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Effects of the lack of forest management on spatiotemporal dynamics of a subalpine *Pinus cembra* forest

Francesco Giammarchi^a, Giorgio Vacchiano^b, Andrea Bertagnolli^c, Maurizio Ventura^a, Pietro Panzacchi^a, Paolo Cherubini^d and Giustino Tonon^{a,e}

^aFaculty of Science and Technology, Free University of Bolzano, Bolzano, Italy; ^bDipartimento di Scienze Agrarie, Forestali e Alimentari, Università degli Studi di Torino, Grugliasco, TO, Italy; ^cMagnifica Comunità di Fiemme, Cavalese, TN, Italy; ^dSwiss Federal Research Institute for Forest, Snow and Landscape Research, Birmensdorf, Switzerland; ^eMountFor Project Centre, European Forest Institute, San Michele a/Adige, TN, Italy

ABSTRACT

Knowledge about the stand structure and dynamics of subalpine forests is crucial to preserve their multifunctionality. In the present study, we reconstructed the spatiotemporal dynamics of a subalpine *Pinus cembra* forest in the eastern Italian Alps in response to natural disturbances and forest management. We adopted a concurrent point pattern, dendroecological and growth dominance (GD) analysis. We mapped and measured all trees of *Pinus cembra* and *Larix decidua* in a 1 ha plot. We analyzed intra- and interspecific spatial patterns and spatial autocorrelation of tree size and age. We explored establishment dynamics and shifts in competition by analyzing growth suppression/release patterns and GD trends. Results showed a clumped, uneven-aged, multilayered structure where pine was dominant. The synergic action of ecological and human-induced factors is discussed to explain the prevalence of pine over time. Spatial pattern and autocorrelation analyses suggest a different colonization strategy of the two species, in which pine established after small-scale perturbations and experienced a stronger inter- and intra-specific competition. The interruption of tree establishment and shift in GD toward large trees resulting from the lack of forest management are the most important findings of this research. This highlights the importance of an active management to avoid the homogenization of the forest structure that is generally associated with a reduction in biodiversity and protective ability of forests.

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Introduction

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

In the absence of human influence, the main drivers of species composition and growth of the larch–stone pine subalpine forests are summer temperatures (Pfeifer et al. 2005; Tinner & Kaltenrieder 2005; Casalegno et al. 2010), snow

cover (Frey 1983), microtopography (Schönenberger 1985; Holtmeier 2009) and natural disturbances. These latter are usually characterized by high-frequency (seasonal to yearly), low- to mid-severity events, such as avalanches, rockfall or larch budmoth (*Zeiraphera griseana* Hubner) outbreaks (Baltensweiler 1964; Nola et al. 2006). The occurrence of major disturbances such as fires or bark beetle outbreaks (Veblen et al. 1994) has been ascertained, starting from the mid-Holocene (Blarquez et al. 2009), but their role in regulating species composition is uncertain and seemingly variable between sites (Genries et al. 2009). In the past, the influence of climate and natural disturbances has been obfuscated by human impact, such as livestock grazing and tree cutting. Starting from the twentieth century, because of the depopulation of mountain areas and the adoption of more conservative forestry systems, natural factors have returned to be the predominant drivers of forest dynamics (Motta & Lingua 2005), especially at higher altitudes (Lingua et al. 2008).

Currently, forest management at the timberline presents the challenge of preserving long-term ecological integrity and supplying environmental services (Dorren et al. 2004) in face of extreme climate, peculiar soil and geomorphological conditions and high frequency of disturbances. Therefore, knowledge of the stand structure and dynamics of high-

elevation forests in response to the abovementioned drivers is crucial for their sustainable management, for instance to maintain their protective function (Brang et al. 2006). However, few monitoring experiments have been set up in Alpine high-elevation forest ecosystems (Wunder et al. 2008), and they generally lack sufficient timespan, if compared to the temporal length of these forests' dynamics. To this end, evidence of past dynamics and response to perturbations can be inferred by retrospective analyses. Among these, dendroecological techniques aimed at dating past increases (releases) and/or decreases (suppressions) of tree growth (Rubino & McCarthy 2004) can provide important information on the dynamic response of forests to perturbations (Camarero et al. 2000), especially when this analysis is associated with the study of spatial distribution of trees. In this context, spatial pattern distribution can be seen as the result of the interaction between establishment dynamics, intra- and interspecific competition, past climate, type of disturbances and forest management (Moeur 1993; Dale 1999; Tonon et al. 2005).

In light of the previous considerations, the aims of the present study were (1) to analyze the current spatial patterns of trees in a high-elevation Swiss stone pine forest of the eastern Italian Alps, focusing on interspecific (larch vs. pine) and inter-size (small vs. large trees) spatial relationships; (2) to reconstruct the process of forest establishment and (3) infer, by a concurrent dendroecological analysis of tree age, release/suppression events and growth dominance (GD), which past natural and anthropogenic drivers brought to the current forest structure.

Materials and methods

Study site

The study area is located in the Natura 2000 site IT3120128 "Alta Val di Stava" (TN, Italy) (46°19'79"N, 11°32'26"E). The 1775 ha site, at an average elevation of 1840 m asl (max. 2345 m asl, min. 1249 m asl), is dominated by coniferous woodlands (52%); subalpine scrub, alpine grasslands and rocks that cover about 15% of total land area. The most common forest habitats are acidophilus Norway spruce (*Picea abies* (L.) Karst.) stands in the mountain belt (15% of total land area), and mixed European larch–Swiss stone pine stands (36%) in the subalpine belt up to the tree line, at about 2200 m asl (coded 9420 and 9410, respectively, by the EU Habitat Directive 92/43/EEC). The area was a grazed woodland during the eighteenth and nineteenth century (Ridolfi 2009). The abandonment of the traditional silvo-pastoral system reportedly occurred at the beginning of the twentieth century, except for the flat highlands that are still presently managed as pastures (Provincia Autonoma di Trento 2013). We selected a patch of European larch–Swiss stone pine forest at an elevation of 1860 m asl, and in 2009 we established a permanent 100 × 100 m plot in which we carried out our study. The plot is dominated by Swiss stone pine with a minor presence of European larch and few trees of European rowan (*Sorbus aucuparia* L.) and Norway spruce (*P. abies* Karst.). The understory is composed by a thick layer

of *Rhododendron ferrugineum* L., *Vaccinium myrtillus* L. and *Vaccinium vitis-idaea* L. Average slope angle is 25° with a North-North-East aspect. Mean temperature is 3.9°C (mean minimum temperature: −15°C; mean maximum temperature: 23°C) and the cumulated mean annual precipitation is 1100 mm (Passo Lavazè meteorological station). The parent material is limestone. Due to its nontrivial slope, it is unsure whether the study area has ever been managed as a pasture. In the Trento province, all public forests have been subject to management plans since 1954 (Ferrari 1988), based on close-to-nature silvicultural criteria (Wolynski et al. 2009). In particular, the forest under scrutiny was managed by selection cutting until 1966, when a mudflow permanently damaged the nearby forest road and active management ceased (Ridolfi 2009).

Field sampling and tree mapping

Within the plot, all living trees were mapped on a Cartesian coordinate system by a total station (Leica, UK), permanently tagged and measured for species, stem height and stem diameter. The diameter was measured at 130 cm height for large trees (diameter at breast height [dbh] ≥7.5) and at the root collar (rcd) for small trees (dbh <7.5 cm). Additionally, two 33 × 100 m perpendicular transects were delimited (55% of the plot area), crossing the center of the plot. Within the transects, an increment core was taken at 80 cm height from both large and small trees, parallel to slope in order to avoid sampling compression wood and obtaining biased measurements (Cook & Kairiukstis 1990). Coring height was chosen to maximize the accuracy of true age estimates, while avoiding the most asymmetric part of the basal stem. A total of 229 large trees of pine and 31 large trees of larch were sampled, that is, 47% and 49% of all the respective large trees in the plot. Concerning small trees, 55 pines and 10 larches were sampled, corresponding to 24% and 20% of each species in the whole plot. In order to compute the mean age difference between stem base and 80 cm height, we cut 10 Swiss stone pine and 10 European larch small trees outside the experimental area. From each felled stem, we collected a cross section at the stem base and at 80 cm and counted tree rings. The difference between the mean ring counts at collar and at 80 cm height was subsequently added to ring counts at coring height, in order to obtain a corrected estimate of tree age (Motta & Lingua 2005). Given the exploratory nature of the study and being a beginning step for advanced studies, the statistical analyses used in this paper are generally basic when compared to more up-to-date techniques (Druck-enbrod 2005; Ise & Moorcroft 2008; Renshaw 2009; Shimatani & Kubota 2011).

Dendroecological analysis

Following tree cores preparation by sanding with increasingly graded sandpaper, tree-ring width and number were measured by means of a LINTAB6 station and TSAP-Win software (Rinntech, Heidelberg). Individual tree-ring series were cross-dated and standardized using a negative exponential curve (Fritts et al. 1969) to remove age-related trends, while

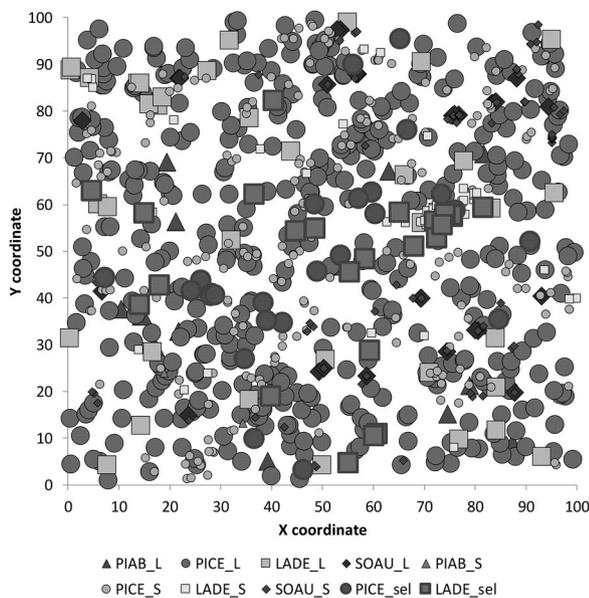


Figure 1. Mapped spatial distribution of both small and large trees of all species within the 1-ha plot. The 25 trees of Swiss stone pine and European larch that were used for the growth release/suppression analysis are highlighted with thick dark borders. PIAB_L: large Norway spruce; PICE_L: large Swiss stone pine; LADE_L: large European larch; SOAU_L: large European rowan; PIAB_S: small Norway spruce; PICE_S: small Swiss stone pine; LADE_S: small European larch; SOAU_S: small European rowan; PICE_sel: Swiss stone pine trees selected for growth release/suppression analysis; LADE_sel: European larch trees selected for growth release/suppression analysis.

preserving growth fluctuation related to past disturbances (Fritts 1976; Cook & Kairiukstis 1990). Standardization was performed through the ARSTAN package (Cook 1985). In order to identify past disturbance periods, radial growth release and suppression analysis (Lorimer 1985; Motta et al. 1999) was performed on 25 detrended tree-ring series of Swiss stone pine and 25 of European larch, evenly distributed in the two transect areas (Figure 1). Only the oldest 25 trees available for each species were selected in order to have a broader time span, while avoiding a huge unbalance in the size sample before and after the period of major establishment, bias that would have taken place if we started to include younger trees. After computing 5-year running median segments starting from the first recorded year for each species (segments 1753–1757 for Swiss stone pine; segments 1830–1834 for European larch), we identified a release when the 5-year median growth was $\geq 50\%$ of the median of the previous 5 years, and a suppression if it was $\leq 50\%$. Median values were chosen instead of simple average as they better represent the non-normality of tree-growth patterns (Rubino & McCarthy 2004). Release and suppression data were expressed as the percentage of trees showing release/suppression among the total number of trees analyzed in each 5-year period.

Point pattern analysis

Several methods have been proposed to describe point pattern spatial patterns (Diggle 1983). The main aim of these methodologies is to assess whether trees have a random, regular or clumped spatial distribution, in order to infer the nature, intensity and duration of processes that

may have originated the observed spatial structure (Diggle 1983; Camarero et al. 2000; Tonon et al. 2005). For this purpose, both a second-order analysis based on Ripley's K function (Ripley 1977), which calculates the variance of the distance between all possible point pairs within a given bidimensional space with a radius d (Duncan 1991), and the refined nearest-neighbor Diggle's G function (Diggle 1983), which is based on the distance between the event of a sample and its nearest neighbor, were computed for all the trees of the plot. Ripley's K was linearized by a square root transformation to $L(d)$, which has an expected value of zero under a Poisson distribution (Ripley 1979; Moer 1993; Haase 1995). Obtained spatial patterns can be described, at any distance, as significantly clumped, regular or random when $L(d)$ or $G(w)$ is, respectively, higher, lower or within a given quantile bound generated by n randomized iterations of tree positions within the plot. Both univariate analyses were carried out on all trees pooled, and separately on each species (Swiss stone pine, European larch) and size class (large and small trees), under the complete spatial randomness (CSR) null hypothesis, by using a Monte Carlo 99% confidence interval. Bivariate analyses were performed to assess the spatial relationship between large and small trees of stone pine ($N=481$ and 224, respectively) and larch ($N=63$ and 49). We used Ripley's K_{12} function (Lotwick & Silverman 1982; Diggle 1983) in its square root transformation $L_{12}(d)$, and its noncumulative equivalent Neighborhood Density Function (NDF) (Condit et al. 2000). Values of $L_{12}(d)$ or Relative Neighborhood density greater, lower or within a Monte Carlo 99% confidence interval, respectively, indicate positive association (attraction), negative association (repulsion) or spatial independence between the two analyzed populations. A CSR null hypothesis for the two populations was assumed. All point pattern functions were computed by the SpPack Excel add-in (Perry 2004), with a distance lag of 1 m, generating 499 Monte Carlo simulations of tree locations and applying a toroidal edge correction for Ripley's K (Bailey & Gatrell 1995; Haase 1995) and edge correction (Gignoux et al. 1999) for Diggle's G and NDF. The distance range was reduced from 1–15 m to 1–5 m because in the last 10 m no evident change was ever detected. Moreover, given the establishment in small groups typical of such forests, it is normal that most of the interactions are taking place in the first meters. Finally, spatial autocorrelation of tree height, diameter and age was calculated for all trees, and for large and small trees separately, by means of noncumulative Moran's I index (1950), which ranges from -1 (negative autocorrelation) to 1 (positive autocorrelation), zero indicating the absence of spatial autocorrelation (Fortin et al. 2002). Moran's I was also 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 significance at each distance. All-directional spatial correlograms were computed for sets with 10 or more pairs of points available at all distances (Tonon et al. 2005), and tested for significance ($P < .05$), using the Bonferroni procedure to correct for the dependence among the autocorrelation coefficients calculated for each distance. Given that age data were available only in the two perpendicular transects, Moran's I for this parameter was calculated only on a subsample of the population.

Growth dominance

In order to assess past changes in competitive environment, we used tree-ring data from the two transects to compute the temporal trend of stand GD. GD relates the distribution of growth rates of individual trees within a stand to tree sizes (Binkley et al. 2003). According to Binkley (2004), stand development entails a systematic change in the GD of stands, articulated in four distinct stages. For each year m since the establishment of the oldest large tree, we used radial increments to back-calculate the dbh of each large tree, its volume using dbh-volume equations (Scrinzi et al. 2010) and its volume increment as the difference between volume in year m and volume in year $m-1$. We chose the appropriate site index for volume equations by computing average height at 100 years of all cored Swiss stone pines. Subsequently, we plotted cumulative increment vs. cumulative volume of trees arranged from the smallest to the largest one for each year (i.e. a GD curve), and computed a GD coefficient GD (Fernández et al. 2011) to quantify the dominance level in each year:

$$GD = \frac{\sum_{i=1}^{n-1} P_{Vi} - P_{Ci}}{\sum_{i=1}^{n-1} P_{Vi}}$$

where P_{Vi} is the cumulative stem volume up to the i -th individual in relation to total stem volume, and P_{Ci} is the cumulative volume increment up to the i -th individual in relation to total volume increment. The GD curve would follow a 1:1 line if the proportional contributions of each size class of trees were the same for volume as for volume increment. If larger trees accounted for a greater proportion of increment than for stand volume (positive dominance), the stand dominance curve would fall below the 1:1 line (GD >0). Stands where relatively low growth rates of larger trees account for a smaller portion of total stand increment than of stand volume would show a “reverse” GD (curve above the 1:1 line, GD <0) (Fernández et al. 2011): the large, structurally dominant trees would not dominate the growth of the stand. Since in the first half of the chronology the sample size was small and no information was available on the former stand structure, we chose to compute the GD index only starting from 1920.

Results

Species composition and size structure

The stand had a density of 593 large trees and 371 small trees per hectare and a basal area of 36.55 m² ha⁻¹. *Pinus cembra* was the dominant species for both number of large trees and basal area (81% and 86%, respectively), followed by European larch (11% and 9%, respectively) (Table 1). European rowan and Norway spruce were rarer, constituting only 6% and 2% of the large trees group (Table 1). Dominant height and mean diameter were 18.58 m and 27.63 cm, respectively (Table 1). Distribution of diameters approximated a negative exponential curve typical of uneven-aged subalpine forests (Meyer 1943), with a large number of small trees and progressively decreasing with increasing size class (Figure 2(a)). Pine was represented in almost all diameter classes up to

Table 1. Species mixture, total basal area and stand characteristics of the 1-ha area. Absolute values and relative abundance (%) referred to both small (DBH<7.5 cm) and large trees populations (DBH>7.5 cm). Stand characteristics referred to large trees population only

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

Note: g_m : average basal area; h_{mg} : height at average basal area diameter; Hd: dominant height (average height of the tallest 100 large trees); d_{mg} : diameter at average basal area; V : standing volume.

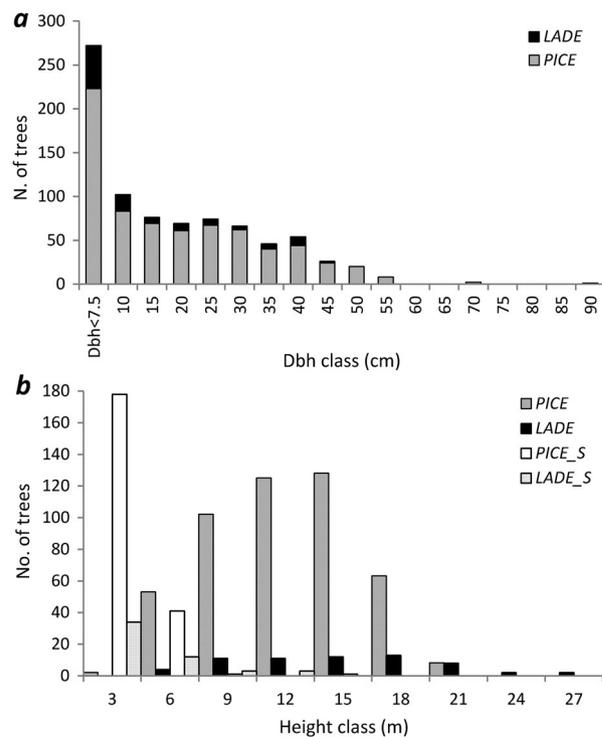


Figure 2. Diameter (a) and height class (b) distribution of large and small trees. In (a) all small trees have been included in one single class with dbh<7.5 cm. PICE = *P. cembra*; LADE = *L. decidua*; PICE_S = *P. cembra* small trees; LADE_S = *L. decidua* small trees.

the largest (90 cm). Larch occurred in both small and large diameter classes with the same proportion (Figure 2(a)). The height distribution of large trees showed a bell-shaped curve with a maximum at 12–15 m, whereas small trees were almost completely grouped in the first 3 m class (Figure 2(b)).

Age-structure, growth release/suppression and GD analyses

The mean length of site chronologies was 256 years (1753–2009) and 179 years (1830–2009) for Swiss stone pine and European larch, respectively. Average tree-ring width was 1.05 mm (max. width 2.10 mm; min. width 0.25 mm) for Swiss stone pine and 1.04 mm (max. width 2.05 mm; min.

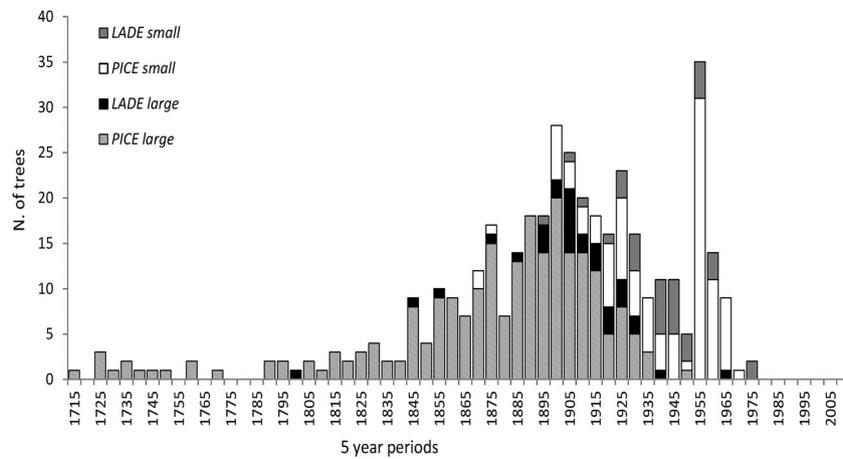


Figure 3. Age-structure of the studied stand shown in 5-year interval classes. Large trees (*large*) and small trees (*small*) of both species have been represented separately. PICE = *P. cembra*; LADE = *L. decidua*.

width 0.13 mm) for European larch. When apportioned into 5-year periods, age-structure showed a bell-shaped curve (Figure 3). Most of the current large trees established between years 1845 and 1935, with a peak from 1900 to 1910. While pine was found in all age classes, larch was only sporadically present before 1900. After a peak of natural regeneration in the second half of the 1950 decade, no Swiss stone pine established after 1970 (age of the youngest living small tree), and no European larch after 1975. Visual assessment of the release/suppression analysis results showed regular shifts with a periodicity of about 20–25 years for Swiss stone pine, especially in the earlier part of the time series (Figure 4). Two periods of growth release of Swiss stone pine occurred at the end of the nineteenth century and at the beginning of the twentieth century, and coincide with the observed strong establishment of this species. Moreover, a marked event occurred in the 1950 decade, causing a strong suppression of larch growth and a simultaneous release of Swiss stone pine, followed by an inverse reaction of both species. With the exception of these events, growth releases and suppressions never show a frequency higher than $\pm 30\%$ throughout the twentieth

century. Results from the GD analysis showed that it was always reversed (<0). GD values were decreasing from 1920 until a minimum in 1950, pointing to an increasingly consistent role of small trees in biomass production. However, from this minimum to 2010, GD increased, meaning that small trees biomass production constantly decreased in favor of large trees (Figure 5).

Spatial distribution of trees

Univariate point pattern analysis showed a clear tendency toward clumping of large trees of the investigated species (all species individually and combined) at all considered distances (Figure 6(a), (c) and (e)). Swiss stone pine $L(d)$ peaked at 1 m distance, farther in larch. Small trees exhibited clumping at all distances, with higher aggregation in the first meters for *Pinus cembra*. These results were confirmed also by Diggle's G function, as $G(w)$ values showed aggregation at all considered distances for small trees, both combined and separately (Figure 7(b), (d) and (f)), as well as aggregation for large trees at least until 3 m (Figure 7(a), (c) and (e)). For what concerns $L_{12}(d)$ bivariate point

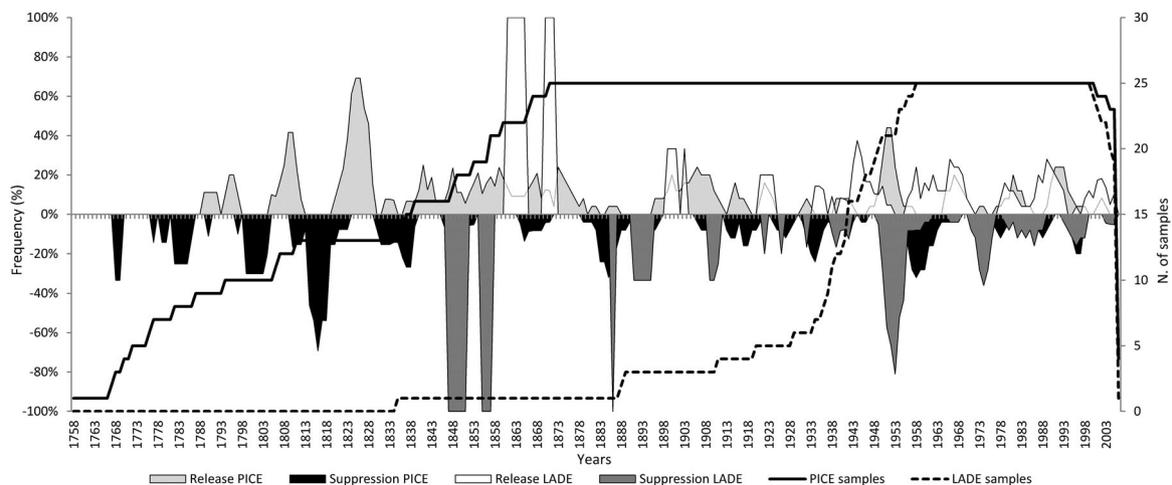


Figure 4. Frequency of growth release and growth suppression periods in PICE = *P. cembra* and LADE = *L. decidua*. The frequency represents the percentage of trees showing growth releases/suppressions among the whole sample. Secondary y-axis: number of trees implemented in the sample.

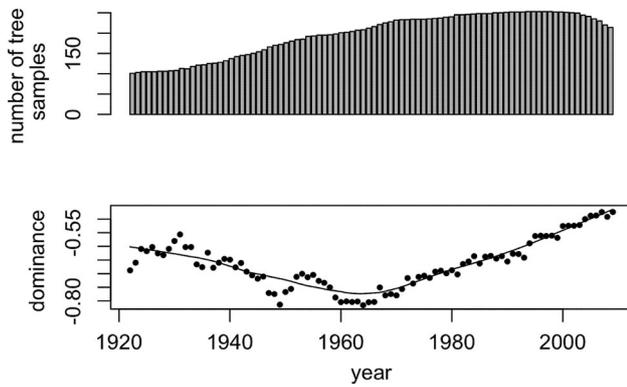


Figure 5. GD analysis chart. In the upper part is the amount of trees implemented in the sample. In the lower part, the GD (growth dominance) trend (continuous line) and single values (dots) over time.

pattern analysis, large trees vs. small trees of both species combined showed spatial attraction for all distance lags (Figure 8(a)). Intra-specific patterns, according to $L_{12}(d)$, exhibited continuous spatial attraction for pine and from 3 m to 5 m for larch (Figure 8(b) and (c)), whereas inter-specific patterns showed a random distribution between

pine and larch large trees (Figure 8(d)) and a significant attraction between Swiss stone pine and European larch small trees (Figure 8(e)). Similarly, the noncumulative bivariate point pattern analysis (NDF) showed attraction in the first and fourth lags between large and small trees of both species combined (Figure 9(a)), as well as intra-specific attraction up to 2 m for pine (Figure 9(b)) and from 3 to 5 m for larch (Figure 9(c)). A random spatial distribution was observed between pine and larch large trees (Figure 9(d)) and significant attraction between small trees of the same species (Figure 9(e)). Correlograms (all species pooled) showed significantly positive ($P < .05$) autocorrelation of diameter in the first meter in large trees, and up to 2 m in small trees (Figure 10(a)). Positive autocorrelation was detected at all distances for large trees height and at 1, 2 and 5 m for small trees (Figure 10(b)). For large trees only, age was positively autocorrelated (Figure 10(c)), diameter was positively autocorrelated only for pine at 2 m (Figure 10(d)), whereas height was at 1 m for larch and from 2 m to 5 m for pine (Figure 10(e)). Age was positively autocorrelated only for large trees of pine (Figure 10(f)). A significant and positive autocorrelation of both diameter and height was detected in the small trees layer of Swiss stone pine

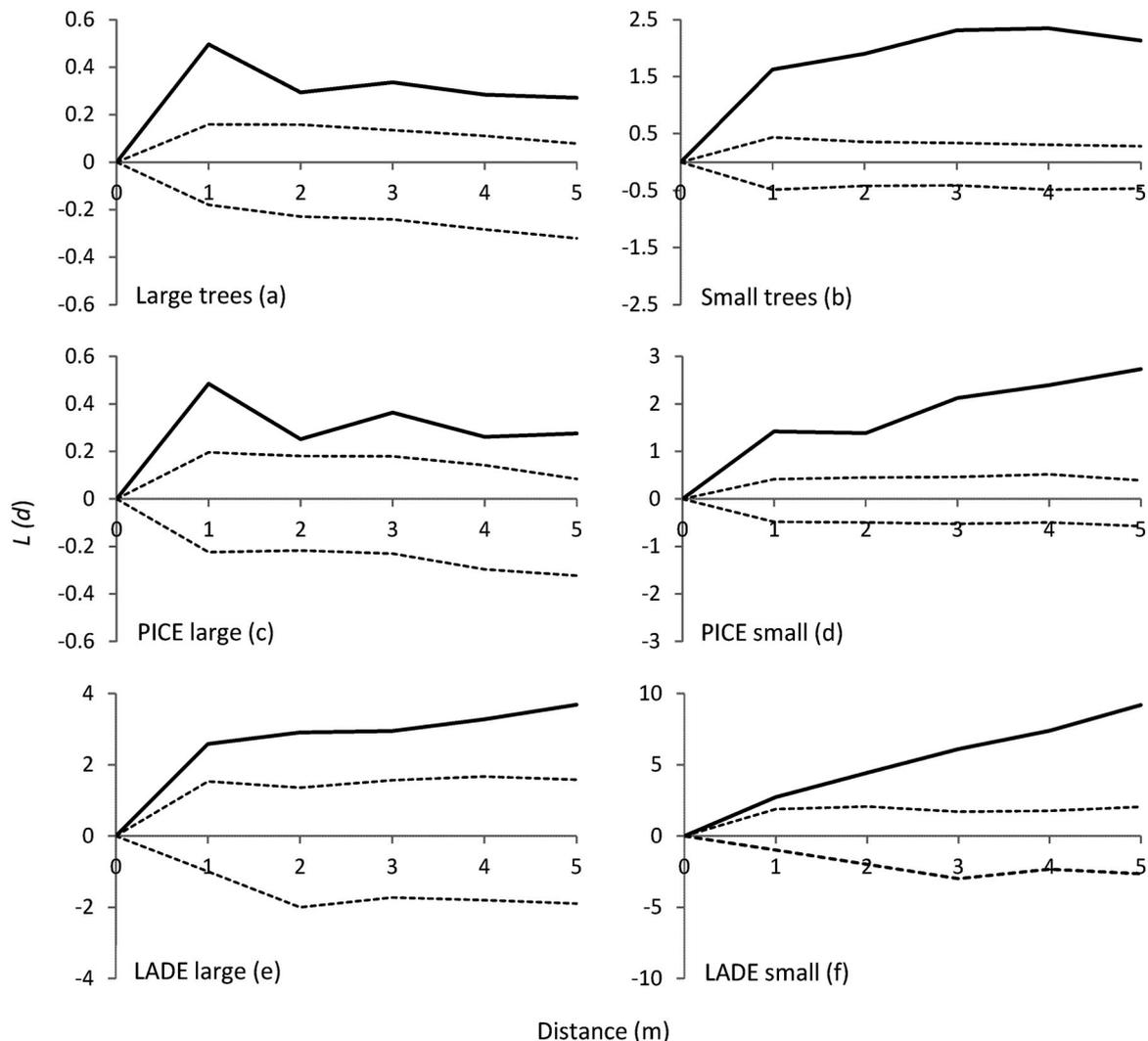


Figure 6. Univariate point pattern analysis of large and small trees pooled, and Swiss stone pine and European larch separately. $L(d)$ square root transformation is shown (continuous line), with a 99% Monte Carlo confidence envelope (dashed line). PICE = *P. cembra*; LADE = *L. decidua*.

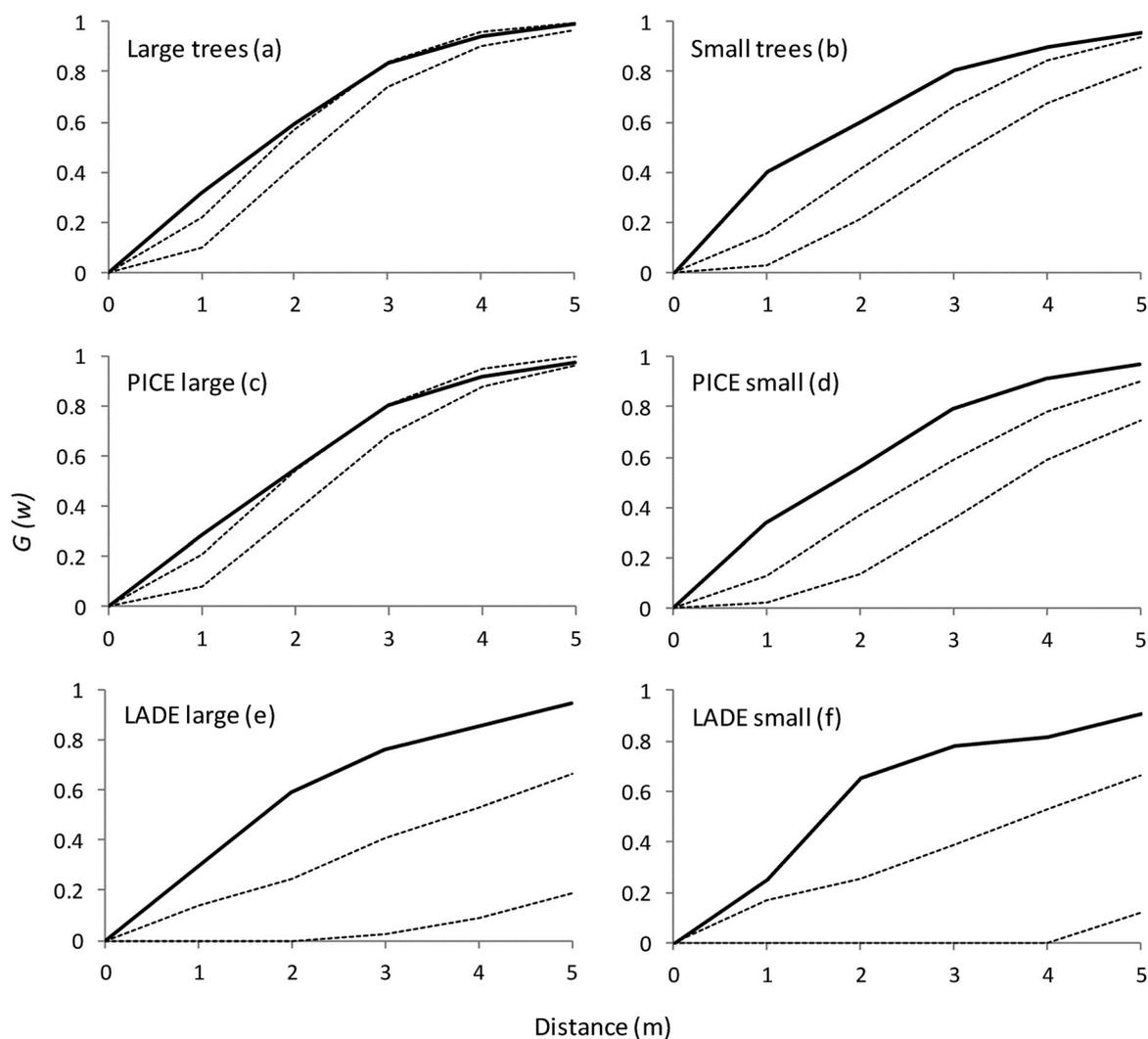


Figure 7. Diggle's G function analysis for large and small trees pooled, and Swiss stone pine and European larch separately. $G(w)$ is shown (continuous line), with a 99% Monte Carlo confidence envelope (dashed line). PICE = *P. cembra*; LADE = *L. decidua*.

at almost all distances, whereas larch was never autocorrelated, set aside from height at 5 m (Figure 10(g), and (h)). Unlike large trees, significant age autocorrelation was discernible in small trees only at 2 m for larch and 4 m for pine (Figure 10(i)).

Discussion

Unlike previous studies on Alpine tree-line forests, which were focused on mixed pine–larch woods (Carrer & Urbinati 2001; Motta & Lingua 2005; Lingua et al. 2008), the present study considers a stand clearly dominated by Swiss stone pine. Past disturbance regime, land-use and microclimate conditions seem to have favored Swiss stone pine over European larch in the past. Historically, in grazable Alpine woodlands, pine was generally removed, whereas larch was promoted by landowners because of its lighter crown, suitable for the growth of the herbaceous layer (Garbarino et al. 2011). Nevertheless, age-structure analysis showed that the oldest living trees are pines and almost no larch trees are found dating back to a period prior to the end of the nineteenth century (Figure 3). This suggests that the stand had only marginal

grazing relevance, while timber production might have been important, even though not as intensive as in lower altitude Norway spruce forests of the same valley. In this regard, the circa 20-year-long release–suppression cycles occurring in the early stand history hint at a utilization of the forest with a utilization frequency of the abovementioned length (Figure 4). Therefore, we cannot formulate any hypothesis about the harvest intensity and silvicultural principles used in the eighteenth and nineteenth centuries, but we cannot exclude similarities with selection cutting currently applied in several parts of the Alps. An additional hypothesis that could explain the dominance of Swiss stone pine is that during the last centuries, because of its resistance to weathering, larch timber was largely used for construction all over the Alps (Gambetta et al. 2004). Therefore, local foresters could have preferentially targeted European larch, felling large and mid-sized trees and hence making it impossible to trace the establishment of this species back to the nineteenth century.

Besides historical reasons, the dominance of Swiss stone pine can be explained through ecological processes. For instance, the absence of events that significantly altered

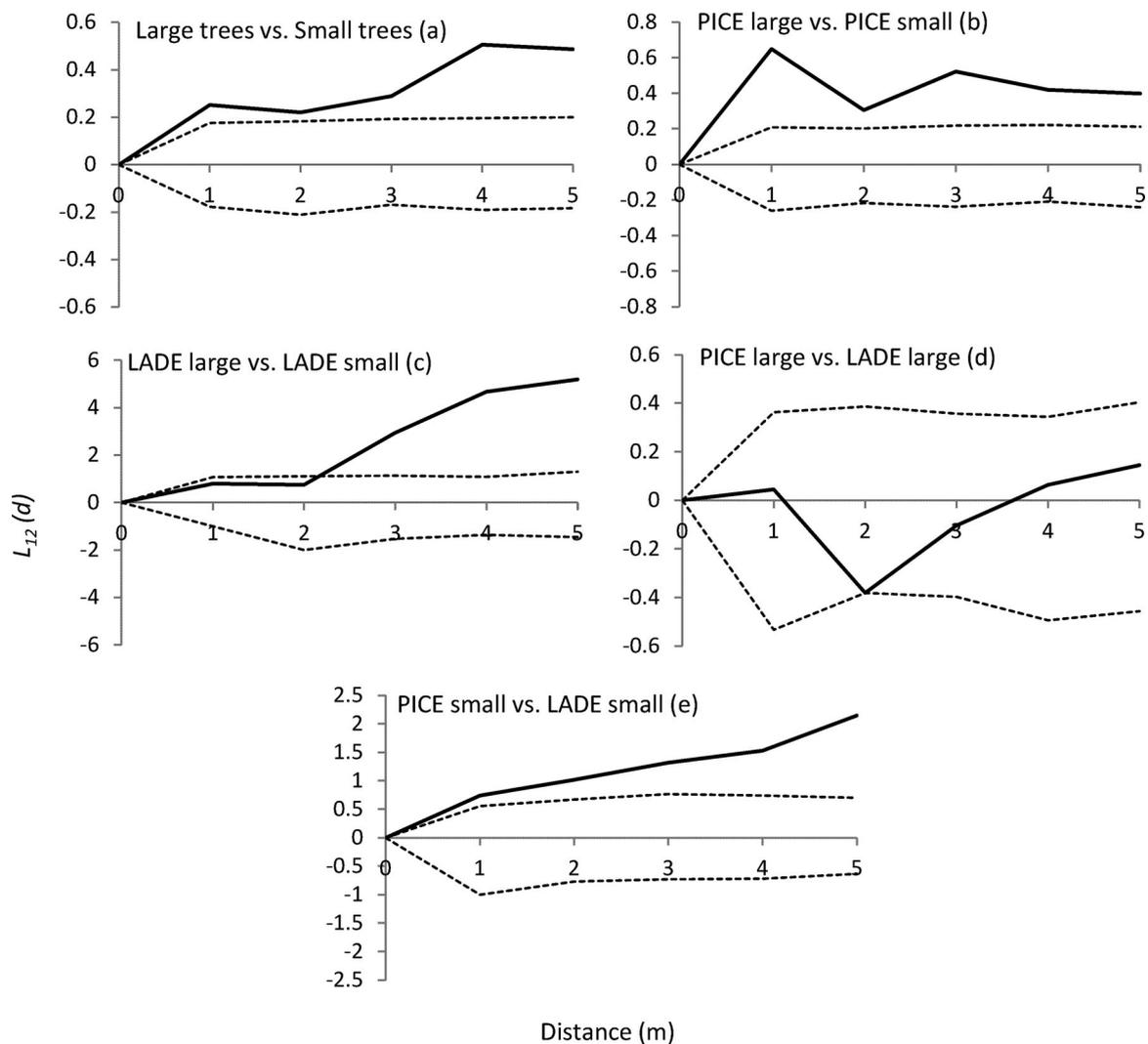


Figure 8. Bivariate point pattern analysis: between large trees and small trees (pooled); intra-specific for Swiss stone pine and European larch separately; interspecific comparing large trees and small trees of both species separately. Square root transformation $L_{12}(d)$ is shown (continuous line), with a 99% Monte Carlo confidence envelope (dashed line). PICE = *P. cembra*; LADE = *L. decidua*.

growth dynamics and species composition could have negatively affected European larch, as it demands high light availability and bare or disturbed soil to germinate, whereas a relatively undisturbed stand with cold aspect, as occurs in this study, allowed Swiss stone pine to establish easily (Li & Yang 2004). In addition, the dense rhododendron understory makes the germination of species with light seeds, such as larch, quite difficult. For these reasons, the dominance of Swiss stone pine in the large trees layer seems to be the result of a synergic combination of ecological and human-induced factors. On the other hand, small trees showed a more balanced species composition and a higher relative frequency of *L. decidua* than the large trees population (Figure 3). This could be due to the higher frequency of small-scale disturbances, for example, more frequent utilizations, that promoted the establishment of this pioneer species, at least until active forest management was carried on. In addition, both European larch and Swiss stone pine were able to endure growth suppression for a very long time, since individuals with dbh < 7.5 cm and ages of 93 and 75 years have, respectively, been sampled. The ability to survive for several

decades under forest canopy conditions is traditionally considered a trait of shade-tolerant species (Lorimer 1983), but these findings highlight how both European larch and Swiss stone pine may exhibit a higher ecological plasticity to this extent, also in light of the harsh environmental conditions experienced in subalpine forests which slow down growth rates.

Establishment of the current large trees cohort was temporally limited to a time span of about 40 years (1885–1925). Moreover, the last harvesting in this area was carried out at the beginning of the 1960s. This was confirmed by a high frequency of tree establishment from 1955 to 1965 (Figure 3). Larch budmoth outbreaks have been reported to occur in cycles 8–10 years apart (Baltensweiler & Fischlin 1988) and to spread eastwards starting from the Upper Engadine valley, following the predominantly westerly winds blowing through the Alpine arc (Baltensweiler & Rubli 1999). Consistently to our study, outbreaks have been registered in the eastern Alps (Büntgen et al. 2009) as well as in other areas of the Alpine region in the early 1950 (Price et al. 2006). In this regard, the most severe growth suppression

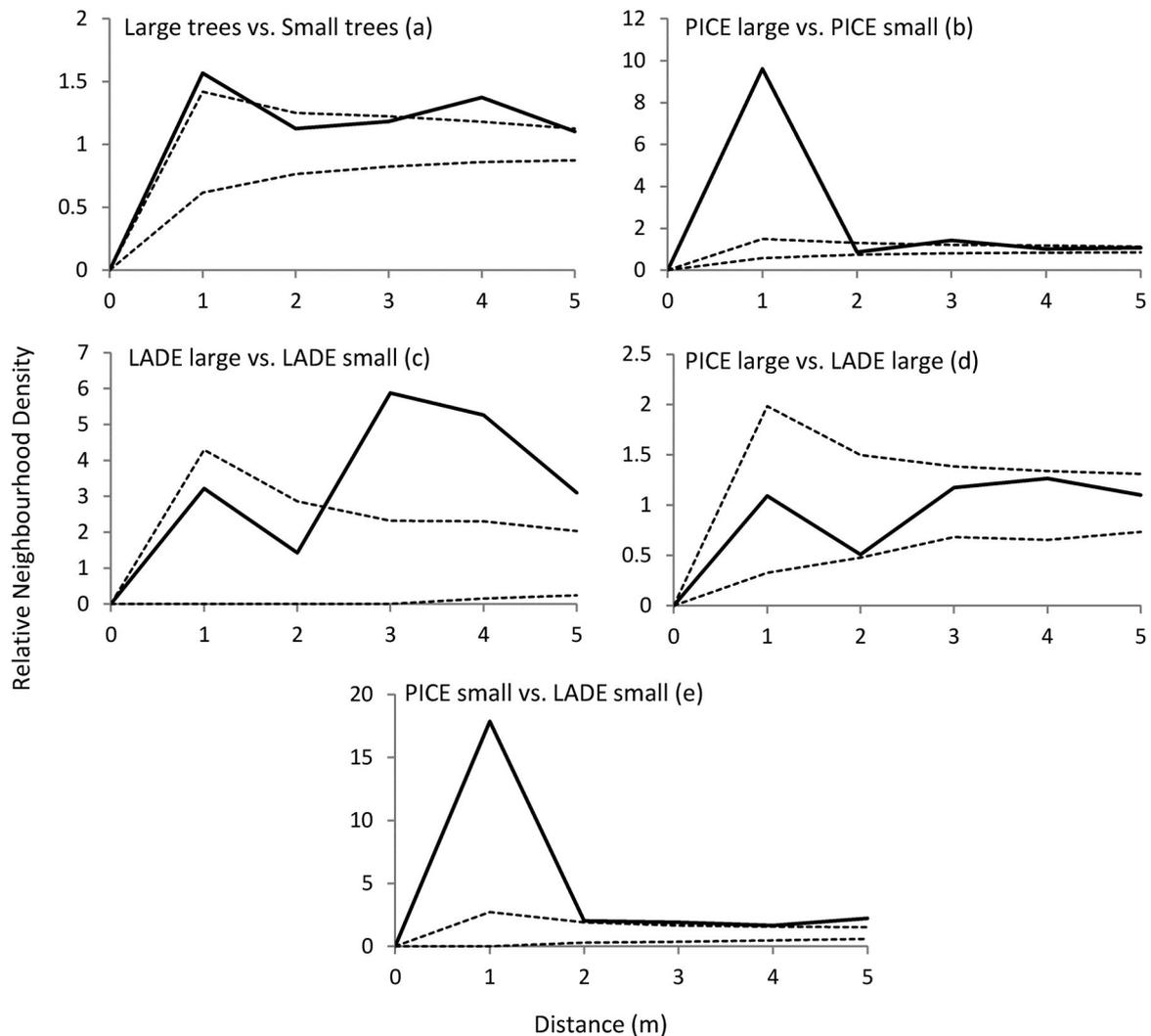


Figure 9. Relative neighborhood density between large trees and small trees (pooled); intra-specific for Swiss stone pine and European larch separately; interspecific comparing large trees and small trees of both species separately. Relative neighborhood density is shown (continuous line), with a 99% Monte Carlo confidence envelope (dashed line). PICE = *P. cembra*; LADE = *L. decidua*.

we could detect was the one of European larch during the 1950 decade and the contemporary release of Swiss stone pine growth (Figure 4). This event could be related to a larch budmoth outbreak. As a consequence of defoliation, larch experienced a strong and sustained reduction in growth, supported also by direct observation of tree-ring and latewood width, with an observed negative pointer year in 1953 followed by a circa 3-year period of reduced yearly and latewood growth (Baltensweiler et al. 2008). Swiss stone pine seems to have benefited from the availability of resources made possible by the suppression of larch, showing a quasi-simultaneous increase in growth. However, the most important finding of this study is the lack of small trees establishment after 1970, coinciding with the cessation of active management that occurred in 1966. Moreover, as pointed out by the GD analysis (Figure 5), the relevance of small and large trees in biomass production changed in the middle of the twentieth century favoring the latter, hinting at a changed contribution of the two classes, likely triggered by the interruption of forest management. Therefore, the absence of small-scale natural perturbations and silvicultural

tending is leading to the reduction of suitable microsites for seed germination and saplings establishment of both species, and consequently, the stand is evolving toward a new phase characterized by a less heterogeneous age-structure.

To this end, although they are pertaining only to the current state of the forest, results about spatial structure reinforce previous considerations about changes in the stand structure. Tree spatial pattern was clumped at all distances in both large and small trees, particularly for distances <3 m (Figures 1, 6 and 7). Aggregated patterns are typical of high-elevation subalpine forests and originate from facilitative processes in the regeneration phase (Brang et al. 2001; Motta & Lingua 2005). Trees tend to establish in groups, thus obtaining mutual ecological advantages against strongly limiting environmental factors (wind, snow, erosion, etc.) (Callaway & Walker 1997). The feeding behavior of the spotted nutcracker is a further cause of clumped spatial pattern for Swiss stone pine. Small trees of all species pooled exhibited a positive spatial association with the large trees population (Figures 8 (a) and 9(a)), confirming the preference for clumped patterns

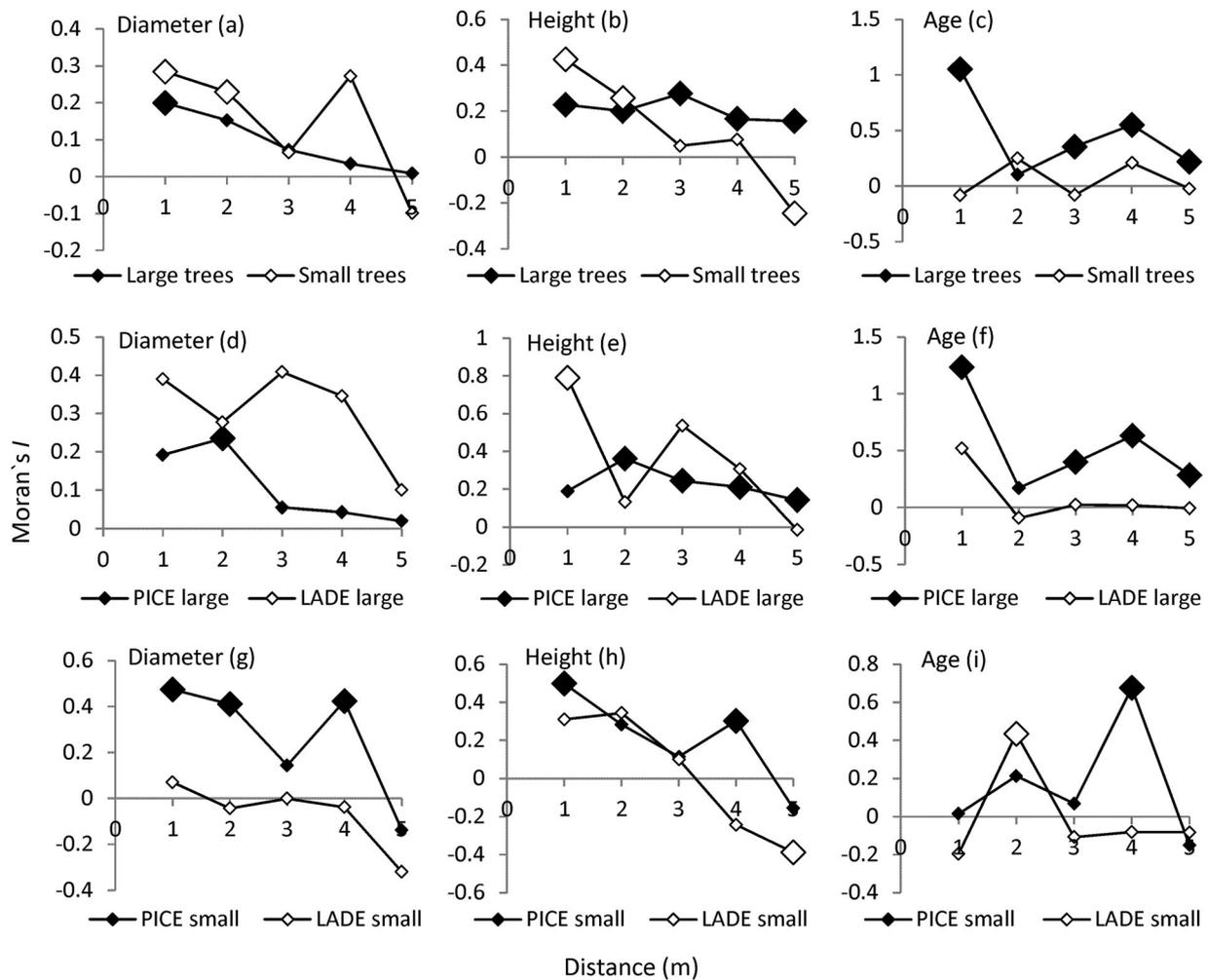


Figure 10. Moran's I correlograms for diameter, height and age of large and small trees (pooled) and Swiss stone pine and European larch separately. Double-sized markers: spatial autocorrelation significant at $P < .05$. PICE = *P. cembra*; LADE = *L. decidua*.

and the facilitative influence of large trees on regeneration processes. However, this outcome seems to depend on the dominance of Swiss stone pine also in the small trees layer, as the two species showed a different behavior when considered one at a time. In fact, while Swiss stone pine exhibited spatial association at short distances (Figures 8(b) and 9(b)), larch regeneration occurred preferentially between 3 and 5 meters from large trees (Figures 8(c) and 9(c)), confirming the light-demanding trait of this species and the preference for canopy gaps. Considering large trees only, Swiss stone pine exhibited a positive autocorrelation for age and height, whereas larch did not show a positive autocorrelation for almost any of the distance lags of all the parameters (Figure 10(d), (e) and (f)). This suggests a different colonization strategy and/or competition experienced by the two species. Pine trees established more quickly after small-scale perturbations (individuals of similar age in a small space) and experienced a stronger competition (individuals of different diameter in a small space) than larch. The general positive age autocorrelation of large trees, especially Swiss stone pine, is contrasted by the absence of age autocorrelation of small trees (Figure 10(i)). This discrepancy suggests that the formation of regeneration nuclei of the dominant species in the past has been faster than today. The long suppression

period that small trees can tolerate is a likely explanation for the different age autocorrelation patterns between the large tree and small tree populations. Nevertheless, the absence of forest management in the last 50 years might have represented a crucial factor in determining the slowdown of the regeneration dynamics.

Conclusions

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

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Disclosure statement

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