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Fine-scale population dynamics help to elucidate community assembly patterns of epiphytic lichens in alpine forests

Juri Nascimbene [a, b], Sophie Ackermann [b], Matteo Dainese [c, *], Matteo Garbarino [d], Marco Carrer [b]

[a] Museo di Scienze Naturali dell'Alto Adige, via Bottai 1, 39100, Bolzano, Italy
[b] Dipartimento Territorio e Sistemi Agro-Forestali, University of Padova, Viale dell'Università 16, I-35020, Legnaro, PD, Italy
[c] Department of Animal Ecology and Tropical Biology, University of Würzburg, Biocenter, Am Hubland, 97074, Würzburg, Germany
[d] Department of Agricultural, Food and Environmental Sciences, Università Politecnica delle Marche, Via Brecce Bianche 10, I-60131, Ancona, AN, Italy

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A B S T R A C T

We examined the main and interactive effects of factors related to habitat filtering, dispersal dynamics, and biotic interactions, on tree-level population dynamics of a subset of species composing the epiphytic lichen pool in an alpine forest. We tested these processes evaluating the population size of 14 lichen species on six hundred and sixty-five trees within a 2 ha plot located in a high elevation alpine forest of the eastern Italian Alps. Our results indicate that community assembly patterns at the tree-level are underpinned by the simultaneous effects of habitat filtering, dispersal, and biotic interactions on the fine-scale population dynamics. These processes determine how the single species are sorted into community assemblages, contributing to tree-level community diversity and composition patterns. This corroborates the view that the response of lichen communities to environmental gradients, in terms of compositional and diversity shifts, may reflect differential species responses to different drivers.

1. Introduction

Habitat filtering, dispersal dynamics and biotic interactions are the main processes that determine community assembly (Lortie et al., 2004). The importance of each process may, however, depend on environment type, organism traits, and spatial scale of analysis (e.g., Guisan and Thuiller, 2005). The niche-based model emphasizes the role of habitat filtering in determining species patterns, especially at the fine-scale, while the neutral model (Hubbell, 2001) stresses the importance of dispersal dynamics at both broad (Wisz et al., 2013) and fine (Hanski, 1999) spatial scales, in connection with habitat connectivity and dispersal ability of the species (Snäll et al., 2004, 2005). Biotic interactions also contribute to determine community assembly at different spatial scales (Wisz et al., 2013), based on the concept that species are not independent entities and interact with other species.

Overall, these processes influence the co-occurrence of the species within communities, which in turn determines community diversity and composition. In this perspective, the analysis of population dynamics in terms of influence of environmental factors, dispersal, and biotic interactions on the performance of single components of the community, may contribute to elucidate the mechanisms behind community assembly patterns (Lortie et al., 2004).

Epiphytic lichens are a functionally important and species-rich component of alpine forests (e.g. Nascimbene et al., 2014). They contribute to the water and nutrient cycling by retaining precipitation in the canopy and fixing atmospheric nitrogen (cyanobacterial lichens), and increasing microhabitat complexity and the diversity of forest invertebrate fauna, which in turn serve as food for a variety of passerine bird species (Ellis, 2012). Moreover, several species are worthy of conservation being included in red-lists (e.g. Nascimbene et al., 2013). Several studies have already assessed the effects of different drivers of epiphytic lichen community diversity and composition. In particular, there is a wide consensus about the role of host tree features and stand conditions (Johansson et al., 2007; Jüriado et al., 2009; Mežaka et al., 2012; Nascimbene et al., 2012), as well as dispersal dynamics (Löbel

* Corresponding author.
E-mail address: matteo.dainese@uni-wuerzburg.de (M. Dainese).

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et al., 2006a). Recent findings also support the role of species interactions in determining lichen distribution patterns (Maestre et al., 2008). For instance, the inter-specific competition in saturated epiphyte communities leads to dominant species outcompeting pioneers (for an overview see Ellis, 2012), and photobiont sharing could facilitate lichen establishment in forests (Rikkinen et al., 2002). However, the exploration of the mechanisms determining the observed community patterns is still scanty, hindering a deeper understanding of the general rules driving lichen community assembly along environmental gradients.

In this study, we developed a fine resolution analysis to test the main and interactive effects of factors related to different processes, namely habitat filtering, dispersal, and biotic interactions, on tree-level population dynamics of a subset of species composing the lichen pool in an alpine forest. This approach is expected to help to elucidate how species are sorted into tree-level communities, contributing to a more mechanistic view of community assembly patterns of epiphytic lichens on their host trees.

2. Materials and methods

2.1. Study site

We examined a 2 ha plot located in the eastern Italian Alps at an elevation of 1900 m (latitude: 46.23° N; longitude: 11.32° E; Fig. 1). The climate is characterized by strong daily and annual temperature fluctuations. Mean annual temperature is 4.6 °C and mean annual precipitation is c. 950 mm, with a peak during summer and a dip between December and February. Vegetation belongs to Vaccinio-Piceetea (Larici-Cembretum), with Norway spruce (*Picea abies*), stone pine (*Pinus cembra*), and European larch (*Larix decidua*) as dominant tree species. The area is subject to the dynamics of many high-elevation forests in the Alps, where a substantial reduction of livestock activities and a decreased intensity of silvicultural practices during the last century triggered a change in forest tree composition, with larch, the initial dominant tree species, being replaced by stone pine and spruce (Carrer and Urbinati, 2001). This change in tree cover has resulted in increasing stem density and canopy closure. Management activities ceased in the 1990s, and the area is now used for long-term ecological studies (Carrer and Urbinati, 2001).

2.2. Sampling design and data collection

Trees taller than 130 cm were mapped with a GPS station and georeferenced using an electro-optical distance meter. For each tree, lichen species (Fig. 1), diameter at breast height (DBH), and crown dimension were recorded by measuring two orthogonal diameters (Carrer and Urbinati, 2001). Tree age was also determined through increment coring. Full details of the sampling protocol for forest structure is reported in Carrer and Urbinati (2001) and Carrer et al. (2013).

A previous floristic survey (Nascimbene, 2013) yielded 66 epiphytic lichens including 31 microlichens (crustose growth form, including 8 calicioid lichens) and 35 macrolichens (foliose and fruticose growth form). In the present study, species were selected according to three criteria: (*i*) common species reported in the previous survey; (*ii*) species that can be identified in the field with the naked eye or the help of a magnifier; (*iii*) species representing different growth forms and reproductive strategies. Species with low occurrence frequency (<10%) were excluded from analysis to allow for robust statistical modelling. Only *Letharia vulpina*, one of the most typical species in this type of alpine forest (Nascimbene et al., 2014) was included despite its apparent local rarity. We aimed to represent approximately 20% of the local species pool. This selection process yielded a subset of 14 species (see Supplementary material Appendix A, Table A1), including 10 macrolichens whose dispersal is mainly by vegetative propagules, and 4 microlichens (crustose growth form) whose dispersal is by sexual spores. The imbalanced proportion between micro- and macrolichens was related to the practical constraints imposed by the application of criteria (*i*) and (*ii*).

Reproductive strategies and growth forms were determined following Nimis and Martellos (2008). On trees with a DBH > 15 cm,

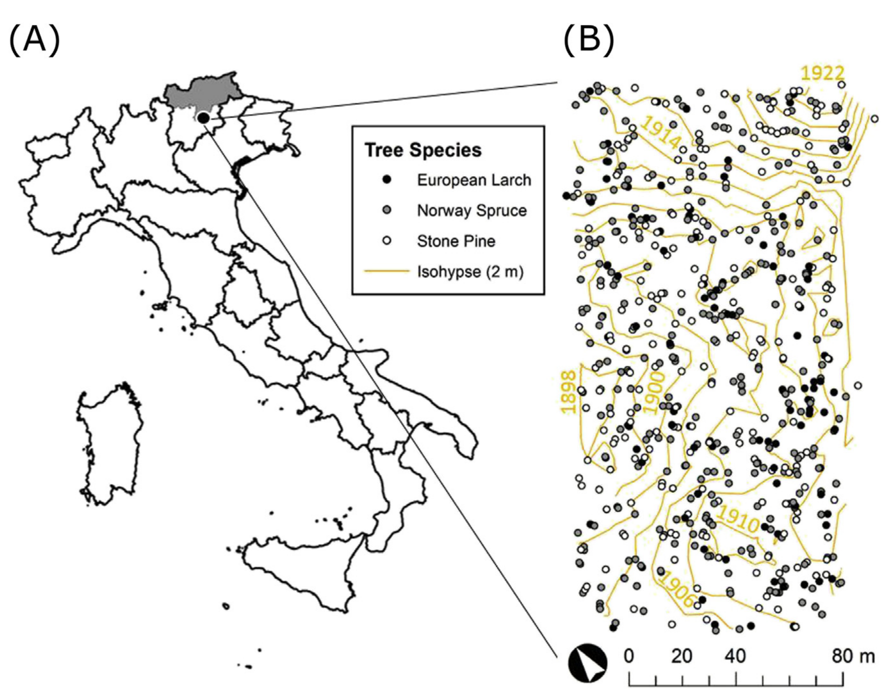

Fig. 1. (A) Study area, (B) study site: a 2 ha plot located in the eastern Italian Alps at an elevation of 1900 m (latitude: 46.23° N; longitude: 11.32° E).