

# Spatial structure along an altitudinal gradient in the Italian central Alps suggests competition and facilitation among coniferous species

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## Abstract

**Questions:** What is the structure of the anthropogenic upper forest-grassland ecotone and are there differences in the spatial relationships between the tree species involved?

**Location:** Valfurva Valley, Italian central Alps.

**Methods:** We conducted a spatial distribution and structure analysis in three 1-ha permanent plots along an altitudinal gradient, from the treeline to the sub-alpine forest. We reconstructed the age structure from cores from each individual with diameter > 4 cm at 50 cm height.

**Results:** All tree species and age classes examined had a clumped structure. The cluster tendency was more evident at the treeline where the environmental conditions are more severe. In the sub-alpine forest there was a repulsion between *Pinus cembra* and *Pinus mugo* but at the treeline *P. cembra* was frequently found downslope from *P. mugo*.

**Conclusions:** Although human influence has been the main driving force in shaping the present forest structure, in the last few decades natural dynamics have become the predominant force acting on forest structure and processes, showing a higher magnitude as altitude increases. Our results emphasize the existence of facilitating and interfering mechanisms between different species. *P. cembra* seems to be favoured compared to the other tree species.

**Keywords:** Forest-grassland ecotone; *Larix decidua*; Moran's *I*; *Pinus cembra*; *Pinus mugo*; Ripley's *K*; Spatial interaction.

**Abbreviations:** CSR = Complete spatial randomness; GIS = Geographic information system; LU = Livestock unit; PPA = Point pattern analysis; UTM = Universal transverse mercator.

## Introduction

Forest structure is the result of past dynamics and complex interactions among many processes acting on a stand (Moravie & Audrey 2003; Chen et al. 2004). Tree spatial distribution in a stand depends on several factors, including environmental heterogeneity (Valverde & Silvertown 1997), development stage (Oliver 1981), competition among individuals and populations (Duncan 1991), seed dispersal and regeneration success (Rozas 2003). Distribution is also affected by the disturbance regime (Oliver & Larson 1996), resulting from stochastic processes such as windthrows (Nagel et al. 2006), fire (Harper et al. 2005), insect outbreaks (Camp 1999) and diseases (Dobbertin et al. 2001).

Human disturbance affects forest structure (e.g. Curtin 1995; Pommerening 2002; Motta & Lingua 2005), directly through exploitation and livestock grazing or indirectly by altering natural processes. This is particularly evident at the upper treeline in the Alps (Paulsen & Körner 2001; Erschbamer et al. 2003; Motta et al. 2006a), where forest distribution and limits are strongly related to human land use over past millennia. Forest structure and composition were simplified (e.g. uneven aged mixed stands transformed into even aged pure stands) according to human needs (Motta & Garbarino 2003). The treeline was lowered because of livestock grazing (Cairns & Moen 2004) and fire, which was used to maintain alpine meadows free from trees (Carcaillet 1998; Tinner & Theurillat 2003; Ali et al. 2005).

In the Italian Alps it is hard to find a natural treeline due to the extensive use of mountain areas for summer farming (Motta & Nola 2001). In the last few decades, however, a decrease in domestic grazing pressure has occurred throughout the Alps following the widespread abandonment of marginal pastures (Bebi & Baur 2002; Dullinger et al. 2003; Motta et al. 2006a).

Few studies have been conducted on the structure of forest to alpine meadow ecotones in the Alps (Motta &

Nola 2001). How these high-altitude ecosystems will react in the long term to current environmental changes, both anthropogenic and natural, is still uncertain (Kräuchi et al. 2000). Moreover, because upper treeline ecotones were extensively human-influenced in the Alps, it is particularly important to understand the structural changes of these formerly artificial ecotones as a result of (mainly) changing land use. The present structure may influence future changes (Holtmeier & Broll 2005). Through studying tree spatial patterns we may better understand the environmental processes in treeline ecotones (Camarero et al. 2000; Chen et al. 2004), including possible future responses to global change (Camarero & Gutierrez 1999).

When analysing forest structure, it is not only important to investigate overall tree spatial patterns, but also to examine the spatial interactions between different co-occurring species in order to fully understand plant community organization (Baumeister & Callaway 2006) and biological diversity (Durrett & Levin 1998). Interaction between different species can be both facilitative and competitive, and can shift from facilitation to competition in a stress gradient (Callaway et al. 2002). Recently, species interactions in a stress gradient have been widely discussed (Maestre & Cortina 2004; Körner 2003, 2004; Lortie et al. 2004; Maestre et al. 2006; Lortie & Callaway 2006). The gradient can be geographical (i.e. when limitations change with elevation) or temporal (i.e. when conditions change during a growth season) (Tielbörger & Kadmon 2000; Kikvidze et al. 2006). The facilitative or competitive interactions can be both direct and indirect (Pages & Michalet 2003; Pages et al. 2003).

The aims of the study were thus: (1) to assess the actual structure of forest stands along an altitudinal gradient, (2) to analyse the establishment dynamics of the stands, (3) to analyse the species spatial interactions and (4) to understand the ongoing processes and dynamics.

## Material and Methods

### Study area

The study was conducted in the upper Valtellina Valley in Stelvio National Park, located in the Italian central Alps (10°25'13" E; 46°26'16" N). Altitudes ranged from 2150 to 2450 m a.s.l., and the aspect was mainly north-east. The mean annual rainfall (period 1921–1990) varies between 860 mm at S. Caterina di Valfurva (1740 m a.s.l.), 5 km from the study site, and 737 mm at Bormio (1225 m a.s.l.), 7 km from the study site. The mean annual temperature at Bormio is 2.2 °C (1921–1990). The forest is a *Pinus cembra* stand with *Larix decidua*, *Picea abies* and *Pinus mugo*. The forest soils are podzols with a silicate bedrock.

### Field work and sampling

We established three 1 ha (100 m × 100 m) permanent plots along an altitudinal gradient: one in the treeline ecotone, one immediately below the timberline and one inside the sub-alpine forest.

In order to identify the different zones, we defined the tree limit as the highest location of individuals > 2 m tall (Holtmeier 2003), while the closed forest was identified by a canopy cover > 30%. The treeline ecotone was considered as the transitional zone between the closed forest and the upper tree limit, while the timberline was defined as the upper limit of the closed forest.

All trees (individuals with a diameter at 50 cm height ≥ 4 cm), snags (standing dead trees with a diameter at 50 cm height ≥ 10 cm), logs (downed, dead wood with a diameter ≥ 10 cm) and stumps (cut-surface with diameter ≥ 10 cm) were identified, labelled with numbered plastic tags, mapped with a total station and georeferenced in UTM (universal transverse mercator) co-ordinates system using a GPS with metric precision. For each tree the following parameters were recorded: species, diameter at 50 cm height, diameter at 1.30 m height (DBH), total height, height of the lowest living branches (upslope and downslope), and four radii of the vertical crown projection along the two directions marked by the plot axes (to the nearest 0.1 m). To be able to study the age structure, an increment core was taken upslope at 50 cm height from each tree. In the laboratory, all the cores were fixed to wooden supports and sanded to a high polish for annual tree-ring counts. When the samples did not reach the pith, we estimated the pith location using the method of Motta & Nola (2001). Individuals with rotten cores and those for which it was not possible to estimate the number of missing rings to the pith were not considered for further analyses. The estimated age reported for all trees is the age at 50 cm height above the root collar. Since we did not crossdate the cores due to the young age of most trees and because of the potential errors in estimating missing rings, the age structure was constructed for ten year classes (Payette et al. 1990).

Regeneration (trees with height ≥ 10 cm and diameter at 50 cm < 4 cm) was mapped and measured in a 2000 m<sup>2</sup> transect (20 m × 100 m) located inside the plot, parallel to the slope contour.

### Land use

The treeline plot is classified as pasture in the management plans of the municipality of Bormio, the owner of the land. Livestock pressure in rangelands decreased during the last half of the 20th century, from 420 sheep in 1950: 0.3 LU.ha<sup>-1</sup>.a<sup>-1</sup> (LU = Livestock Unit) to 60 sheep and 24 cows in 1996: 0.17 LU.ha<sup>-1</sup>.a<sup>-1</sup>, and

finally to 13 cows, 4 horses and 78 sheep in 2005: 0.07 LU.ha<sup>-1</sup>.a<sup>-1</sup>.

The other two plots (timberline and sub-alpine forest) are both classified as forest and belong to the same management unit. The exploitation is currently very limited (0.12 % of timber volume per year in the last 20 years) and concentrated in the lower part of the management unit, where the sub-alpine forest plot is located. Selective cutting is applied, with the main aim of providing firewood for the inhabitants with rights on public forest land.

### *Spatial analysis*

Point pattern analysis (PPA) techniques were applied using tree-stem mapped data (Moeur 1993) to characterize the tree spatial patterns within the plots. These techniques are based on the use of all point-to-point distances, corresponding in our case to tree-to-tree distances, with the main aim of describing two-dimensional distribution patterns (Haase 1995). To determine whether the distributions of trees, single species or classes of trees were random, regular or clumped, the univariate Ripley's  $K(t)$  function was used (Ripley 1977). Ripley's  $K(t)$  is a second order analysis that provides information at multiple scales, comparing distance of all pairs of points.

Ripley's  $K(t)$  was computed with the formula:

$$K(t) = \frac{1}{n^2} A \sum_{i=1}^n \sum_{j=1}^n \frac{I_i(\delta_{ij})}{w_{ij}}, \text{ for } i \neq j \quad (1)$$

where  $A$  is the plot area with  $n$  trees,  $I_i$  is a counter variable which is set to 1 if the distance  $\delta_{ij}$  between tree  $i$  and tree  $j$  is less or equal to  $t$  (corresponding to the lag distance) and  $w_{ij}$  is a weighting factor to correct for the edge effects (Haase 1995).

We used the following square root transformation  $L(t)$  that makes the  $K(t)$  function linear, stabilizes its variance and has an expected value of approximately zero under the Poisson assumption (Diggle 1983, Moeur 1993):

$$L(t) = \sqrt{\frac{K(t)}{\pi}} - t \quad (2)$$

Monte Carlo simulations were used to assess the significance of deviation from the complete spatial randomness (CSR) assumption, generating 10000 random spatial patterns that provided a 99% confidence envelope (Manly 1997). The spatial pattern is defined as clumped, random or regular (hyperdispersed) if the  $L(t)$  values are greater than, equal to or lower than the confidence envelopes, respectively. The analysis was applied in each plot on the overall tree population, single species, young trees (< 100 years) and old trees (> 100 years).

We used AutoCAD 2004 (Autodesk Inc., San Rafael, CA, US) to reconstruct each single tree canopy using the

four radii collected. The resulting layers, representing the canopy cover of each plot, were then exported into a GIS (geographic information system).

The typical structure of the sub-alpine forest is characterized by small groups of trees (often described by the German term 'Rotten'; see Zeller 1993), we identified groups by selecting all trees with an overlapping surface between their crowns. We then extracted the co-ordinates of the centroid of each group to assess their spatial structure.

To investigate the relationships between two point patterns we examined bivariate spatial interactions using the  $K_{12}(t)$  function, which is a generalisation of  $K(t)$  for a bivariate point process (Andersen 1992; Upton & Fingleton 1985; Moeur 1993). The  $K_{12}(t)$  function was computed as follows:

$$K_{ij} = (n_1 n_2)^{-1} A \sum_{i=1}^{n_1} \sum_{j=1}^{n_2} w_{ij}^{-1} I_i(\delta_{ij}) \quad (4)$$

and then

$$K_{12}(t) = \frac{n_2 K_{12}(t) + n_1 K_{21}(t)}{n_1 + n_2} \quad (5)$$

where  $n_1$  and  $n_2$  correspond to the number of events in the two classes of points.

A square root transformation (Lotwick & Silverman 1982; Moeur 1993) was again applied, according to the following formula:

$$L_{12}(t) = \sqrt{\frac{K_{12}(t)}{\pi}} - t \quad (6)$$

To test the significance of deviation from the null hypothesis of spatial independence, we calculated the 99% confidence intervals from toroidal shifts of one class of trees with respect to another. Values of  $L_{12}(t)$  greater than, equal to or lower than the 99% confidence envelopes reveal positive association (attraction), spatial independence and significant negative association (repulsion), respectively, between the two analysed classes. Attraction is defined as a tendency for trees of two groups to be closer than what would occur if they were independently distributed, while repulsion is defined as a tendency between trees belonging to two groups to be farther apart than what would occur if they were independently distributed (Peterson & Squiers 1995). The analyses were only done for classes with more than 15 trees (Camarero et al. 2000). When significant interactions were detected, the bivariate pattern analysis was also computed considering cardinal directions (Haase 2001) to reveal eventual anisotropic relationships. We performed the  $K(t)$  and  $K_{12}(t)$  analyses starting from 1 m to 50 m, applying a 1 m lag distance, not exceeding half the length of the 100m plot dimension, to limit the influence of the margin effects (Haase 1995). Univariate and bivariate indices were calculated using the software

SPPA 2.0 (Haase 2001).

To infer the existence of competition or facilitation processes, the analysis was conducted in each plot between the different species, and between young (<100 years) and old trees (>100 years).

To evaluate whether spatial patterns were correlated to tree age, we computed Moran's  $I$  coefficient (Moran 1950; Legendre & Legendre 1998) according to the following formula:

$$I(d) = \frac{N \sum_i \sum_j w_{ij} (x_i - \bar{x})(x_j - \bar{x})}{W \sum_i (x_i - \bar{x})^2}, \text{ for } i \neq j \quad (7)$$

where  $I(d)$  is the value of Moran's coefficient for a distance class  $d$ ,  $N$  is the total number of mapped tree locations,  $x_i$  ( $i=1, \dots, N$ ) is the age of the tree,  $w_{ij}$  is a counter variable which is set to 1 if the distance between points  $i$  and  $j$  is within  $d$ , otherwise equals to 0, and  $W = \sum w_{ij}$ .

We analysed neighbouring points using 1 m distance classes from 1 m up to 50 m, consistent with Ripley's  $K$  analysis.

A correlogram, where autocorrelation values are plotted in the ordinate against the distance ( $d$ ) among the points (abscissa), was drawn for each plot. The global significance of the correlogram was tested at the  $\alpha' = \alpha/\nu$  ( $\nu$  = number of tests) significance level according to the Bonferroni method (Legendre & Fortin 1989).

The significance of deviations from what was expected in each distance class was tested by calculating the variance of  $I(d)$  under the null hypothesis of randomisation, by means of standard normal deviates  $z(d)$ .

Distance classes that contained less than 30 neighbouring points were excluded from the analysis because the assumption of normality could be invalid for small groups (Duncan & Stewart 1991). Spatial autocorrelation was computed for tree age with the Excel add-in Rookcase (Sawada 1999).

## Results

### Stand composition and characteristics

As expected, there was reduction in tree density with increasing altitude (Table 1). In the treeline plot, *Pinus cembra* was the most frequent species, with 79.7% of the individuals. The other species present were *Larix decidua* (10.8 %) and *P. mugo* (8.9%), while only one individual of *P. abies* was found. Deadwood was almost absent: only 2 stumps, 1 snag and 1 log were found.

In the timberline plot, *P. cembra* was again the most frequent species (84.8%), followed by *P. abies* (6.1%), *P. mugo* (6.1%) and *L. decidua* (3.0%). The total basal area was 11.01 m<sup>2</sup>.ha<sup>-1</sup>, of which 98.2% was *P. cembra*. The deadwood volume was 5.64 m<sup>3</sup>.ha<sup>-1</sup>, mainly comprised logs (density = 21/ha) and snags (6/ha).

In the sub-alpine forest plot, 53.4% of the individuals were *P. cembra* and accounted for 76.4% of the basal area. *L. decidua* and *P. abies* made up 33.1% and 9.6% of the trees, and 18.4% and 3.9% of the basal area, respectively, while *P. mugo* was less abundant (3.9% of individuals; 1.28% of basal area). The amount of deadwood was 2.42 m<sup>3</sup>.ha<sup>-1</sup>, mainly composed of stumps (38/ha) and less by logs (11/ha) and snags (8/ha).

### Age structure

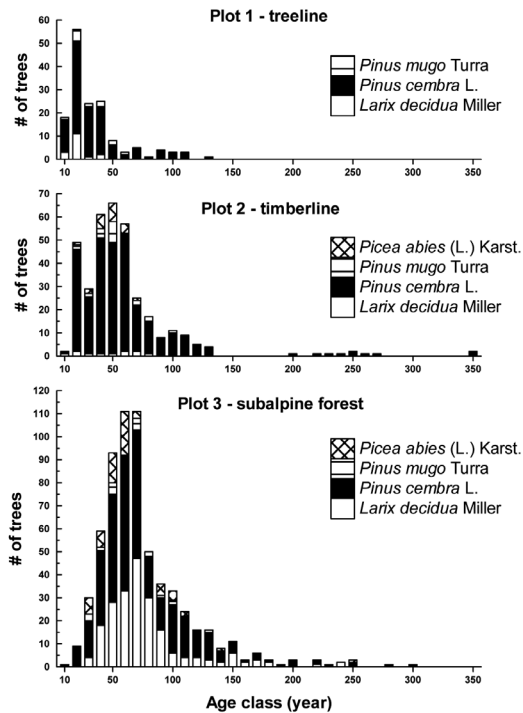
We successfully determined the age at 50 cm height for 94% of the trees. The age structure varied between the plots (Fig. 1). In the treeline plot, 81% of the trees were < 45 years (median = 25, 5th percentile = 13; 95th percentile = 94) and the oldest tree was a *P. cembra* that was 130 years old.

At the timberline plot, the most frequent age classes were from 40 to 60 years (median = 50, 5th percentile = 18; 95th percentile = 115). *P. cembra* trees were the

**Table 1.** Main topographic and stand characteristics of the sampled plots.

	Treeline plot	Timberline plot	Sub-alpine forest plot
Mean altitude (m a.s.l.)	2350	2250	2190
Aspect	NE	NE	NE
Mean slope (°)	27	21	21
Number of trees (n/ha)	158	374	674
Species composition of trees (n/ha)	<i>Pinus cembra</i> (125) <i>Larix decidua</i> (17) <i>Pinus mugo</i> (15) <i>Picea abies</i> (1)	<i>Pinus cembra</i> (317) <i>Larix decidua</i> (11) <i>Pinus mugo</i> (23) <i>Picea abies</i> (23)	<i>Pinus cembra</i> (360) <i>Larix decidua</i> (223) <i>Pinus mugo</i> (26) <i>Picea abies</i> (65)
Basal area total (m <sup>2</sup> .ha <sup>-1</sup> )	0.99	11.01	24.39
Quadratic mean diameter (cm)	9.34	19.66	21.55
Number of saplings (n/ha)	980	6350	9015
Species composition of saplings (%)	<i>Pinus cembra</i> (97.0) <i>Larix decidua</i> (1.0) <i>Pinus mugo</i> (1.0) <i>Picea abies</i> (0.7)	<i>Pinus cembra</i> (99.3) <i>Picea abies</i> (1.0)	<i>Pinus cembra</i> (97.6) <i>Larix decidua</i> (1.7) <i>Pinus mugo</i> (0.3) <i>Picea abies</i> (0.4)
Deadwood (m <sup>3</sup> .ha <sup>-1</sup> )	0.04	5.64	2.42





**Fig. 1.** Age structure of trees in the treeline, timberline and sub-alpine forest plots.

only individuals over 80 years old, where the oldest tree was 352 years. There was evidence of tree establishment in recent decades, although most trees in the ten year class had diameters at 50 cm height < 4 cm and were not recorded. There was also a lack of individuals between the 130 and 200 year classes.

In the sub-alpine forest plot, the age class distribution was significantly skewed towards the older age classes (median = 65 years; 5th percentile = 33; 95th percentile = 148). In this plot, all the species were represented in almost all age classes, except for the < 20 year classes, where only *P. cembra* was found. The oldest tree was a 302 year old *P. cembra*.

### Spatial patterns

All trees, tree species and age classes were significantly clumped ( $P < 0.01$ ) in all plots at short distances - up to 20 m. Only *P. mugo* showed a slightly different pattern (Fig. 2).

The group distribution was clumped at the treeline (5-21 m;  $P < 0.01$ ) and was more regular at short distances both at the timberline (1-2 and 4-5 m) and inside the sub-alpine forest (2-6 m).

In the treeline plot, positive spatial association (attraction) was found between *P. cembra* and *L. decidua* up to 11 m and between *P. cembra* and *P. mugo* at 3 m and > 9 m (Fig. 3).

We also found significant spatial attraction between *P. cembra* and *P. mugo* in the timberline plot. A significant positive interaction was found between young trees (less than 100 years old) and trees older than 100 years up to 14 m (Fig. 3).

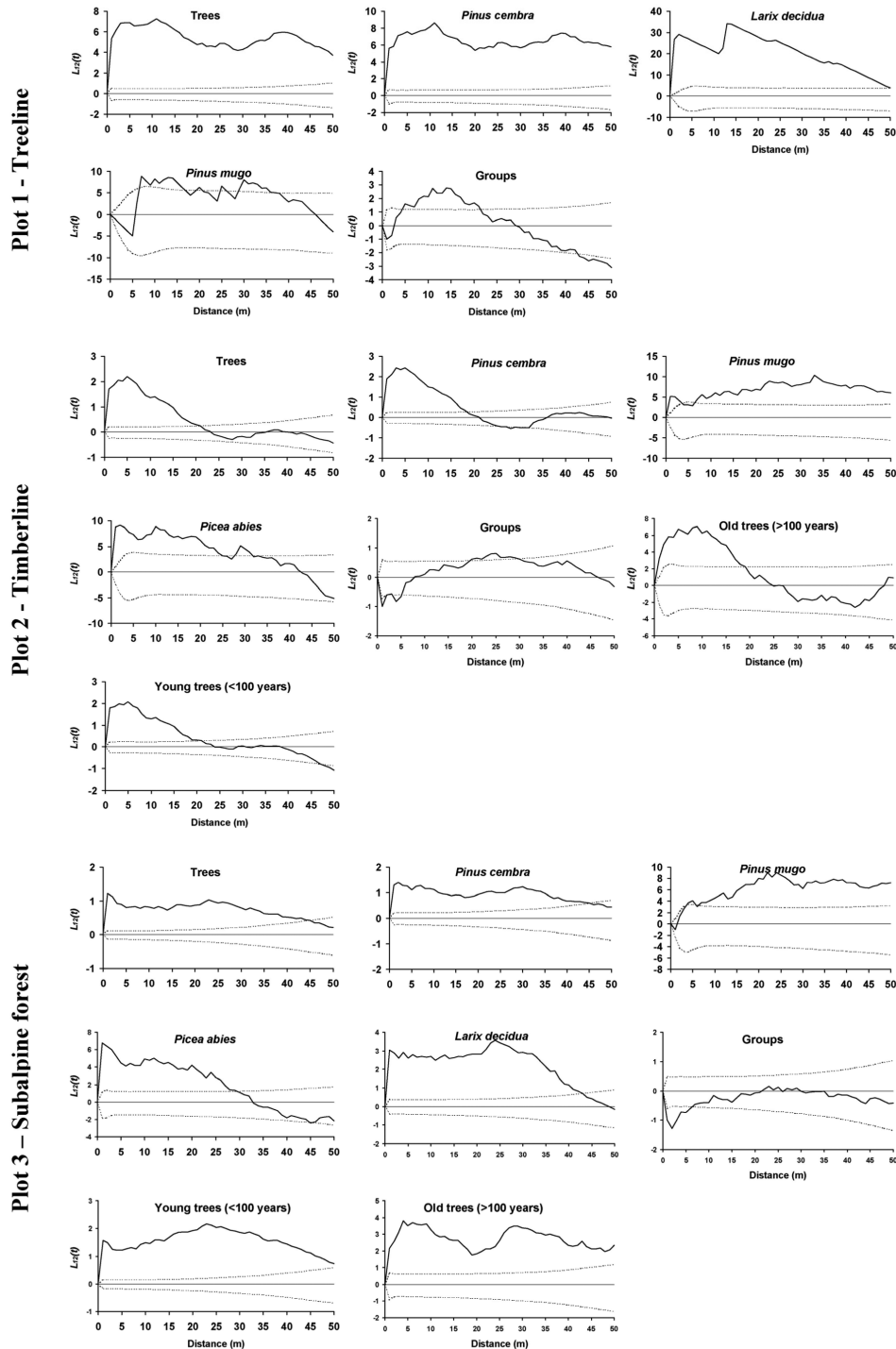
In the sub-alpine forest plot an opposite relationship was found: the two analysed age-classes showed repulsion at > 4 m. Attraction was also found between *P. cembra* and *L. decidua* (up to 3 m) and between *L. decidua* and *P. abies* (over 2 m). Inside the forest, *P. cembra* displayed a negative interaction with *P. mugo*.

The *P. cembra* - *P. mugo* relationship was the only one that showed clear, significant anisotropic interactions, displaying different patterns according to direction (Fig. 4). In the treeline plot *P. cembra* revealed aggregation with *P. mugo* downslope and a slight repulsion upslope (10 m). Since in this plot, the mean crown diameter of *P. mugo* was 4.5 m (radius < 3 m), attraction begins only from the edge of the canopy, and not inside it. In the timberline plot attraction was only found at short distances, while in the forest plot a negative interaction was detected, which was isotropic.

All Moran's  $I$  spatial correlograms were globally significant at  $P < 0.05$  (Bonferroni corrected test), revealing the existence of an age spatial structure (Fig. 5). Only significant positive autocorrelation values occurred at the treeline plot for the overall tree population both at smaller and at longer distances, while for *P. cembra* negative values were found at 13, 25 and 33 m, suggesting the presence of older trees within patches of younger trees. The positive values for the smaller distances are very high, more than the typical range (-1 to +1), that occasionally may be obtained (Legendre & Legendre 1998). In the timberline plot negative significant values for *P. cembra* were found at short distance (6m). Inside the forest significant negative autocorrelation values were found at long distances, revealing the presence of larger patches with similar age.

### Discussion

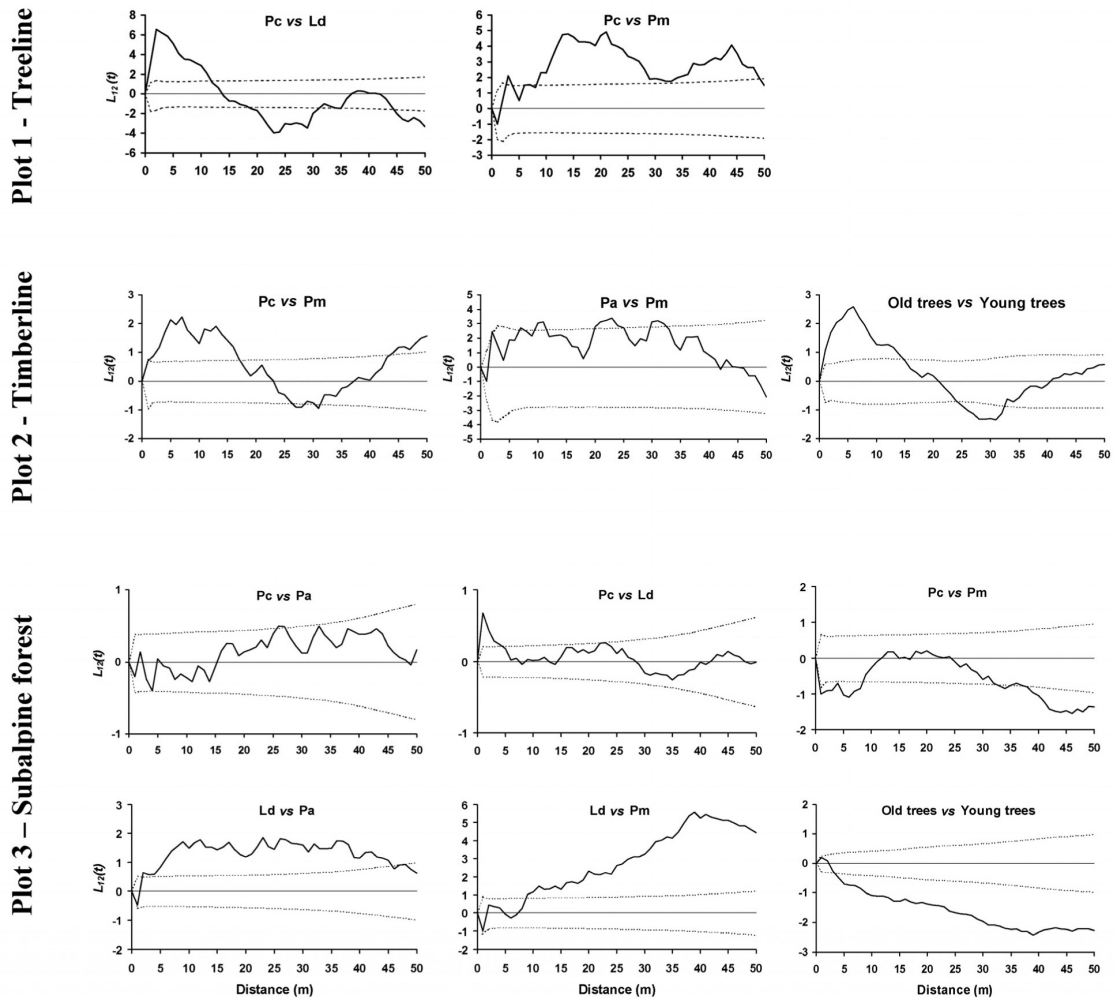
The establishment of the present tree population at the treeline began ca. 135 years ago and the almost total lack of stumps, decaying logs or root mounds in the plot suggests the absence of a tree population at that time. At the timberline, and inside the sub-alpine forest, the main establishment period also started in the second half of the 1800s, but older trees belonging to the former pastured woodlands were present. Holtmeier (2003) underlines that in the European Alps, timberline forest stands are characterized by two wide age classes, with some trees that are hundreds of years older than the other trees. This much older component is a relict of the previous forest



**Fig. 2.** Ripley's  $K(t)$  for the overall trees, tree species, groups and age classes in the three plots. Dashed lines are the confidence envelopes (99%). The square root transformation,  $L(t)$ , was applied. Only graphs with statistically significant difference from the CSR (complete spatial randomness) hypothesis are shown.

removed by human activities, made up by scattered trees that could not influence the pasture negatively. When human impact and livestock grazing decreased or ceased, a new tree population established around the old trees. The

dynamics of tree establishment in our area seem to be dominated by an in-filling process, with trees establishing in the open spaces between scattered individuals or patches of existing trees, consistent with other observations made



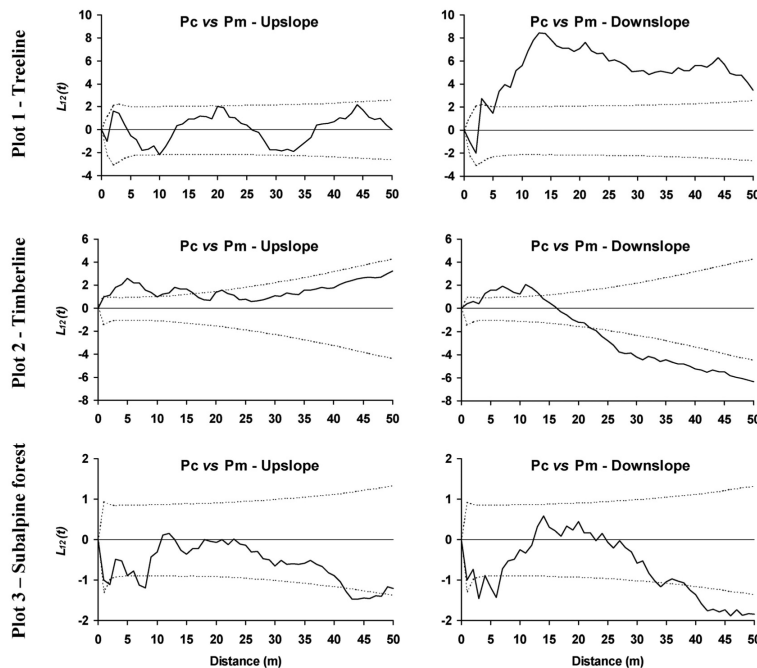
**Fig. 3.** Ripley's  $K_{12}(t)$  for tree species and age classes in the three plots (Pc = *Pinus cembra*; Ld = *Larix decidua*; Pa = *Picea abies*; Pm = *Pinus mugo*). Dashed lines are the confidence envelopes (99%). The square root transformation,  $L_{12}(t)$ , was applied.

in forest-pasture ecotones (Slatyer & Noble 1992; Manning et al. 2007; Weisberg et al. 2007). This process is evident in the upper part of the studied gradient, where young trees occur close to the older ones, both because previously established trees can improve site conditions and because they already occupy the most suitable sites. Inside the forest, segregation among these age classes is probably due to silvicultural management. With the removal of mature trees, free space is available for a new generation of trees, causing repulsion between old and young individuals.

The larger amount of deadwood at the timberline suggests a low intensity of human disturbance, especially compared to the forest, where snag and log volume was reduced due to silvicultural operations (Motta et al. 2006b). Instead, stumps are the only type of deadwood that are always present in both human affected and natural forest ecosystems. The presence of recently cut, slightly decayed stumps in the sub-alpine forest confirms the

present exploitation of forest resources by man.

Regeneration is abundant at all three altitudes. *L. decidua* is lacking in the regeneration layer within all the plots, whereas *P. cembra* is abundant, regardless of the main cover. *L. decidua* is a shade intolerant tree, whose recruitment is negatively sensitive to thick litter layers. Consequently, it depends on disturbances that expose the mineral soil for establishment (Risch et al. 2003). In the past, such disturbances were provided by human activities, directly through logging operations in the forest or indirectly by grazing. Livestock trampling can expose mineral soil (Mast et al. 1997), favouring the establishment of wind-dispersed seeds. The decreased livestock grazing in the study area over the last 55 years ( $-77\% \text{ LU} \cdot \text{ha}^{-1} \cdot \text{a}^{-1}$ ) could have caused a decline in *L. decidua* establishment on abandoned alpine pastures. On the contrary, the establishment of *P. cembra* seedlings, which is mainly related to European nutcracker (*Nucifraga caryocatactes*) hoarding activity, is currently abundant,



**Fig. 4.** Anisotropic Ripley's  $K_{12}(t)$  for *Pinus cembra* and *Pinus mugo*. Dashed lines are the confidence envelopes (99%). The square root transformation,  $L_{12}(t)$ , was applied.

especially at higher altitudes. This bird related dispersal is more evident above the timberline, consistent with the corvid behaviour (Holtmeier 2003), resulting in the highest age spatial autocorrelation values in the short distances among *P. cembra* inside the treeline plot. Furthermore, it should be noted that the number of *N. caryocatactes* in the Italian Alps has probably increased in the last 30 years as it was legally protected in the 1970s. Prior to the 1970s, the bird was considered a pest and could be hunted all year round (Motta & Lingua 2005).

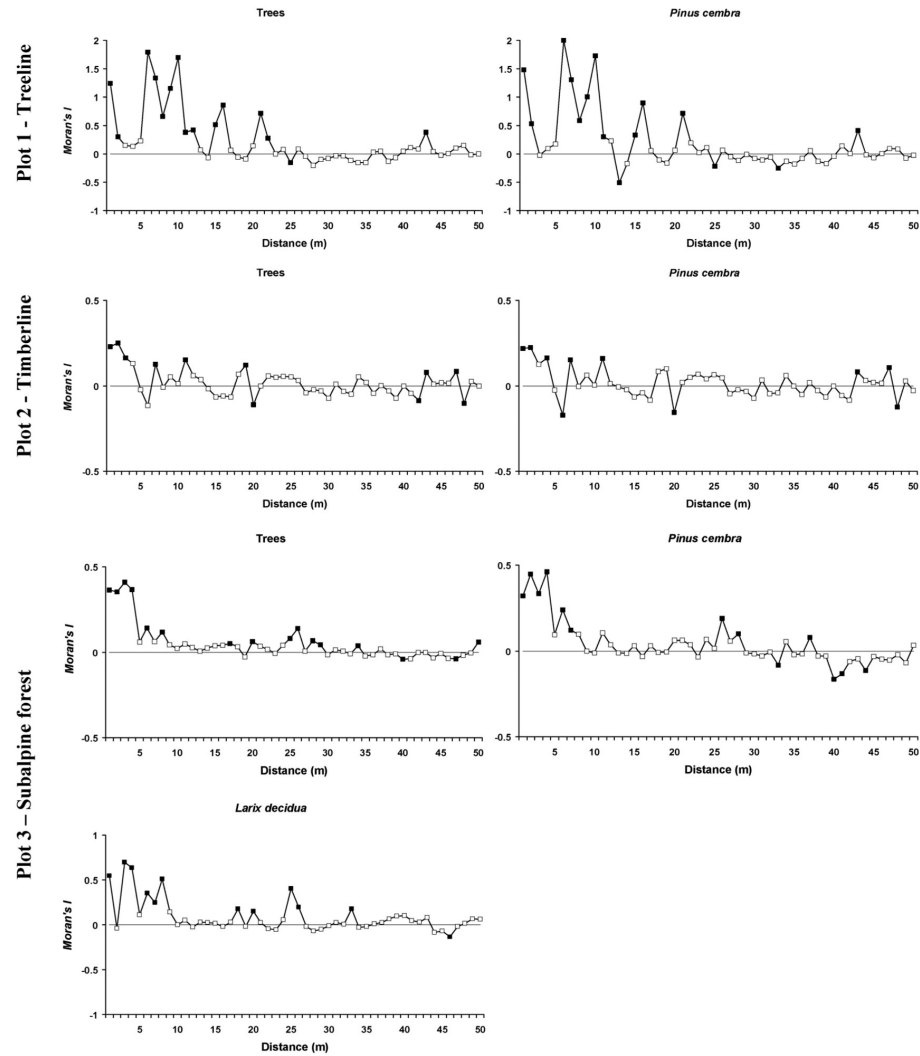
The presence of abundant *P. cembra* regeneration, together with the absence of *L. decidua* regeneration, could eventually lead to a secondary successional pathway characterized by replacement of *L. decidua* with *P. cembra* (Motta & Lingua 2005). In contrast, some studies have shown that a possible increase in air temperature could give *L. decidua* a competitive advantage over *P. cembra* and *P. abies* (Anfodillo et al. 1998; Carrer et al. 1999). However, the current successional pathway began after human influences ceased, or at least decreased, and this could probably confound the eventual effects of climatic change.

Since high-elevation forests are typically dominated by long-lived species (200–500 years or more), with long reproductive life spans (Lloyd 1997), the described successional dynamics are likely to occur over a long period. In fact, in communities characterized by long-lived dominant species, the effects of changing conditions on the forest structure often occur with a substantial time delay (Watt 1947; Von Holle et al. 2003).

The tendency to form a clustered horizontal structure was found within all the plots and for all the species. This is the typical behaviour within the sub-alpine altitudinal belt. The groups are generally mixed, as no repulsion was found between different species. The importance of the association between trees in the sub-alpine belt is well known (Zeller 1993; Schönenberger 2000; Bebi et al. 2001). Tree patches can improve microsite conditions in treeline ecotones (affecting snow thickness, soil characteristics and microclimate), offer physical support, reduce soil compaction and erosion and create protection from herbivores (Smit et al. 2005). This association often suggests some nurse effects of the neighbouring plants, through direct or indirect contributions to the performance of the saplings, by providing shelter from extreme temperatures and high irradiance and improving water and nutrient availability, aided by a below-ground mycorrhizal component (Hasselquist et al. 2005).

The spatial distribution of tree clusters reveals different patterns along the gradient. At the treeline the groups show aggregation, avoiding the less favourable sites, whereas there is a more regular pattern at lower elevations. Inside the forest, the groups tend to occupy all the available space. The forest effect acts to improve microclimate conditions and reduces limitations in the potential establishment sites (James et al. 1994) and could, therefore, explain the differences in the groups' spatial patterns, while differences within groups in terms of species and age composition are probably more related to past human interventions.





**Fig. 5.** Moran's  $I(d)$  correlograms for the age of the overall trees and tree species (with more than 30 individuals) in the three plots. ■ = significant autocorrelation values ( $P < 0.05$ ).

Concerning species spatial interactions, the positive relationship between *P. mugo* and *P. cembra* at the treeline and at the timberline confirms that established *krummholz*-like trees can improve environmental conditions favouring the downslope establishment of new individuals (Bekker 2005). In a scattered tree distribution, typical of a treeline ecotone, the high crown density of *krummholz*, as well as their clumped spatial distribution and growth form can provide microenvironments more favourable to establishment than those created by isolated trees (Tranquillini 1979; Hadley & Smith 1987; Camarero et al. 2000). The presence of *krummholz*-like trees and dense and compact *krummholz* mats can enhance snow accumulation and alter snow distribution and accumulation, reducing wind abrasion, needle dehydration and frost damage to vegetation (Tranquillini 1979; Grace & Norton 1990; James et al. 1994; Camarero & Gutierrez 2002). This could be a key factor for tree growth and especially for seedling establishment and survivorship, which may shape future

forest species composition, along with the influence of climatic change (Theurillat & Guisan 2001).

*P. mugo* crowns start closer to the ground compared to the other tree species in the stand and they may have provided more wind shelter. *P. cembra* seedling survival in the sub-alpine belt is strongly influenced by the duration of snow cover, because the species is highly vulnerable to cryophilic parasitic fungi (Senn et al. 1994). Its establishment downslope from *P. mugo* could thus be mostly related to the reduced snow presence downslope from *krummholz* trees.

Several interacting abiotic factors operate together in governing facilitative mechanisms (Baumeister & Callaway 2006). Recently, studies on seedling-canopy tree interactions have demonstrated a shift from facilitation at high altitudes to competition at lower altitudes (Callaway 1998; Callaway et al. 2002; Germino et al. 2002). The highlighted *P. cembra*-*P. mugo* relationship is consistent with this hypothesis. Inside the forest, where the closed

woodland creates better environmental conditions, the two conifer species are in competition for resources, as indicated by the distinct negative spatial interactions. In the harsh conditions outside the forest, *P. cembra* seems to establish preferentially leeward but outside the *P. mugo* crown, while at the timberline an isotropic shelter effect was found. As shown by Haase (2001), in the case of anisotropic spatial distribution, the physical aspects of facilitation predominate. Since the aggregation was detected downslope and outside the crown of *P. mugo*, we can assume that there is a 'shield effect' rather than a 'nurse effect' with regard to *P. cembra*. Improving site conditions for downwind individuals has been suggested by Holtmeier (2003) and Bekker (2005). Baumeister & Callaway (2006) observed a similar situation in the *Pinus flexilis* - *Pseudotsuga menziesii* relationships in a forest-grassland ecotone in Montana (US).

The spatial interaction between *P. mugo* and *P. cembra* provides further evidence of an ongoing dynamics that could, in the long term, favour *P. cembra* over *L. decidua* in the Alps (Piussi 1994; Risch et al. 2003; Motta & Lingua 2005). The encroachment of grassland and other non-forest habitats by pine *krummholz* reduces the parts of the landscape where *L. decidua* recruits more effectively and grows faster than late successional species. Furthermore, a pronounced negative effect of *Pinus* cover on recruitment and growth of *L. decidua* has been noted in other studies (Dullinger et al. 2005).

Human impact has been the major driving force in shaping the investigated forest ecosystem. Over the last few decades, however, natural dynamics have become more important, mainly as a consequence of the decrease in grazing and forest exploitation. *P. cembra* seems to be favoured in the new conditions, where it is able to compete with other tree species for establishment. Competition and facilitation dynamics between tree species may, therefore, play an important role on the evolution of this formerly human shaped environment and should be investigated in long-term monitoring research.

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