



Patterns of beta-diversity along elevational gradients inform epiphyte conservation in alpine forests under a climate change scenario



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ABSTRACT

We explored the patterns of beta-diversity of forest epiphytic bryophytes and lichens along elevational gradients to elucidate the potential impact of climate change on these functionally relevant components of the forest biota of the Alps. Eight elevational gradients were selected from a regional forest database matching the requirement of hosting spruce-dominated forests within the whole elevational range of this forest type (900–1900 m). We calculated the decay of species compositional similarity along the gradients, considering the beta diversity components, turnover and richness difference. We then assessed the importance of temperature in explaining variation in these components of beta diversity along the elevational gradients by using a distance-based redundancy analysis. Our results warn against the impact of climate change on epiphytic bryophyte and lichen communities in alpine spruce forests. This impact could be more rapid (higher rate of similarity decay) and severe for lichens, triggering species loss with temperature warming. In contrast, temperature warming is expected to cause relevant shifts in species composition to bryophyte communities, despite allowing to maintain species richness through species replacement. The contrasting mechanisms (species loss vs species replacement) by which climate influences bryophyte and lichen communities, suggest that conservation strategies should be tailored to each organism group. In particular, for bryophytes conservation efforts should be assigned to forests at each band of the elevation gradient which hosts peculiar assemblages. In contrast, for lichens priority for conservation should be assigned to forests at higher elevation that currently host the largest species pool. In this context, forest management is the primary tool available to mitigate the effect of climate change and to give a chance to delay the local extinction of several species.

1. Introduction

Rapid climate change is threatening biodiversity globally (Bellard et al., 2012), becoming one of the main challenges for conservation (Dawson et al., 2011). However, only a few studies have addressed beta-diversity patterns along climatic gradients to predict the effects of global change on the terrestrial biota and to improve the effectiveness of conservation practices (Socolar et al., 2016). In this framework, elevational gradients are among the most suitable model templates for testing species diversity-climate relationships (McCain and Grytnes, 2010; Graham et al., 2014) as they encompass several clines in climatic factors over a relatively short distance (Acharya et al., 2011; Lomolino, 2001; Körner, 2007).

The analysis of beta-diversity along environmental gradients is a powerful tool to understand how species richness is generated and maintained (Bishop et al., 2015; Graham et al., 2014). This approach has a great potential for informing conservation practices (Socolar

et al., 2016). Beta-diversity is the component of regional diversity that accumulates as a result of compositional differences between sites (Harrison et al., 1992). In other words, it is a measure of the variation in species composition between sites which results from two distinct processes, species turnover and species loss or gain that generates richness differences among sites (Carvalho et al., 2012; Legendre, 2014 and references therein). Turnover occurs when species of one site are replaced by different species in other sites, while richness difference results in a nested pattern caused by species gain and loss in which the species-poor sites are a subset of the richer sites (Atmar and Patterson, 1993; Baselga, 2012). The patterns of these two components of beta-diversity along environmental gradients have substantial implications for conservation (e.g. Legendre et al., 2005; Socolar et al., 2016). For instance, high rates of species turnover among sites would imply favouring multiple, spatially separated reserves before single large protected areas to maximize biodiversity conservation (Franklin, 1993). In contrast, high rates of richness difference among sites (nestedness

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would suggest that it is better to protect biodiversity hotspots (Cutler, 1994).

Epiphytic bryophytes and lichens are among the most sensitive organisms to climate change in forest habitats (Nascimbene et al., 2016; Nascimbene and Marini, 2015; Spitale, 2016) and their conservation should be urgently included in forest management through specific strategies and practices that could buffer the negative effects of changing climatic conditions (e.g. Ellis et al., 2009). The physiology of these organisms is closely coupled to ambient temperature and moisture, which influence water saturation of thallus (the undifferentiated vegetative body of bryophytes and lichens) and desiccation tolerance (Green et al., 2008). Increasing ambient temperature may impact these epiphytes due to increased respiratory carbon losses (Schroeter et al., 2000; Wagner et al., 2012). Moreover, high temperature influences thallus rewetting and water content, inducing frequent and severe desiccation events that hinders the photosynthetic activity (Insarov and Schroeter, 2002). These processes are mediated by thallus morphology (Merinero et al., 2014) and, for instance, crustose lichen species are more resistant to high temperatures because of their capacity to withstand drought events, whereas foliose and fruticose growth forms are more desiccation-sensitive (Larson, 1981). Among bryophytes, desiccation tolerance differs between mosses and liverworts: the latter are usually more sensitive to drought than the former (Oliver et al., 2000). Also in this case, this could be due to their different morphology, as in most cases the conducting system in liverworts is even simpler than in mosses.

The influence of climate change on the beta-diversity patterns of epiphytic bryophytes and lichens is still poorly explored (Socolar et al., 2016), hindering the development of effective conservation measures that could mitigate the impact of global change on these organisms. In this study, we explored beta-diversity patterns of forest epiphytic bryophytes and lichens using distance decay of pairwise similarity (Nekola and White, 1999; Mori et al., 2015) coupled with elevational gradients to elucidate the potential consequences of climate change on these organisms in mountain forests of the Alps. In particular, we hypothesized that pairwise similarity of both bryophyte and lichen communities decreases with increasing difference in elevation between sites (Bishop et al., 2015), because of the effect of changing climatic conditions along the gradient. However, this pattern could be generated by the contrasting mechanisms of species turnover and richness difference (species gain or loss). For this reason, for each organism group we partitioned the pairwise beta diversity into its two components (richness difference and turnover) and then we tested their relationships with the temperature elevational gradient. Since thallus morphology influences the response of bryophyte and lichen communities to climate, we then tested its effect on the relationships between beta-diversity components and temperature.

2. Materials and methods

2.1. Study area

We carried out the study in the alpine region of South Tyrol (N Italy) covering 740,000 ha (Fig. 1). The climate is largely influenced by elevation (Fig. 2), ranging from temperate conditions in the Adige Valley area, with a mean annual temperature of 11–12 °C, to alpine tundra conditions above 1700 m a.s.l., with a mean annual temperature of 2–3 °C. Precipitation across the region is variable, ranging from < 600 to 1400 mm yr⁻¹. The conditions are the driest in the east-west orientated Venosta Valley in the western part of the study area, and the wettest in the central northern and eastern part of the study area. Given the high geological diversity of the study area, the bedrock varies from hard siliceous, to metamorphic, porphyric and carbonatic rocks, while soils are usually podsoles and rendzinas (on calcareous bedrock).

Between 600 and 2100 m a.s.l. the landscape is dominated by forests that cover an area of 370,000 ha, of which 52% are spruce forests

that are managed for timber production in even-aged and multilayered, uneven-aged, stands. In both cases, management is based on progressive thinning and exploitation (1.6 m³ ha⁻¹ yr⁻¹) of mature trees.

2.2. Study organisms

Bryophytes and lichens contribute greatly to the biodiversity of alpine forests (Nascimbene et al., 2014), underpinning important ecological functions and ecosystem services (Elbert et al., 2012; Zedda and Rambold, 2015). For example, they contribute to both C and N biogeochemical cycles and to water regulation. These aspects are relevant in the European Alps where the regulatory function of forest ecosystems is fundamental for controlling and maintaining efficient water fluxes along the watersheds (Zedda and Rambold, 2015).

Bryophytes and lichens are poikilohydric organisms. Thus, their eco-physiology is directly related to climatic conditions (Oliver et al., 2000). The water uptake is broadly similar between mosses and lichens: the larger the surface area to weight ratio, the more rapid the water uptake (Larson, 1981). Lichens have three main thallus growth forms: crustose, foliose and fruticose. Due to their relatively large size, the latter are included in the morphological group of macrolichens, while the former, due to their smaller size, are defined as microlichens. Lichens with a crustose growth form are expected to better resist drought events than foliose and fruticose forms because of higher desiccation tolerance. Crustose lichens have a lower surface-to-volume ratio (i.e. less surface exposed to the atmosphere), resulting in a higher tolerance to desiccation, water loss being restricted to the upper exposed surface (Büdel and Scheidegger, 2008).

Bryophytes are organisms able to cope with drought and desiccation through a complex balance of mechanisms related to physiology, morphological features and colony architecture. Among bryophytes, few liverworts have specialized conducting tissues in their gametophytes and none have these structures in the sporophyte. Liverworts have therefore a generally lower tolerance to drought and desiccation than mosses, which have conducting cells in both generation phases (Ligrone et al., 2012).

2.3. Sampling design

Eight distinct elevational gradients were selected (Fig. 1) on the basis of the regional forest database matching the requirement of hosting spruce-dominated forests within the whole elevational range of this forest type (900–1900 m a.s.l.). The site selection was made to span the entire regional rainfall gradient (c. 600–1200 mm yr⁻¹).

Since we were interested in evaluating the climatic effects of elevation, the structural heterogeneity was minimized by selecting stands of forests as similar as possible.

In each site, a pair of forest stands with mature trees were selected at three different elevational steps (900–1200 m a.s.l.; 1400–1600 m a.s.l.; 1800–1900 m a.s.l.; Fig. 1). Despite the different size of the three elevational steps, the 95% confidence intervals of temperature are comparable among them (1.1 °C in the lowest step, 0.9 °C in the intermediate step, and 0.8 °C in the highest step). A 13 m radius plot was randomly placed in each forest stand and in each plot, five mature spruce individuals were randomly selected for the lichen and bryophyte survey, for a total of 240 trees.

The lichen and bryophyte survey was conducted according to the European guidelines for lichen monitoring, that allow robust estimate of epiphyte diversity (Asta et al., 2002). Epiphyte diversity was sampled using two standard frames of 10 × 50 cm which were attached to the tree trunk at the north and south cardinal points with the shorter lower side at 100 cm from the ground. To better capture epiphyte diversity, two additional standard frames were placed at the base of the trunk on the same cardinal points. All epiphytes (lichens and bryophytes) inside the frames, including sterile crustose lichens, were listed and their frequency was computed as the number of trees in each plot on which

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