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

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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

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management and climatic scenarios (Frelich, 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 Urbinati, 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 Urbinati, 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 commonly seen in many valleys in the Alps (Carrer and Urbinati, 2001; Didier, 2001; Garbarino et al., 2013).

2.2. Field sampling and samples preparation

Each 1-ha plot was traced using a closed polygon laid out with a theodolite and an electro-optical distance meter (Wild T2). All trees taller than 50 cm were identified, labelled and the following features recorded: topographic position and elevation at the base of the stem, species, diameter at 50 cm (D_{50}) to the nearest centimetre, total height.

Tree age was determined through increment coring using the following procedure: in trees with $D_{50} \geqslant 4$ cm one or two cores were taken at 50 cm from the ground at least 120° apart from one another. In trees with a $D_{50} < 4$ cm no coring was performed but, where possible, age at D_{50} was determined by counting the annual whorls. All increment cores were prepared conforming to the standard procedures (Stokes and Smiley, 1968) and ring widths were measured to the nearest 0.01 mm. Each ring width series was checked, corrected and dated both visually and using the COFECHA computer program (Holmes, 1983). Each tree was assigned the age of the longest tree-ring series that represents the age at 50 cm above the root collar.

2.3. Spatial analysis

Univariate and bivariate point pattern analysis (PPA) techniques were applied using tree-stem mapped data (Moeur, 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 $\lambda K(r)$, which represents the expected number of points within distance r of an arbitrary point of the process that is not counted (Rip-