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Patterns of plant trait–environment relationships along a forest succession chronosequence

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ABSTRACT

Land-use change due to socioeconomic factors leads to the abandonment of traditional intensive coppice management in large areas of the mountainous landscapes of the Apennines (Italy). In this study we explored the multivariate relationship between plant species traits, stage of forest succession and environmental gradients. We focused on community-level patterns in plant traits of the vegetation of beech forest understory along the regeneration chronosequence initiated after cessation of coppicing. We hypothesized that the correlations between the traits and environmental factors should increase with succession age due to the decreasing role of chance.

Landscape-level heterogeneity, i.e. changing elevation, slope, exposition, bedrock and forest stand age was assessed using a stratified random sampling design. Sixty sites were sampled for stand structure and species composition. We focused on 14 plant traits related to persistence, growth and dispersal. The recently developed data-analytical method, Model-Based Recursive Partitioning, was used to disentangle the relationships between patterns of plant traits and environmental gradients.

About half (seven) of the studied plant traits showed significant correlations with succession stand age, elevation, inclination, heat index and bedrock. Contrary to the low number of trait–environment correlations in early succession, eight traits showed significant relationships with one or more abiotic factors in older stages of the post-coppice development. Stand age had the highest independent explanatory power, explaining 40% of variance of SLA, more than 17% of variance of short-distance seed dispersal and more than 15% of variance of both long-term connection and extensive perennial root. Among the other abiotic factors, elevation explained 27% of variance of SLA, inclination explained 6–8% of variance of long-term connection, extensive perennial root, thickening and large bud bank.

The observed trait–environmental relationship is assumed to be driven by various environmental factors operating at various levels of complexity. While forest succession in relatively homogeneous landscapes might be driven mainly by environmental factors related to forest succession itself and associated abiotic changes (such as changes in light and soil moisture patterns), in heterogeneous landscapes the succession pathways may be structured by landscape-level environmental factors such as inclination. However, in the present study, forest stand age had the highest explanatory power for most of the investigated traits, supporting the assumption of the overall strong impact of succession-driven environmental factors in trait–environment relationships.

1. Introduction

Vegetation changes, omnipresent at all temporal and spatial scales, are a result of aging and death of species, species interactions with the environment and changes in land management (Koniak and Noy-Meir, 2009). Although these causal relationships are undoubtedly true and corroborated, the underlying ecological and physiological processes driving these patterns are not

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well understood and remain the focus of much research effort (Shipley et al., 2006; Westoby and Wright, 2006). Processes shaping the patterns of vegetation dynamics have traditionally been approached by quantifying the changes in plant species composition over time. Plant taxonomy (species identity) is undoubtedly an important messenger of ecological and evolutionary information, yet this information is often only very remotely relevant to understanding processes. In this context, plant species traits have proven to be a very effective tool in analyses of these relationships in quest of understanding the crucial processes shaping the patterns and dynamic pathways within ecosystems (Lavorel and Garnier, 2002; Garnier et al., 2004). Leaf ecomorphological and physiological traits, for instance, were found to show remarkable covariance with environmental conditions at both landscape (Garnier et al., 2004; Dahlgren et al., 2006; Castro et al., 2010) and global (Wright et al., 2004) scales, hence demonstrating that plant functional traits carry important (albeit not yet fully understood) information allowing better understanding of ecological processes (*e.g.* Lavorel et al., 1997; Garnier et al., 2004; Kahmen and Poschlod, 2008; Castro et al., 2010). Trait-based approaches have been used successfully to evaluate complex ecosystem responses to human disturbance, as in grasslands (*e.g.* Lavorel et al., 1998; Barbaro et al., 2000; Kahmen and Poschlod, 2008; Mládek et al., 2010), forest ecosystems (*e.g.* Graae and Sunde, 2000; Verheyen et al., 2003; Aubin et al., 2007) and beyond.

Diverse environmental conditions in developing coppiced forests act as filters on plant functional traits pertinent to dispersal and demands for light (Mason and MacDonald, 2002; Decocq et al., 2004; Bartha et al., 2008; Canullo et al., 2011). Specifically, in the herb layer the light-demanding species with low specific leaf area (SLA) might be replaced by low light tolerating species (with high SLA), while species with persistent seed bank might be replaced by species not forming any seed banks during forest succession (Brown and Warr, 1992; Dahlgren et al., 2006). Canullo et al. (2011) showed that clonal traits respond to forest succession in coppiced beech forests. They found that species with highly integrated genets with high persistence and low mobility tend to be more successful in the initial stages of succession. Herb layer plays an important role in these beech forest ecosystems. In impoverished European post-glacial deciduous forests the herb layer supports about 90% of the plant species richness (Seidling, 2005). It is the herb layer in these forests that appears to be particularly sensitive to disturbance, including sudden changes of environmental condition (Moffatt and McLachlan, 2004; Flinn and Vellend, 2005; Gilliam, 2007; Aubin et al., 2008) and human interventions (Andersson et al., 2000; Spellemberg, 2005).

In this study we aimed to explore the multivariate relationships between selected functional traits of species in the forest herb layer, stages of forest succession and environmental gradients at the landscape scale. We focused on community-level patterns of plant traits of beech forest understory vegetation along the regeneration chronosequence initiated after cessation of coppicing. The objectives of our study include identification of relationships between abiotic conditions of the studied ecosystem and the plant functional traits related to persistence, growth and dispersal responding to forest changes along a chronosequence.

Margalef (1968) suggested that the occurrence of plant species in late succession phases in forest ecosystems should be more accurately predictable from prevailing soil and light conditions. On the other hand, species presence in early succession should be more under control of chance events (such as propagule availability). Thus, for any given forest site, patterns of community assembly should become more predictable as succession progresses (Christensen and Peet, 1984; Harrelson and Matlack, 2006; Erfanzadeh et al., 2010). In our study we test this hypothesis using plant functional traits and employ the recently developed Model-Based Recursive Partitioning (MOB; Zeileis et al., 2008) to this goal. In this method the trait–environment relationships are tested for significant differences according to a certain input variable (such as succession age), by maximizing differences of trait–environment relationships between groups of the input variable.

2. Materials and methods

2.1. Study area

The study area is located in the southern part of the Marche Region (Central Apennines, Italy) in the Monti Sibillini National Park (Fig. 1). The area falls within the temperate climatic zone, with mean annual precipitation ranging from 1100 to 1400 mm and mean annual temperatures spanning 8–12 °C (Amici and Spina, 2002). The bedrock is formed mainly by Mesozoic and Tertiary limestones, with some Tertiary arenaceous marly flysch sandstone in the southernmost part. The limestone soils (Skeleti-Calcaric Phaeozems and Calcari-Humic Leptosols) are poorly structured and have low water-holding capacity (ASSAM, 2006). Soils supported by sandstones (Calcaric Cambisols, Eutri-Endoleptic Cambisols) are generally deep and well structured (50–100 cm) and have high water-holding capacity.

The area represents a silvipastoral system where coppice management with short time rotation (25–30 years) is traditionally applied to a large extent (more than 70%), also including beech (*Fagus sylvatica*) forests. This silvicultural practice was an important characteristic of the socioeconomic structure until the 1950s of the last century (Pavari, 1999; Amorini and Fabbio, 2001; Debussche et al., 2001). Depopulation and changes in socioeconomical conditions over the last decades led to a pronounced drop in local demand for small size timber, firewood and charcoal (Ciancio et al., 2006). Therefore, the characteristic extensive land use practices and, in particular, the traditional coppice management of these systems are being gradually abandoned in 21% of present beech woodlands.

We studied the beech forest communities of the montane belt. The tree layer is dominated by deciduous *Fagus sylvatica* accompanied by *Acer obtusatum*, *Acer platanoides*, *Acer pseudoplatanus*, *Corylus avellana*, *Fraxinus excelsior*, *Laburnum anagyroides*, *Sorbus aria* and locally abundant evergreen *Ilex aquifolium* and *Taxus baccata*. The beech forests cover about 10,000 ha in the study area, 90% of which are active or abandoned coppices with standards (IPLA, 2001). This silvicultural system is common in European Mediterranean countries, where it covers an area of about 23 million hectares (UN/ECE-FAO, 2000; Ciancio et al., 2006). In this system, a clear felling of stems is carried out at selected rotation ages (25–30 years for beech) and some mature trees (so-called "standards") are retained over two or three normal coppicing rotation cycles, usually with a density of 80–140 trees per hectare (Coppini and Hermanin, 2007). After felling, regeneration proceeds by creation of a dense shrub layer, usually beneath a sparse canopy layer retained after individual or group harvesting (Matthews, 1989; Fig. 2). Gradually, a complex (vertically and horizontally heterogeneous) tree stand is formed through resprouting suckers and mature trees (Bartha et al., 2008).

2.2. Sampling design and environmental variables

We chose 60 forest stands using a stratified sampling design based on an historical survey to represent the various stages of forest succession and landscape heterogeneity (Bartha et al., 2008). The following stratification criteria were used: age since last coppicing, bedrock (limestone and sandstone) and elevation classes (1000–1200 m and 1200–1400 m) (Table 1). The elevation threshold clearly delimits two altitudinal beech communities that are also