Convergent space–time tree regeneration patterns along an elevation gradient at high altitude in the Alps

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Article info

Article history:
Received 21 February 2013
Received in revised form 16 April 2013
Accepted 17 April 2013

Keywords:
Forest dynamics
Larix decidua
Picea abies
Pinus cembra
Trees spatial pattern

ABSTRACT

In most mountain regions forests growing at high altitude have fundamental ecological roles and other benefits to humans. A key factor affecting the structure and evolution of these forest stands is the spatial and temporal dynamics of natural regeneration. Sound empirical knowledge is therefore important to support management prescriptions aimed at guaranteeing the space and time continuity of the forest cover through proper natural regeneration.

By means of a spatial distribution and structure analysis in three 1-ha permanent plots along an elevation gradient at high altitude, we assessed the small-scale processes and interaction between canopy cover and regeneration establishment in a temperature limited environment. Particular attention has been paid to the interaction among three tree species (Larix decidua, Picea abies and Pinus cembra) and their specific regeneration behaviour.

The spatial pattern of regeneration is very similar in all the tree stands in spite of the increasingly limiting environmental conditions with elevation and the significant differences at species and stand level. On the contrary, the small-clustered organization of individuals, typical of a high elevation area, only becomes visible at the highest sites considering the age spatial structure.

Significant differences in stand structure, composition and history in addition to differences in species autoecology, mode and strategy of seed dispersal and growth are not enough to result in parallel differences in the distribution patterns of regeneration. Given that successful regeneration is one of the most significant bottlenecks for high elevation forest maintenance, any management approach should take this into account in order to better sustain the future stand structure and dynamics with likely future changes in environmental conditions.

1. Introduction

In most mountain regions high elevation forests play a fundamental ecological role and provide many benefits to humans. For example, in the Alps the protective function of high elevation forests has always been recognized as essential although human impact on these forests has been high for centuries (Carcaillet and Brun, 2000). Indeed, natural disturbance regimes have very often been overwhelmed by anthropogenic activities aimed mainly at timber production and livestock grazing; this results in a significant reduction of the forested area and in a modification of the composition, structure and spatial patterns of remaining forests (Motta and Lingua, 2005).

The ecological and social benefits from these ecosystems may only remain stable through natural regeneration that can guarantee the continuity of wide forest cover in both space and time (Dorren et al., 2004). A better understanding of the spatial and temporal dynamics of natural regeneration, and the conditions that may promote it, is therefore of great importance not only from a scientific perspective but also for the sustainability of management (Hofgaard, 1993a). The pattern of seedling recruitment is the result of a broad array of factors, including abundance and location of parent trees, yearly variation in seed production, type and distribution of seedbeds, microclimate, pathogens and seedling predators (Brang, 1998; Gray and Spies, 1998; Greene et al., 1999; Kozlowski, 2002). Stand structure exerts a considerable influence on these factors, e.g., through light availability in the understory, soil temperature and nutrient mineralization, which regulate seed germination, initial seedling development, and competing vegetation (Canham et al., 1990; Coates, 2002). Considering the broad spatial and temporal scales usually associated with forest dynamics, the regeneration patterns and processes may be interpreted more successfully from long-term observations. Indeed, only with a systematic assessment of how processes and structures vary in space and time will be possible to develop realistic and reliable models concerning, for example, future stand development under strongly changing conditions.

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http://dx.doi.org/10.1016/j.foreco.2013.04.025
management and climatic scenarios (Freligh, 2002; Holtmeier, 2009; Rasche et al., 2011). In this perspective, long-term research plots are becoming an increasingly valuable tool to analyze natural dynamics in forests where there have been past human disturbances mixed with natural ones (Carrer and Urbanati, 2001; Motta and Edouard, 2005; Lingua et al., 2008; Navarro-Cerrillo et al., 2013). Spatial analysis could help in this task mainly in those ecosystems, such as high elevation forests, where a specific limiting factor (e.g. temperature) and, more generally, the harsh environmental conditions drive the distribution patterns of trees either directly or through several significant feedback mechanisms (McIntire and Fajardo, 2009).

The present study was conducted on three permanent plots located at different elevations in the Dolomites area of the Italian Alps where a long-term monitoring project was established in 1994. Spatial patterns and age structure of trees within stands were analyzed to provide a critical insight into the role of small-scale processes and the interaction between canopy cover and regeneration establishment in a temperature-limited environment. We hypothesized to observe (i) an increase of regeneration patchiness together with a parallel increase of the environmental stressful condition with elevation. This is in line with the current knowledge on the spatial pattern and dynamics of regeneration in most of the temperature-limited forests (Holtmeier, 2009; Körner and Riedl, 2012); (ii) some evidence, in the spatial pattern of regeneration, related to the site-specific stand history and successional stages and (iii) a distinct spatial pattern among the three species with differing life history traits.

According to these underlying hypotheses, our specific objectives were to: (i) infer the role of increasing limiting conditions on the regeneration pattern and dynamics; (ii) delineate the interaction among three conifer species and between mature versus the regeneration stages; (iii) evaluate the species-specific tree recruitment according to the different seed dispersal and regeneration needs and strategies.

2. Materials and methods

2.1. Study sites

The study sites are located in a high-elevation forest in the eastern Italian Alps on a NE slope of Croda da Lago (46°27′N; 12°08′E) in the Ampezzo Dolomites. Permanent plots are at decreasing elevation: 2200 m for the treeline (C1) plot, 2100 m for the timberline (C2) plot and 1950 m for the subalpine (C3) one. The bedrock is dolomite and limestone with shallow rendzic leptosol soils at higher elevation and deeper brown soils more common at the subalpine level. The climate is characterized by dry winters, with most of the precipitation occurring during summer and early autumn; the coldest and warmest months are usually January and July, respectively, while the growing period typically lasts from June to August. All the three sites are less than two km apart from each other and share the same North–East aspect and gentle slope (Carrer and Urbanati, 2006; Carrer et al., 2007).

The area features the typical composition and stand history of high-altitude Alpine forests with three conifer species: Larix decidua (European larch, hereafter larch), Pinus cembra (Swiss stone pine, hereafter pine) and Picea abies (Norway spruce, hereafter spruce) and signs of past human disturbances. Stump dating and local management plans confirmed that there had been no major harvesting for the last two centuries in C1 and C2 and more recently, 50 years, in C3. Livestock grazing decreased significantly during the last century and especially after World War II, as the turning point between the regeneration and the following stages (regeneration versus mature individuals) at different spatial scales. At this altitude, where trees can easily live hundreds of years with considerably slow growing processes, size rather than age can better represent the regeneration phase. Hence, we considered regeneration all the trees smaller than 5 m in height. This roughly corresponds to 1/3 of the mature-tree height but primarily, it represents the important ecological threshold of the maximum snowpack depth recorded for this Dolomite area (ISPRA, 2013). In winter, a tree taller than 5 m surely has at least part of the crown outside the snowpack with all the consequences that this means (i.e. no protection from winter injuries, reduced vulnerability to fungi attack, etc.) (Holtmeier, 2009). We considered this height as the turning point between the regeneration and the following life stages. To identify significant interactions occurring within the regeneration, we proceeded in three steps analyzing: (i) the second-order effects in the univariate patterns looking at the global or species-specific distribution of the regeneration; (ii) the second-order effects in the bivariate patterns, testing, within the regeneration, the interactions between different species, and (iii) the second-order effects in the bivariate patterns, at both global and species-specific level, focusing on the interactions between regeneration and mature trees. In this case we consider as mature trees all the individuals taller than 10 m.

Univariate and bivariate point pattern analysis (PPA) techniques were applied using tree-stem mapped data (Moere, 1993) to characterize both the tree spatial patterns within the plots and the association of the patterns of two tree species or two ontogenetic stages (regeneration versus mature individuals) at different spatial scales. At this altitude, where trees can easily live hundreds of years with considerably slow growing processes, size rather than age can better represent the regeneration phase. Hence, we considered regeneration all the trees smaller than 5 m in height. This roughly corresponds to 1/3 of the mature-tree height but primarily, it represents the important ecological threshold of the maximum snowpack depth recorded for this Dolomite area (ISPRA, 2013). In winter, a tree taller than 5 m surely has at least part of the crown outside the snowpack with all the consequences that this means (i.e. no protection from winter injuries, reduced vulnerability to fungi attack, etc.) (Holtmeier, 2009). We considered this height as the turning point between the regeneration and the following life stages. To identify significant interactions occurring within the regeneration, we proceeded in three steps analyzing: (i) the second-order effects in the univariate patterns looking at the global or species-specific distribution of the regeneration; (ii) the second-order effects in the bivariate patterns, testing, within the regeneration, the interactions between different species, and (iii) the second-order effects in the bivariate patterns, at both global and species-specific level, focusing on the interactions between regeneration and mature trees. In this case we consider as mature trees all the individuals taller than 10 m.

We used pair-correlation functions (g) (Stoyan and Stoyan, 1994), a second order statistic closely related to Ripley’s K function (Ripley, 1977) that provides information at multiple scales, comparing the distribution of distances of all pairs of points, in our case the tree-to-tree distances, of the patterns. We chose the g function instead of K-function in order to avoid any misinterpretation of results due to the cumulative effect of the latter that can confound effects at larger distances with effects at shorter distances, challenging the detection of the scale of the departure from a null model (Perry et al., 2006). In contrast, the pair-correlation function is non-cumulative and uses only points separated by a certain distance r. In this way, it may allow specific scales to be identified where significant point–point interactions occur (Wiegand et al., 2007). Ripley’s K function can be defined using the quantity k(r), which represents the expected number of points within distance r of an arbitrary point of the process that is not counted (Rip-
ley, 1976), where \( z \) is the intensity of the pattern in the study area. The pair correlation function \( g(r) \) is related to the derivative of the \( K \) function, i.e., \( g(r) = K'(r)/(2\pi r) \) (Ripley, 1977; Stoyan and Stoyan, 1994). Likewise, the bivariate extensions of \( K(r) \) function, \( K_{ij}(r) \) can be defined as the expected number of pattern 2 points within distance \( r \) of an arbitrary pattern 1 points, divided by the intensity \( z_2 \) of pattern 2. The bivariate \( g_{ij}(r) \) follows straightforwardly (Diggle, 1983; Wiegand and Moloney, 2004).

Bearing in mind that the interpretation of the results could be severely biased by the selection of inappropriate null models, we carefully adopted a different null model for each step of the analysis. The univariate patterns were contrasted with the complete spatial randomness (CSR), i.e., the simplest and most widely used null model in this kind of analysis: it considers that any point of the pattern has an equal probability of occurring at any location within the plot (Wiegand and Moloney, 2004). For the bivariate patterns within regeneration we adopted the heterogeneous Poisson null models to account for first-order effects; in this case the constant homogeneity of CSR was replaced by a function \( a(x,y) \) that varies with location \((x,y)\) but maintains the independence of the occurrence of any point in respect to any other (Wiegand and Moloney, 2004). Lastly, for the bivariate analyses between regeneration and adult trees, we applied the antecedent conditions: since the adult tree had already been present and did not change their position during the establishment of regeneration this null model relies on potentially finding regeneration over the whole plot while keeping the locations of the adult trees fixed (Wiegand and Moloney, 2004).

The 95% confidence intervals for both univariate and bivariate analyses were computed from 999 Monte Carlo simulations (Stoyan and Stoyan, 1994; Wiegand and Moloney, 2004). The univariate spatial pattern was defined as clumped, random or regular (hyperdispersed) if the \( g(r) \) values were greater than, equal to or lower than the confidence envelopes, respectively. In the bivariate analyses, values of \( g_{ij}(r) \) greater than, equal to or lower than the confidence envelopes reveal positive association (attraction), spatial independence and significant negative association (repulsion), respectively, between the two analyzed classes. Attraction and repulsion are defined as a tendency for trees of two groups to be respectively closer or farther apart than would occur if they were independently distributed (Peterson and Squiers, 1995).

We performed the \( g(r) \) and \( g_{ij}(r) \) analyses applying a 1 m lag distance and not exceeding half the minimum length of the plot to limit the influence of the margin effects (Haase, 1995). All analyses were done only for classes with more than 15 trees (Camarero et al., 2000) with the grid-based software Programita (Wiegand and Moloney, 2004) adopting a grid size of 1 m² and a ring width of 5 m.

A local indicator of spatial association (LISA, Anselin, 1995), the Getis-Ord G-Star statistic \( (G^*_i) \) (Getis and Ord, 1992), together with tree age as quantitative variable, was used to describe the spatio-temporal patterns of tree recruitment. The LISA statistics have a number of attributes that make them attractive for measuring association in a spatially distributed variable. Indeed, the well-known spatial autocorrelation statistics such as Moran’s I, Geary’s c and Matern’s variogram, measure at a “global” level and report the “average” spatial pattern in a data set (Cliff and Ord, 1981) since they are not designed to look beyond the general autocorrelation characteristics of the pattern (Ord and Getis, 2001). However, in ecology and forestry, a spatial pattern has hardly ever been observed to apply equally across the study region; this is the reason for the increasing importance of the LISA statistics, which can detect the local clustering around an individual location and add depth to inferences where a single measure of global association may contribute little meaningful information (Lamedica et al., 2011). In practice, local analysis dissects global statistics into their local constituents and highlights local spatial clusters (Anselin, 1995; Fotheringham et al., 2000); notably, the \( G^*_i \) statistic can detect and separate clusters of high values, often referred to as hot spots, from clusters of low values named cold spots (Anselin, 1995).

Adopting the variable tree age, the \( G^*_i \) statistic considers each tree as a centre, one at a time, and searches the nearby area for incidences of more old or young trees compared to mean age. Each tree is then classified as a member or non-member of clusters of either young or old trees. \( G^*_i \) was computed as follows:

\[
G^*_i(d) = \frac{\sum w_{ij}(d)X_j}{\sum X_j} \quad \text{for all } j
\]

where \( G^*_i \) is the measure of local clustering of attribute \( x \) around \( i \), \( x_j \) is the value of \( x \) at location \( j \), and \( w_{ij} \) represents the strength of the spatial relationship between units \( i \) and \( j \) which can be measured as either a binary contiguity variable, as in our case, or a continuous distance-decay measure (Anselin, 1995; Fotheringham et al., 2000). All the local \( G^*_i \) analyses were computed using the Excel add-in Rookcase (Sawada, 1999). According to the previous results we adopted two distance classes: 2 and 10 m. This to assess both the small-scale spatial structure potentially related to the micro-environmental variability, often a very important issue in high-elevation areas, and the medium-scale structure more linked to the processes at stand level (e.g. small gap dynamics).

3. Results

The presence of Norway spruce decreased with elevation until almost disappearing at the treeline, while the other two species mostly show an opposite trend (Fig. 1 and Table 1).

In the C1 plot 192 trees were recorded, with 65% larch, 33% pine and 2% spruce (Table 1). The forest is in a typical recolonization phase with rather young trees, low density (Fig. 1), low competition among individuals and almost without a vertical structure; although the age-class distributions are quite similar, pines are smaller than larches (Fig. 2).

In the C2 plot there are 298 trees taller and 460 smaller than 5 m (Table 1 and Fig. 1) with 65% being larch, 29% pine and 6% spruce. The diameter distribution is typical of an uneven-aged stand (Fig. 2) with a vertical structure showing two clear layers. The diameter distribution and age structure of regeneration highlight a significant and continuous increase in pine presence, and to a lesser extent of spruce, with a corresponding reduction in larch proportion especially in the last decades (Fig. 2).

In C3 plot spruce is the dominant species with 44% of individuals, followed by larch and pine with 29% and 27% respectively. Diameter (Fig. 2) and height (not shown) distribution features a monolayered structure with a dominant layer composed mainly of larch and spruce and a regeneration/dominated layer with pine and secondly spruce, where larch decreases to 3% of individuals. In the last 50 years the age structure shows a decreasing trend in larch establishment (Fig. 2).

3.1. Spatial distribution of the regeneration

The univariate \( g(r) \) function shows for all three species, considered either together or separately, a clear tendency towards aggregation (Fig. 3). However, some species and site differences are appreciable: (i) at the treeline C1 plot larch and pine record the highest and significant small-scale \( g(r) \) values revealing the tight grouping up to a distance of 2 m; (ii) larch aggregation generally shows significant values at wider distance and with a smoother decreasing trend with respect to the evergreen species.
On the contrary, looking at the association between the regeneration of the different species (bivariate $g_{12}(r)$), an almost universal tendency towards segregation has been found in all plots and for all species (Fig. 4). This segregation can be pervasive and still evident at rather long distances, as for larch with pine and spruce in the C2 plot, or a small-scale phenomenon only emerging within a 5–7 m range. Finally, considering the bivariate $g_{12}(r)$ function between regeneration and adult/mature trees (Fig. 5), in both C2 and C3 plots (there are no trees taller than 5 m in the treeline C1) for all the species, excluding pine at C2, there is an overall significant tendency towards segregation within a 10–12 m range. The partition of this pattern among the three species (Fig. 6) confirms the previous results, with the exception of pine that likely tends to regenerate, within a small-scale range of 1–4 m, under the larch cover in both C2 and C3 plot.

### 3.2. Spatial structure of the regeneration

With the Getis’s $G_i$ we were able to localize within the plots (Fig. 7), clusters of even-aged trees older (red spots) or younger (blue spots) than the mean age and to describe the spatiotemporal pattern of tree recruitment. Regeneration seems to establish with

#### Table 1

<table>
<thead>
<tr>
<th>Plot</th>
<th>Elevation (m)</th>
<th>Larch</th>
<th>Pine</th>
<th>Spruce</th>
<th>n</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>$h &lt; 5$ m (%)</td>
<td>$h &gt; 5$ m (%)</td>
<td>$h &lt; 5$ m (%)</td>
<td>$h &gt; 5$ m (%)</td>
</tr>
<tr>
<td>C1</td>
<td>2210</td>
<td>124 (65)</td>
<td>0 (0)</td>
<td>64 (33)</td>
<td>0 (0)</td>
</tr>
<tr>
<td>C2</td>
<td>2090</td>
<td>264 (35)</td>
<td>232 (31)</td>
<td>168 (22)</td>
<td>51 (7)</td>
</tr>
<tr>
<td>C3</td>
<td>1940</td>
<td>17 (3)</td>
<td>125 (26)</td>
<td>66 (13)</td>
<td>66 (13)</td>
</tr>
</tbody>
</table>

#### Fig. 1.

Spatial distribution and height of the regeneration in the three treeline (C1), timberline (C2) and subalpine (C3) plots.

#### Fig. 2.

Tree diameter and age distribution within the three plots. The two inset graphs show the diameter distribution of just the adult and mature trees with height >5 m.
different age cohorts in rather large 10–20 m groups and this tendency is likely more significant in the two plots at higher elevation (C1 and C2). However, with the 2-m scale of analyses it is possible to appreciate a finer pattern composed of very small 1–3 m even-aged patches of trees, with different age among patches, but growing very close to one another. This configuration of the
regeneration pattern is not present in the subalpine C3 plot where, even at a closer look, the spatial structure does not show small clusters and seems significantly coarser.

4. Discussion

The regeneration of all the species in this study shows a clear tendency to aggregation throughout the elevation gradient. This can be considered as both the result of a recolonization process (Goreaud et al., 1997; Didier, 2001) and of active niche selection (Grubb, 1977). Concerning recolonization, most high elevation forests in the Alps were subjected to major human modifications in the past centuries following local forestry uses and practices and to increase the grazing area available for domestic ungulates (Holtmeier, 2009). Historically, mountain shepherds used to uproot pine seedlings and harvest saplings in order to thin the canopy cover and favour the lighter crowns of larch to permit better grass growth conditions (Holtmeier, 1994; Motta and Lingua, 2005). The current forest ecosystem structure clearly shows the signs of this cultural legacy in all three stands, with, for example, the presence of stumps, the dominant layer composed mainly of larch or the significant unimodal diameter distribution at the C3 plot. However, abandonment has also fostered either recolonization processes, as in the treeline C1 plot, or the recruitment of late successional species, as for pine and spruce in both C2 and C3 plots.
Even so, these successional dynamics cannot be considered the major driver of the actual spatial pattern of regeneration. In this case, being in a high-elevation area, the role of site conditions could be critical. That is why, even if the seed dispersal and regeneration strategies of the species are clearly different, a convergence is observed in the recruitment spatial distribution with a significant selection of the favourable sites, or better, a significant avoidance of the worst ones, rather than a random distribution all over the plots. The processes leading to this situation are species-specific: spatial distribution of pine is likely determined by both the dissemination activity of nuthackers and small mammals (Contini and Lavarello, 1982; Crocq, 1990; Zong et al., 2010) and by the high sensitivity of the species to cryophilic fungi-disease (Barbeito et al., 2011). This results in the typical distribution in small patches of the species (Del Favero et al., 1985; Tombback et al., 1993) due to lost seed caches (Camaret et al., 1998) and the strict avoidance of late snow-melting microsites. The very high peak of the $g(r)$ function in the C1 plot should be the consequence of the harshest environmental condition; indeed, this is one of the most efficient and successful ways to recolonize alpine pasture (Didier, 2001). In this case, each group of trees growing in very tight patches represents a sort of isolated system with a symbiotic-like relationship among the components that can benefit from a mutual facilitation that improves microsite conditions, affects local snow thickness, soil characteristics and microclimate and offers physical support and protection from herbivores (Mlinšek, 1975; Smit et al., 2007; Lingua et al., 2008; Körner and Riedl, 2012).

In the wind-dispersed larch and spruce, on the contrary, the same small-scale aggregation should be more directly the result of microsites variability (especially in C1 and C2 plots) that is always a very important factor for the regeneration of these species (Oswald and Neuenschwander, 1993). Small changes in surface conditions can result in significant environmental differences, thus favourable and unfavourable niches can be very close (Schonenberger et al., 1995; Resler et al., 2005; Maher and Germino, 2006). In this way the two conifers can be rather diffuse on a favourable area but also localized in small groups where they find a better chance of survival. For example, on patches of mineral soil and reduced canopy cover density for larch or on dead wood and humps for spruce. (Harmon and Franklin, 1989; Hofgaard, 1993b; Kupferschmid and Bugmann, 2005; Bolli et al., 2007).

The similar spatial distribution of regeneration among the three species does not mean that their patches share the same localization within the plots. Here, the coexisting species show an important niche differentiation that is manifested mainly at the early life stage when the microtopographic conditions, mode of seed dispersal and different needs during ecesis can play a fundamental role (Grubb, 1977; Maher et al., 2005; Maher and Germino, 2006). The bivariate $g_{xy}(r)$ confirms this hypothesis: all the pair-contrasts at all sites [except the $g_{xx}(r)$ for larch and spruce regeneration at C3 (Fig. 4)], highlight various grades of repulsion among the species. This suggests a fine patchy structure where small and almost pure groups of the different species grow separately in the same favourable area of the plots. Nonetheless, species-specific regeneration needs cannot entirely justify such an outcome. For example, the lack of aggregation at very short distance between stone pine and larch has to be considered together with the attraction between pine regeneration and mature or bigger larches, detected at both C2 and C3 plots. This behaviour is often a consequence of the dense grass cover, growing under a light larch canopy or in former pastures, which hampers the small larch seeds reaching the mineral soil. On the contrary stone pine seeds do not face this problem because stump area and hollows around root collar are the nuthacker’s preferred hiding-places for seed caches (Tombback et al., 1993). Moreover, growing at the timberline and subalpine level, larch regeneration is not able to stand the shaded conditions that are ideal for the emergence and survival of pine seedlings and saplings (Motta and Edouard, 2005; Motta and Lingua, 2005).

The significant inter- and intraspecific short-distance repulsion between regeneration and mature trees is present in all three species, except for pine regeneration and just mature larch trees, and is particularly strong in the subalpine C3 plot. This result can be interpreted as evidence of the light and heat requirements of regeneration (Brang, 1998; Motta and Edouard, 2005), which therefore prefers gaps (Kuuluvainen, 1994; Holtmeier, 2009). These needs seem very effective in determining the reciprocal and similar spatial distribution of individuals along the altitudinal gradient despite the increasingly harsh environmental conditions with the corresponding increase in elevation. However, different results emerged considering the age spatial structure of regeneration. Within this new perspective, the small-clustered organization of individuals, typical of a high elevation area, appeared in the treeline and timberline stands but not in the subalpine one. In this case, the more limiting conditions do not seem to affect the spatial distribution but rather just the age structure of the recruitments.

Fig. 7. Interpolated and $z$-transformed local $G$ values computed for the age of regeneration using 2 m (left plots) and 10 m (right plots) distance classes respectively. Red and blue colours depict hot-spot (i.e. groups of trees older than the mean age within the plot) and cold-spot (i.e. groups of trees younger than the mean age within the plot) areas, with the intensity of the colours being proportional to the significance of the local $G$ index. Areas greater than $|2|$ are significant at $P<0.05$. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)
Regeneration highlights a similar spatial structure in both C1 and C2 plots linked with the presence of favourable microsites. The lower number of those sites in C1 with respect to the less limiting conditions in C2 generates a simplified structure at the treeline compared to the timberline where a continuous replacement of small even-aged groups is observed. Although all the tree stands are experiencing successional dynamics, LISA analyses confirm that the C2 stand has a more complex structure and small gap-phase dynamics where regeneration is localized under treefall gaps. For example, the rather large cold spot in the north side of the plot is the likely result of the last important disturbance that removed most of the forest cover around two centuries ago, opening the door to today’s cohort of mainly larch regeneration (Carrer and Urbini, 2001).

This recruitment strategy is even clearer in the subalpine area (C3) where regeneration grows with dense even-aged cohorts as in the north side of the plot on the long and narrow gap opened after a windthrow and on the larger group in the middle. Yet, the reduced significance of spatial autocorrelation at short distance suggests the presence of different aged trees closely interspersed rather than the typical small even-aged groups seen at higher elevation. In this case the less limiting conditions and the denser cover would enhance competition and increase the mortality rate within the group with the effects of shortening its life, weakening the structure and finally inducing a faster degeneration of the group itself.

5. Conclusions

Despite the differences at species (seed dispersal mode, regeneration strategy, ecophysiological behaviour), stand (structure, composition and history) and environmental (conditions are increasingly limiting with elevation) levels, the spatial pattern of regeneration is quite similar in all the tree stands. This convergent behaviour is clearly in contrast with our first hypotheses. Yet, the presence of few outcomes in line with the assumption of the increasing role of competition associated with less stressful conditions (i.e. the greater repulsion among species at the lowest elevation C3 site) are not enough to reframe this general representation. These results seem to mask and partially question the increasingly limiting with elevation) levels, the spatial pattern of regeneration at high elevation are recommended for the world, so further investigations on the spatial and temporal pattern of regeneration at high elevation are recommended for addressing parallel management issues outside the typical Alp-species communities. Information on both spatial pattern and structure have proved to be fundamental in defining forest stand dynamics and to obtain a better focused picture of the successive trajectories of the whole stand. Placed in the correct context according to the various biophysical and social settings, this type of information can provide fundamental clues for improved conservation and management of these highly vulnerable mountain ecosystems.

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