggle 1983) in its square root transformation  $L_{12}(d)$ , and its non-  
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32 160 cumulative equivalent Neighborhood Density Function (NDF) (Condit et al. 2000). Values of  $L_{12}(d)$  or Relative  
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34 161 Neighborhood density greater, lower or within a Monte Carlo 99% confidence interval respectively indicate  
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36 162 positive association (attraction), negative association (repulsion) or spatial independence between the two  
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38 163 analyzed populations. A CSR null hypothesis for the two populations was assumed. All point pattern functions  
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40 164 were computed by the SpPack Excel add-in (Perry 2004), with a distance lag of 1 m, generating 499 Monte  
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42 165 Carlo simulations of tree locations and applying a toroidal edge correction for Ripley's K (Bailey and Gatrell  
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44 166 1995; Haase 1995) and edge correction (Gignoux et al. 1999) for Diggle's G and Neighborhood Density  
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46 167 Function. The distance range was reduced from 1-15 m to 1-5 m because in the last 10 m no evident change  
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48 168 was ever detected. Moreover, given the establishment in small groups typical of such forests, it is normal that  
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50 169 most of the interactions are taking place in the first meters. Finally, spatial autocorrelation of tree height,  
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52 170 diameter and age was calculated for all trees, and for large and small trees separately, by means of non-  
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54 171 cumulative Moran's I index (Moran 1950), which ranges from -1 (negative autocorrelation) to 1 (positive  
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56 172 autocorrelation), zero indicating absence of spatial autocorrelation (Fortin et al. 2002). Moran's I was also  
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58 173 computed by the SpPack Excel add-in (Perry 2004), up to a distance of 5 m with a lag of 1 m, and tested for  
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60 174 significance at each distance. All-directional spatial correlograms were computed for sets with 10 or more pairs  
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176 of points available at all distances (Tonon et al. 2005), and tested for significance ( $P < 0.05$ ), using the  
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178 Bonferroni procedure to correct for the dependence among the autocorrelation coefficients calculated for  
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180 each distance. Given that age data were available only in the two perpendicular transects, Moran's I for this  
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182 parameter was calculated only on a subsample of the population.

### 180 Growth dominance

181 In order to assess past changes in competitive environment, we used tree-ring data from the two transects to  
182 compute the temporal trend of stand growth dominance. Growth dominance relates the distribution of

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3 183 growth rates of individual trees within a stand to tree sizes (Binkley et al. 2003). According to Binkley (2004),  
4 184 stand development entails a systematic change in the growth dominance of stands, articulated in four distinct  
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6 185 stages. For each year  $m$  since the establishment of the oldest large tree, we used radial increments to back-  
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8 186 calculate the dbh of each large tree, its volume using dbh-volume equations (Scrinzi et al. 2010), and its  
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10 187 volume increment as the difference between volume in year  $m$  and volume in year  $m-1$ . We chose the  
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12 188 appropriate site index for volume equations by computing average height at 100 years of all cored Swiss stone  
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14 189 pines. Subsequently, we plotted cumulative increment vs. cumulative volume of trees arranged from the  
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16 190 smallest to the largest one for each year (i.e., a growth dominance curve), and computed a growth dominance  
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18 191 coefficient GD (Fernández et al. 2011) to quantify dominance level in each year:  
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$$193 \quad GD = \frac{\sum_{i=1}^{n-1} P v_i - P C_i}{\sum_{i=1}^{n-1} P v_i}$$

21 194 where  $P v_i$  is the cumulative stem volume up to the  $i$ -th individual in relation to total stem volume, and  $P C_i$  is  
22 195 the cumulative volume increment up to the  $i$ -th individual in relation to total volume increment. The growth  
23 196 dominance curve would follow a 1:1 line if the proportional contributions of each size class of trees were the  
24 197 same for volume as for volume increment. If larger trees accounted for a greater proportion of increment than  
25 198 for stand volume (positive dominance), the stand dominance curve would fall below the 1:1 line ( $GD > 0$ ).  
26 199 Stands where relatively low growth rates of larger trees account for a smaller portion of total stand increment  
27 200 than of stand volume, would show a “reverse” growth dominance (curve above the 1:1 line,  $GD < 0$ )  
28 201 (Fernández et al. 2011): the large, structurally dominant trees would not dominate the growth of the stand.  
29 202 Since in the first half of the chronology the sample size was small and no information was available on the  
30 203 former stand structure, we chose to compute the GD index only starting from the 1920.  
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## 205 Results

### 206 Species composition and size-structure

207 The stand had a density of 593 large trees and 371 small trees per hectare and a basal area of  $36.55 \text{ m}^2 \text{ ha}^{-1}$ .  
208 *Pinus cembra* was the dominant species for both number of large trees and basal area (81% and 86%  
209 respectively), followed by European larch (11% and 9% respectively) (Tab. 1). European rowan and Norway  
210 spruce were rarer, constituting only the 6% and 2% of the large trees group (Tab. 1). Dominant height and  
211 mean diameter were 18,58 m and 27,63 cm respectively (Tab. 1). Distribution of diameters approximated a  
212 negative exponential curve typical of uneven-aged subalpine forests (Meyer 1943), with a large number of  
213 small trees and progressively decreasing with increasing size class (Fig. 2a). Pine was represented in almost all  
214 diameter classes up to the largest (90 cm). Larch occurred both in small and large diameter classes with the  
215 same proportion (Fig. 2a). The height distribution of large trees showed a bell-shaped curve with a maximum  
216 at 12-15 m, whereas small trees are almost completely grouped in the first 3 m class (Fig. 2b).

217

## 218 Age-structure, growth release/suppression and growth dominance analyses

219 The mean length of site chronologies was 256 years (1753-2009) and 179 years (1830-2009) for Swiss stone  
220 pine and European larch, respectively. Average tree-ring width was 1.05 mm (max. width 2.10 mm; min. width  
221 0.25 mm) for Swiss stone pine and 1.04 mm (max. width 2.05 mm; min. width 0.13 mm) for European larch.  
222 When apportioned into 5-year periods, age-structure showed a bell-shaped curve (Fig. 3). Most of the current  
223 large trees established between years 1845 and 1935, with a peak from 1900 to 1910. While pine was found in  
224 all age classes, larch was only sporadically present before 1900. After a peak of natural regeneration in the  
225 second half of the 1950 decade, no Swiss stone pine established after the 1970 (age of the youngest living  
226 small tree), and no European larch after 1975. A visual assessment of the release/suppression analysis results,  
227 showed regular shifts with a periodicity of about 20-25 years for Swiss stone pine, especially in the earlier part  
228 of the time series (Fig. 4). Two periods of growth release of Swiss stone pine occurred at the end of the 19<sup>th</sup>  
229 century and at the beginning of the 20<sup>th</sup>, and coincide with the observed strong establishment of this species.  
230 Moreover, a marked event occurred in the 1950 decade, causing a strong suppression of larch growth and a  
231 simultaneous release of Swiss stone pine, followed by an inverse reaction of both species. With the exception  
232 of these events, growth releases and suppressions never show a frequency higher than  $\pm 30\%$  throughout the  
233 20<sup>th</sup> century. Results from the growth dominance analysis showed that it was always reversed ( $<0$ ). GD values  
234 were decreasing from 1920 until a minimum in the 1950, pointing to an increasingly consistent role of small  
235 trees in biomass production. However, from this minimum to 2010, GD increased meaning that small trees  
236 biomass production constantly decreased in favor of large trees (Fig. 5).

237

## 238 Spatial distribution of trees

239 Univariate point pattern analysis showed a clear tendency towards clumping of large trees of the investigated  
240 species (all species individually and combined) at all considered distances (Fig. 6a, 6c, 6e). Swiss stone pine  $L(d)$   
241 peaked at 1 m distance, farther in larch. Small trees exhibited clumping at all distances, with higher  
242 aggregation in the first meters for *Pinus cembra*. These results were confirmed also by Diggle's G function, as  
243  $G(w)$  values showed aggregation at all considered distances for small trees, both combined and separately (Fig.  
244 7b, 7d, 7f), as well as aggregation for large trees at least until 3 meters (Fig. 7a, 7c, 7e). For what concerns  
245  $L_{12}(d)$  bivariate point pattern analysis, large trees vs. small trees of both species combined showed spatial  
246 attraction for all distance lags (Fig. 8a). Intra-specific patterns, according to  $L_{12}(d)$ , exhibited continuous spatial  
247 attraction for pine and from 3 m to 5 m for larch (Fig. 8b, 8c), whereas inter-specific patterns showed random  
248 distribution between pine and larch large trees (Fig. 8d) and a significant attraction between Swiss stone pine  
249 and European larch small trees (Fig. 8e). Similarly, the non-cumulative bivariate point pattern analysis (NDF),  
250 showed attraction in the first and fourth lag between large and small trees of both species combined (Fig. 9a),  
251 as well as intra-specific attraction up to 2 m for pine (Fig. 9b) and from 3 to 5 m for larch (Fig. 9c). A random  
252 spatial distribution was observed between pine and larch large trees (Fig. 9d) and significant attraction  
253 between small trees of the same species (Fig. 9e). Correlograms (all species pooled) showed significantly

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3 254 positive ( $P < 0.05$ ) autocorrelation of diameter in the first meter in large trees, and up to 2 m in small trees (Fig.  
4 255 10a). Positive autocorrelation was detected at all distances for large trees height and at 1, 2 and 5 m for small  
5 256 trees (Fig. 10b). For large trees only, age was positively autocorrelated (Fig. 10c), diameter was positively  
6 257 autocorrelated only for pine at 2 m (Fig. 10d), whereas height was at 1 m for larch and from 2 m to 5 m for  
7 258 pine (Fig. 10e). Age was positively autocorrelated only for large trees of pine (Fig. 10f). Significant and positive  
8 259 autocorrelation of both diameter and height was detected in the small trees layer of Swiss stone pine at  
9 260 almost all distances, whereas larch was never autocorrelated, set aside from height at 5 m (Fig. 10g, 10h).  
10 261 Unlike large trees, significant age autocorrelation was discernible in small trees only at 2 m for larch and 4 m  
11 262 for pine (Fig. 10i).  
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264 **Discussion**

265 Unlike previous studies on Alpine treeline forests, which were focused on mixed pine-larch woods ([Carrer and](#)  
266 [Urbinati 2001](#); [Motta and Lingua 2005](#); [Lingua et al. 2008](#)), the present study considers a stand clearly  
267 dominated by Swiss stone pine. Past disturbance regime, land-use, and microclimate conditions seem to have  
268 favored Swiss stone pine over European larch in the past. Historically, in grazable Alpine woodlands pine was  
269 generally removed whereas larch was promoted by landowners because of its lighter crown, suitable for the  
270 growth of the herbaceous layer (Garbarino et al. 2011). Nevertheless, age structure analysis showed that the  
271 oldest living trees are pines and almost no larch trees are dating back to a period prior to the end of the 19<sup>th</sup>  
272 century (Fig. 3). This suggests that the stand had only marginal grazing relevance, while timber production  
273 might have been important, even though not as intensive as in lower altitude Norway spruce forests of the  
274 same valley. In this regard, the circa 20-year long release-suppression cycles occurring in the early stand  
275 history hint at a utilization of the forest with a [utilization frequency](#) of the abovementioned length (Fig. 4).  
276 [Therefore](#), we cannot formulate any hypothesis about harvest intensity and silvicultural principles used in the  
277 18<sup>th</sup> and 19<sup>th</sup> century, but we cannot exclude similarities with selection cutting currently applied in several  
278 parts of the Alps. An additional hypothesis that could explain the dominance of Swiss stone pine is that during  
279 the last centuries, because of its resistance to weathering, larch timber was largely used for construction all  
280 over the Alps (Gambetta et al. 2004). Therefore, local foresters could have preferentially targeted European  
281 larch, felling large and mid-sized trees and hence making impossible to trace the establishment of this species  
282 back to the 19<sup>th</sup> century.

283 Besides historical reasons, the dominance of Swiss stone pine can be explained through ecological processes.  
284 For instance, the absence of events that significantly altered growth dynamics and species composition could  
285 have negatively affected European larch, as it demands high light availability and bare or disturbed soil to  
286 germinate, whereas a relatively undisturbed stand with cold aspect, as occurs in this study, allowed Swiss  
287 stone pine to establish easily (Li and Yang 2004). In addition, the dense rhododendron understory makes  
288 germination of species with light seeds, such as larch, quite difficult. For these reasons, the dominance of Swiss  
289 stone pine in the large trees layer seems to be the result of a synergic combination of ecological and human-

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3 290 induced factors. On the other hand, small trees showed a more balanced species composition and a higher  
4 291 relative frequency of *Larix decidua* than the large trees population (Fig. 3). This could be due to higher  
5 292 frequency of small-scale disturbances, e.g. more frequent utilizations, that promoted the establishment of this  
6 293 pioneer species, at least until active forest management was carried on. In addition, both European larch and  
7 294 Swiss stone pine were able to endure growth suppression for a very long time, since individuals with dbh<7.5  
8 295 cm and ages of 93 and 75 years have respectively been sampled. The ability to survive for several decades  
9 296 under forest canopy conditions is traditionally considered a trait of shade-tolerant species (Lorimer 1983), but  
10 297 these findings highlight how both European larch and Swiss stone pine may exhibit a higher ecological  
11 298 plasticity to this extent, also in light of the harsh environmental conditions experienced in subalpine forests  
12 299 which slowdown growth rates.

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19 300 Establishment of the current large trees cohort was temporally limited to a time span of about 40 years (1885-  
20 301 1925). Moreover, the last harvesting in this area was carried out at the beginning of the 1960s. This was  
21 302 confirmed by a high frequency of tree establishment from 1955 to 1965 (Fig. 3). Larch budmoth outbreaks  
22 303 have been reported to occur in cycles 8-10 years apart (Baltensweiler and Fischlin 1988) and to spread  
23 304 eastwards starting from the Upper Engadine valley, following the predominantly westerly winds blowing  
24 305 through the Alpine arc (Baltensweiler and Rubli 1999). Consistently to our study, outbreaks have been  
25 306 registered in the eastern Alps (Büntgen et al. 2009) as well as in other areas of the Alpine region in the early  
26 307 1950 (Price et al. 2006). In this regard, the most severe growth suppression we could detect was the one of  
27 308 European larch during the 1950 decade and the contemporary release of Swiss stone pine growth (Fig. 4). This  
28 309 event could be related to a larch budmoth outbreak. As a consequence of defoliation, larch experienced a  
29 310 strong and sustained reduction in growth, supported also by direct observation of tree-ring and latewood  
30 311 width, with an observed negative pointer year in 1953 followed by a circa 3-year period of reduced yearly and  
31 312 latewood growth (Baltensweiler et al. 2008). Swiss stone pine seems to have benefitted from the availability of  
32 313 resources made possible by the suppression of larch, showing a quasi-simultaneous increase in growth.  
33 314 However, the most important finding of this study is the lack of small trees establishment after 1970,  
34 315 coinciding with the cessation of active management occurred in 1966. Moreover, as pointed out by the growth  
35 316 dominance analysis (Fig. 5), the relevance of small and large trees in biomass production changed in the  
36 317 middle of 20<sup>th</sup> century favoring the latter, hinting at a changed contribution of the two classes, likely triggered  
37 318 by the interruption of forest management. Therefore, the absence of small-scale natural perturbations and  
38 319 silvicultural tending is leading to the reduction of suitable microsites for seed germination and saplings  
39 320 establishment of both species and consequently the stand is evolving towards a new phase characterized by a  
40 321 less heterogeneous age-structure.

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52 322 To this end, although they are pertaining only to the current state of the forest, results about spatial structure  
53 323 reinforce the previous considerations about changes in the stand structure. Tree spatial pattern was clumped  
54 324 at all distances in both large and small trees, particularly for distances < 3 m (Figs. 1, -Fig. 6 and Fig.-7).  
55 325 Aggregated patterns are typical of high-elevation subalpine forests and originate from facilitative processes in  
56 326 the regeneration phase (Brang et al. 2001, Motta and Lingua 2005). Trees tend to establish in groups, thus

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3 327 obtaining mutual ecological advantages against strongly limiting environmental factors (wind, snow, erosion,  
4 328 etc.) (Callaway and Walker 1997). The feeding behavior of the Spotted nutcracker is a further cause of clumped  
5 329 spatial pattern for Swiss stone pine. Small trees of all species pooled exhibited a positive spatial association  
6 330 with the large trees population (Fig. 8a and 9a), confirming the preference for clumped patterns and the  
7 331 facilitative influence of large trees on regeneration processes. However, this outcome seems to depend on the  
8 332 dominance of Swiss stone pine also in the small trees layer, as the two species showed a different behavior  
9 333 when considered one at a time. In fact, while Swiss stone pine exhibited spatial association at short distances  
10 334 (Fig. 8b and 9b), larch regeneration occurred preferentially between 3 and 5 meters from large trees (Fig. 8c  
11 335 and 9c), confirming the light-demanding trait of this species and the preference for canopy gaps. Considering  
12 336 large trees only, Swiss stone pine exhibited a positive autocorrelation for age and height, whereas larch did not  
13 337 show positive autocorrelation for almost any of the distance lags of all the parameters (Fig. 10d, 10e, 10f). This  
14 338 suggests a different colonization strategy and/or competition experienced by the two species. Pine trees  
15 339 established more quickly after small-scale perturbations (individuals of similar age in a small space) and  
16 340 experienced a stronger competition (individuals of different diameter in a small space) than larch. The general  
17 341 positive age autocorrelation of large trees, especially Swiss stone pine, is contrasted by the absence of age  
18 342 autocorrelation of small trees (Fig. 10i). This discrepancy suggests that the formation of regeneration nuclei of  
19 343 the dominant species in the past has been faster than today. The long suppression period that small trees can  
20 344 tolerate is a likely explanation for the different age autocorrelation patterns between the large tree and small  
21 345 tree populations. Nevertheless, the absence of forest management in the last 50 years might have represented  
22 346 a crucial factor in determining the slowdown of the regeneration dynamics.

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### 348 Conclusions

349 Our study is one of the few studies showing how the lack of forest management caused the interruption of  
350 tree establishment and a potential homogenization of the structure, which could negatively affect the ability of  
351 this forest to provide services such as its potential protective role (Dorren et al. 2004). This highlights the  
352 importance of an active, sustainable management in maintaining a heterogeneous structure, with an  
353 uninterrupted recruitment of new individuals.

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56 504 **Tables captions**  
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3 505 **Table 1** Species mixture, total basal area and stand characteristics of the 1-ha area. Absolute values and  
4 506 relative abundance (%) referred to both small (DBH<7.5 cm) and large trees populations (DBH>7.5 cm). Stand  
5 507 characteristics referred to large trees population only.  $g_m$ : average basal area;  $h_{mg}$ : height at average basal area  
6 508 diameter;  $Hd$ : dominant height (average height of the tallest 100 large trees);  $d_{mg}$ : diameter at average basal  
7 509 area;  $V$ : standing volume  
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13 **Figure captions**  
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16 **Figure 1** Mapped spatial distribution of both small and large trees of all species within the 1-ha plot. The 25  
17 513 trees of Swiss stone pine and European larch that were used for the growth release/suppression analysis are  
18 514 highlighted with **thick dark** borders. PIAB\_L: large Norway spruce; PICE\_L: large Swiss stone pine; LADE\_L: large  
19 515 European larch; SOAU\_L: large European rowan; PIAB\_S: small Norway spruce; PICE\_S: small Swiss stone pine;  
20 516 LADE\_S: small European larch; SOAU\_S: small European rowan; PICE\_sel: Swiss stone pine trees selected for  
21 517 growth release/suppression analysis; LADE\_sel: European larch trees selected for growth release/suppression  
22 518 analysis.  
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27 **Figure 2** Diameter (a) and height class (b) distribution of large and small trees. In (a) all small trees have been  
28 520 included in one single class with dbh<7.5 cm. PICE = *Pinus cembra*; LADE = *Larix decidua*; PICE\_S = *Pinus*  
29 521 *cembra* small trees; PICE\_S = *Larix decidua* small trees.  
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32 **Figure 3** Age structure of the studied stand showed in 5-years interval classes. Large trees (*large*) and small  
33 523 trees (*small*) of both species have been represented separately. PICE = *Pinus cembra*; LADE = *Larix decidua*.  
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36 **Figure 4** Frequency of growth release and growth suppression periods in PICE = *Pinus cembra* and LADE = *Larix*  
37 525 *decidua*. The frequency represents the percentage of trees showing growth releases/suppressions among the  
38 526 whole sample. Secondary y axis: number of trees implemented in the sample.  
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41 **Figure 5** Growth dominance analysis chart. In the upper part is the amount of trees implemented in the  
42 528 sample. In the lower part the GD (growth dominance) trend (continuous line) and single values (dots) over  
43 529 time.  
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46 **Figure 6** Univariate point pattern analysis of large and small trees pooled, and Swiss stone pine and European  
47 531 larch separately.  $L(d)$  square root transformation is **shown** (continuous line), with a 99% Monte Carlo  
48 532 confidence envelope (dashed line). PICE = *Pinus cembra*; LADE = *Larix decidua*.  
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51 **Figure 7** Diggle's G function analysis for large and small trees pooled, and Swiss stone pine and European larch  
52 534 separately.  $G(w)$  is **shown** (continuous line), with a 99% Monte Carlo confidence envelope (dashed line). PICE =  
53 535 *Pinus cembra*; LADE = *Larix decidua*.  
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3 536 **Figure 8** Bivariate point pattern analysis: between large trees and small trees (pooled); intra-specific for Swiss  
4 537 stone pine and European larch separately; inter-specific comparing large trees and small trees of both species  
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6 538 separately. Square root transformation  $L_{12}(d)$  is shown (continuous line), with a 99% Monte Carlo confidence  
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8 539 envelope (dashed line). PICE = *Pinus cembra*; LADE = *Larix decidua*.

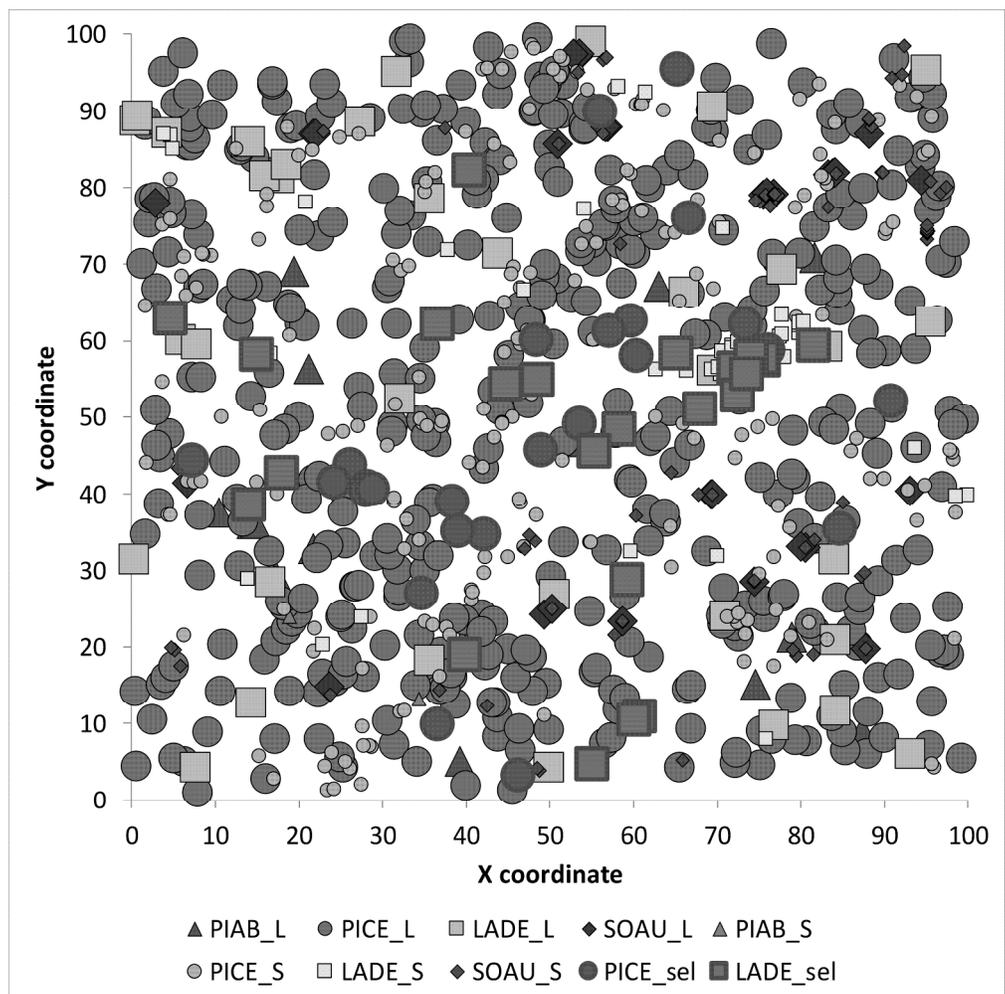
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10 540 **Figure 9** Relative neighborhood density between large trees and small trees (pooled); intra-specific for Swiss  
11 541 stone pine and European larch separately; inter-specific comparing large trees and small trees of both species  
12 542 separately. Relative neighborhood density is shown (continuous line), with a 99% Monte Carlo confidence  
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14 543 envelope (dashed line). PICE = *Pinus cembra*; LADE = *Larix decidua*.

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16 544 **Figure 10** Moran's I correlograms for diameter, height and age of large and small trees (pooled) and Swiss  
17 545 stone pine and European larch separately. Double-sized markers: spatial autocorrelation significant at  $P < 0.05$ .  
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19 546 PICE = *Pinus cembra*; LADE = *Larix decidua*.

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	Large trees	Small trees	Basal area (m <sup>2</sup> ha <sup>-1</sup> )	Stand characteristics	
<i>P. cembra</i>	481 (81%)	224 (60%)	31.50 (86%)	<b>g<sub>m</sub> (m<sup>2</sup> ha<sup>-1</sup>)</b>	0.06
<i>L. decidua</i>	63 (11%)	49 (13%)	3.22 (9%)	<b>h<sub>mg</sub> (m)</b>	13.37
<i>S. aucuparia</i>	34 (6%)	96 (26%)	0.23 (1%)	<b>Hd (m)</b>	18.58
<i>P. abies</i>	15 (2%)	2 (1%)	1.60 (4%)	<b>d<sub>mg</sub> (cm)</b>	27.63
Total	593	371	36.55	<b>V (m<sup>3</sup> ha<sup>-1</sup>)</b>	253.89

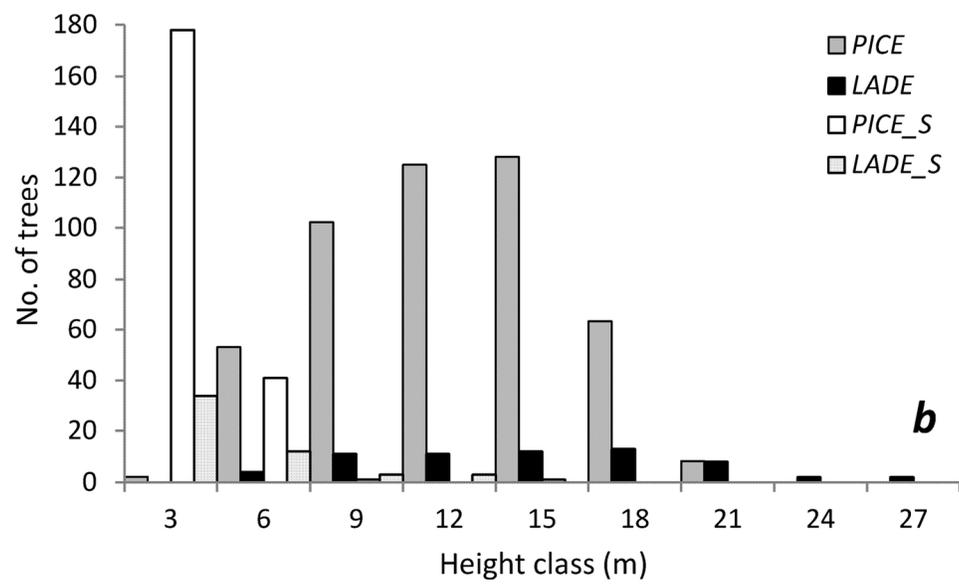
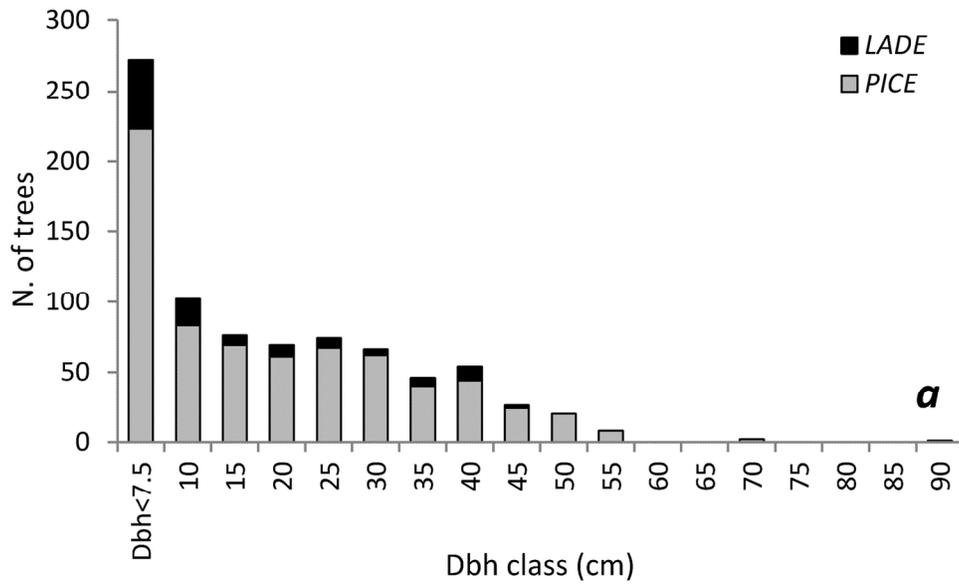
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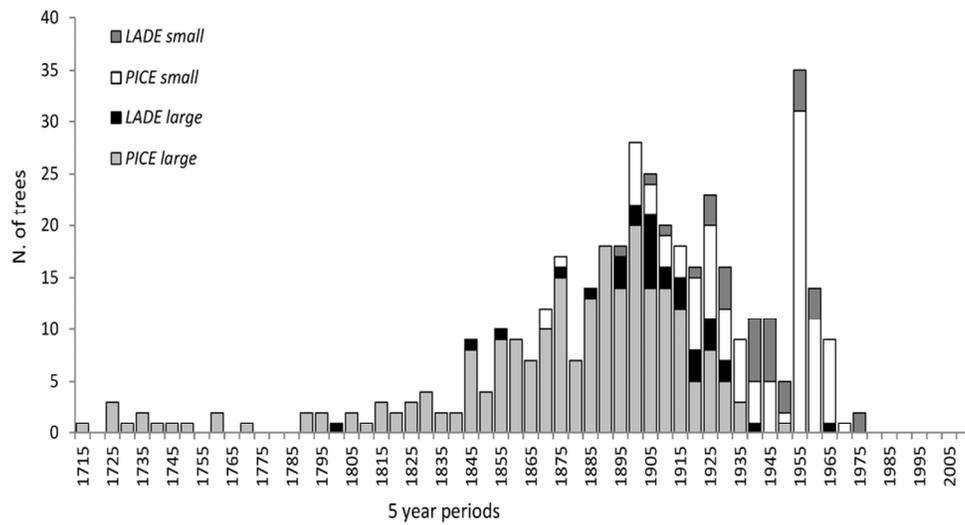
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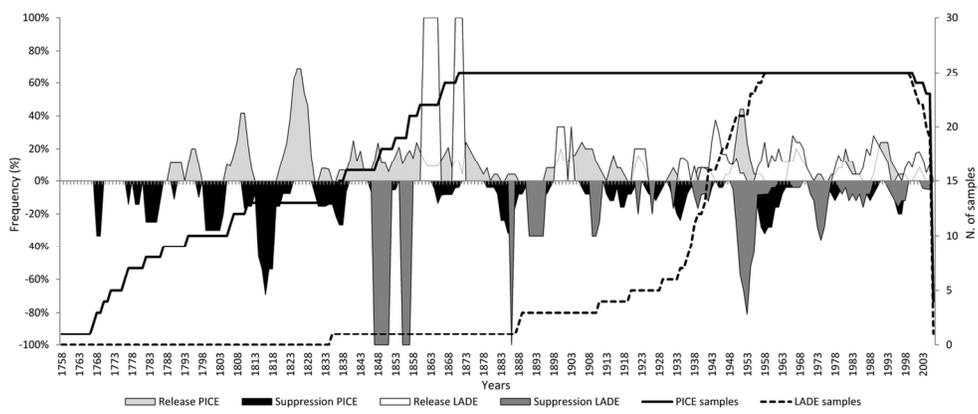
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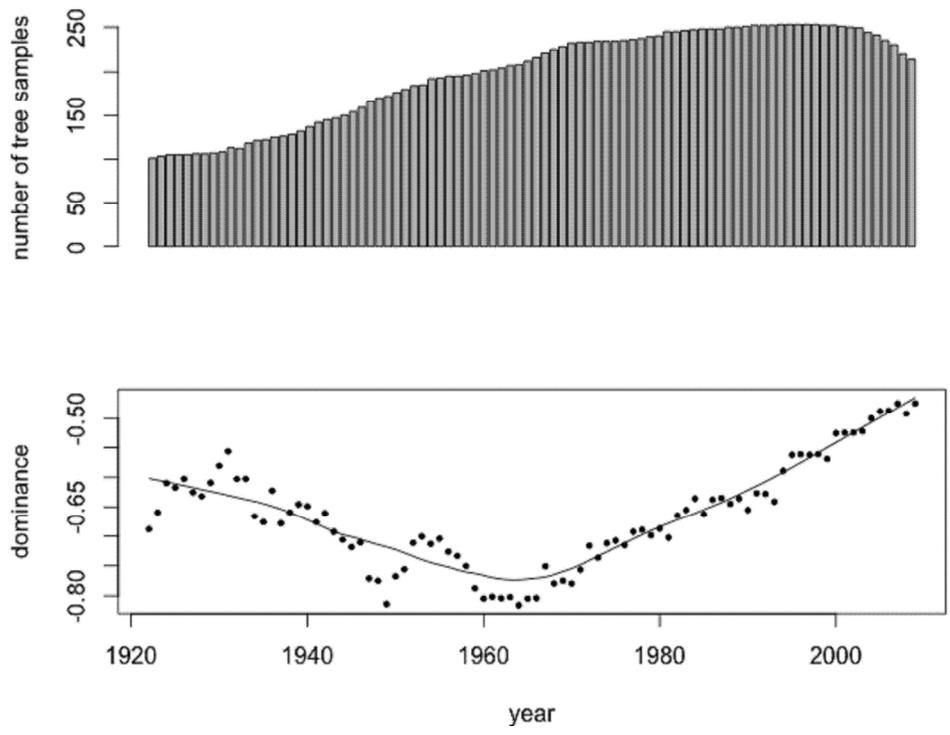
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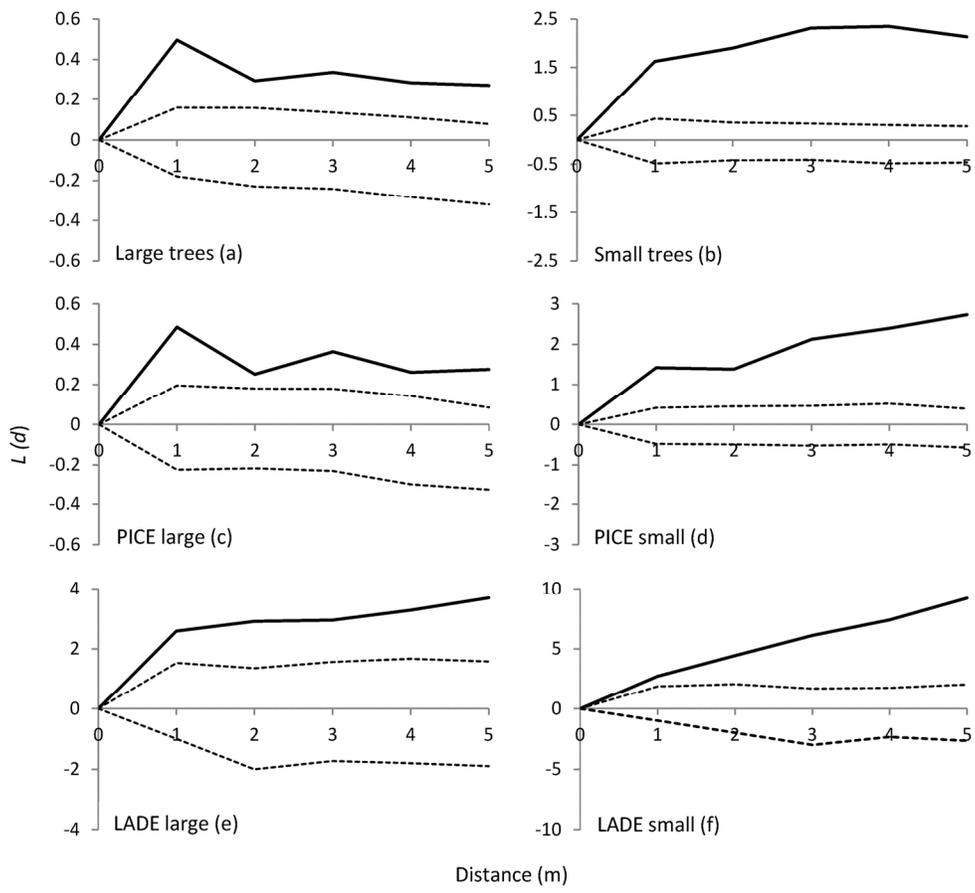
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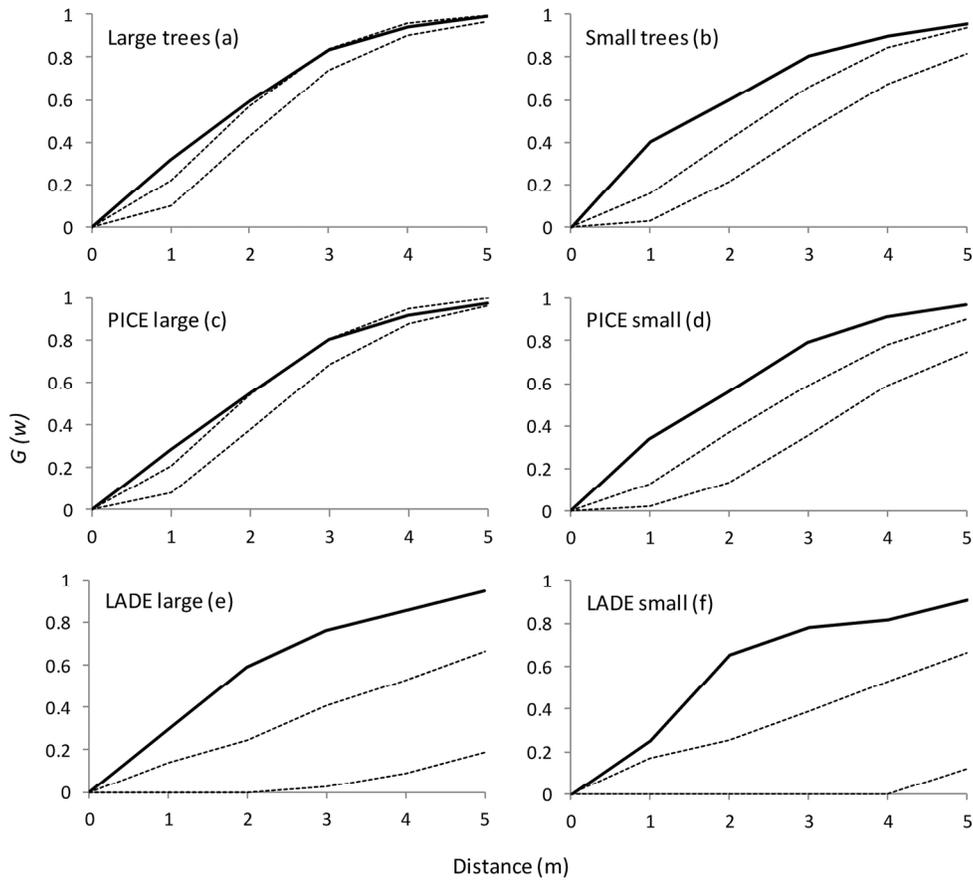
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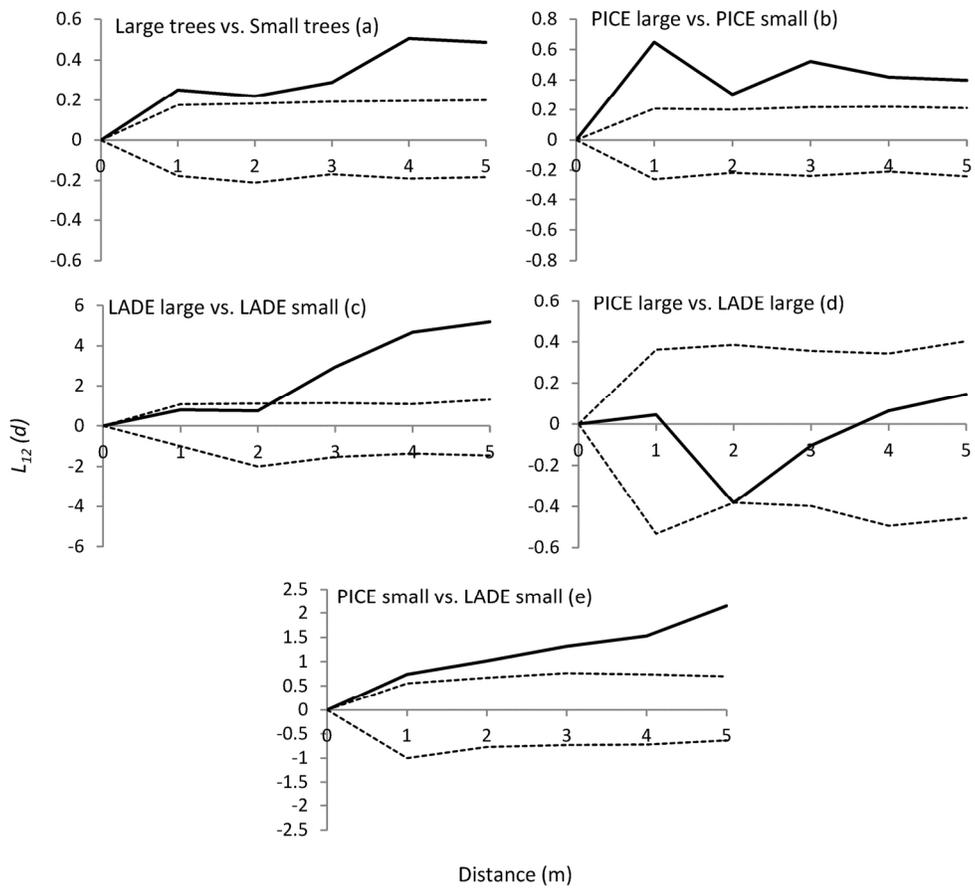


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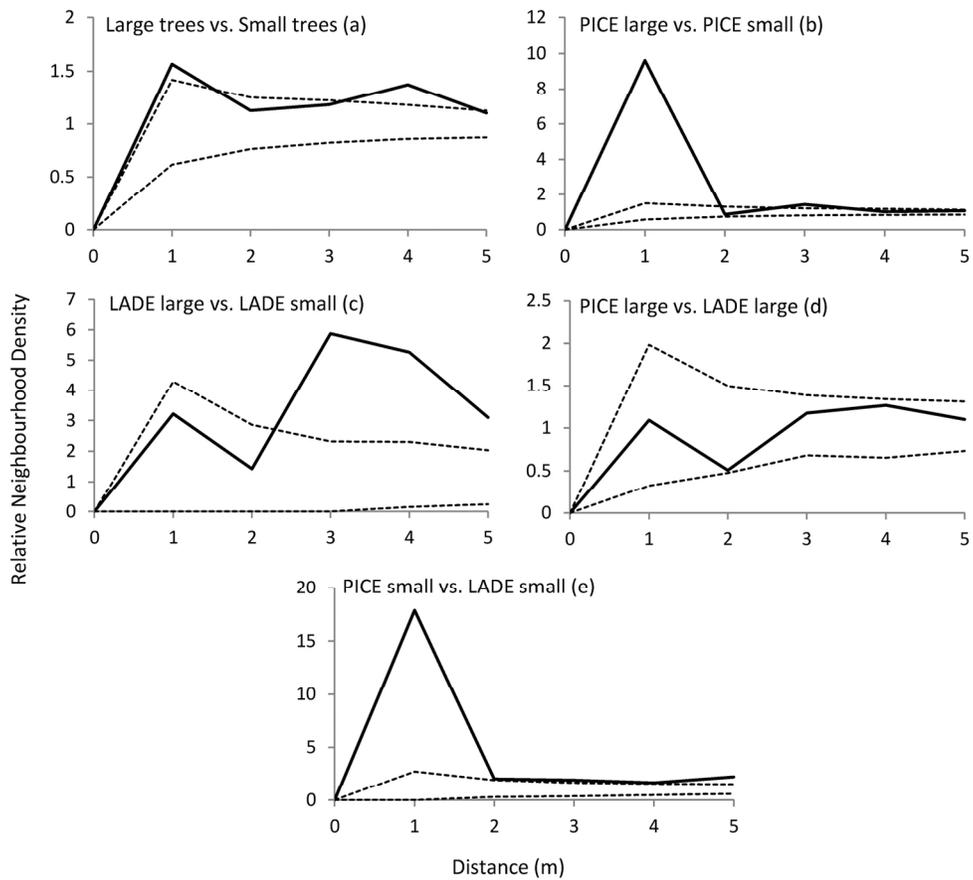
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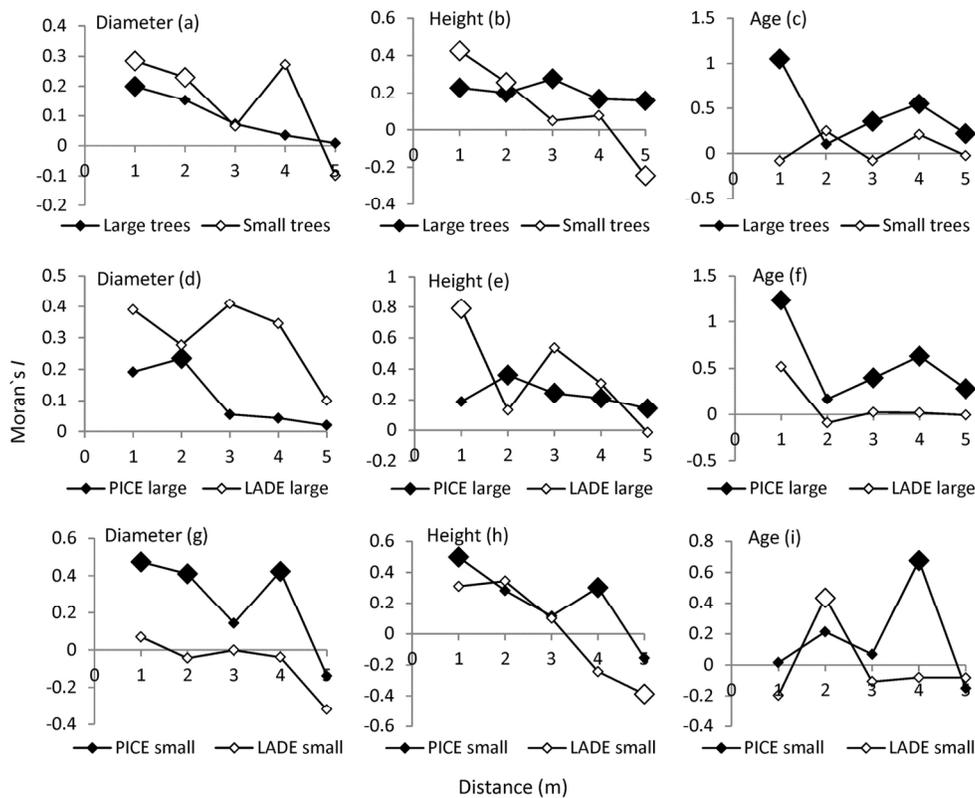
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