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Local dispersal dynamics determine the occupied niche of the red-listed lichen *Seiophora villosa* (Ach.) Frödén in a Mediterranean *Juniperus* shrubland

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ABSTRACT

The red-listed lichen *Seiophora villosa* is associated with undisturbed coastal dune systems dominated by *Juniperus* spp. The clustered distribution of this species suggests that propagative traits may be responsible for its conservation status. We tested whether the local distribution of an *S. villosa* population under undisturbed conditions is limited by habitat filtering or by low dispersal fitness. Using Strip Adaptive Cluster Sampling, we estimated the size of one of the largest undisturbed Italian populations of *S. villosa*. We considered the abundance of both mature and juvenile thalli in relation to geographical and environmental spaces. Multiple regression on distance matrices models were in accordance with the hypothesis that *S. villosa* is occupying only a small portion of its colonizable niche because of a very limited propagation ability. Apart from the co-occurrence of mature thalli, the presence of juvenile thalli was independent of pure spatial and environmental factors.

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Introduction

Epiphytic lichens are an ecologically important component of coastal *Juniperus* habitats, which are characterized by assemblages of predominantly Mediterranean-distributed species restricted to coastal ranges (Nimis and Schiavon, 1986). One such epiphytic lichen, *Seiophora villosa*, is a red-listed macrolichen (Nascimbene et al., 2013) strictly associated with dune environments such as coastal *Juniperus* shrublands (Natura 2000 priority habitat code 2250*).

These habitats are presently threatened worldwide owing to various anthropogenic pressures, such as urban coastal development, tourism, habitat fragmentation, alien species introduction and coastal erosion (McLachlan and Brown, 2006; Picchi, 2008; Prisco et al., 2012; Bertacchi and Lombardi, 2014).

The distribution of *S. villosa* is spatially clustered on both large and local scales (Frödén and Lassen, 2004). The large-scale clustering is mainly due to the effect of habitat fragmentation caused by anthropogenic and natural disturbances such as tourism pressure or dune erosion (Benesperi et al.,

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2013). On a local scale, the clustered distribution of *S. villosa* is purportedly driven by both environmental filtering and the species' dispersal capability as previously reported for other epiphyte species (Öckinger et al., 2005; Schei et al., 2012). However, the importance of different predictors seems to vary with spatial scale (McGill, 2010).

Dispersal is a process fundamental for the persistence and dynamics of a population (Levin et al., 2003). Its relevance in shaping population distribution is particularly important in organisms whose habitats exhibit spatiotemporal dynamics and in patch-tracking organisms, such as several epiphytic lichens (Snäll et al., 2005; Werth et al., 2006).

The recruitment of new individuals in lichen populations depends on two non-mutually exclusive processes (Werth et al., 2006): dispersal limitation, i.e., a limited availability of propagules in a given habitat (Öckinger et al., 2005; Belinchón et al., 2009), and establishment limitation, i.e., the inability of young individuals to become established in a given habitat due to interactions with biotic and/or abiotic factors. This issue recurs in epiphytic communities independently by the colonized habitat. For example, Schei et al. (2012) showed that both local dispersal and environmental conditions influence the spatial distribution and abundance of epiphytic lichen species of the *Lobaria* community at fine spatial scales, in contrast with the assumption of McGill (2010) who suggests that microclimate and dispersal are more important than habitat-related factors at scales $< 10^2$ m.

According to metapopulation theory, both local habitat availability and habitat isolation are important in determining a species' distribution (Hanski, 1999), so that sometimes species may not be able to colonize all suitable habitat because they cannot disperse to isolated habitat fragments (Johansson and Ehrlén, 2003). The abiotic niche of a species, defined using only scenopoetic variables, contributes to shape its colonizable niche. Reductions of the abiotic niche, due to competition and dispersal restrictions, lead to the occupied niche (Soberón, 2007).

In this work, we explored the colonizable versus the occupied niche of *S. villosa* in one of its larger, undisturbed populations situated at the Feniglia dune system (Tuscany, Italy). Basing on a Strip Adaptive Cluster Sampling procedure and by applying unbiased Horwitz–Thompson estimators to the sampled data, we calculated the total abundances of both mature and juvenile thalli in the entire dune system. Then, we used the detailed plot-level dataset for testing two alternative hypotheses for the propagation of *S. villosa*. According to the first hypothesis, *S. villosa* is presently occupying most of its potential niche because many parts of the *Juniperus* shrubland are not a suitable habitat for this species. In this case, the environmental predictors would play a decisive role in shaping the abundance of both mature and juvenile thalli within the population. The second hypothesis predicts that the occupied niche of *S. villosa* is considerably smaller than its colonizable area because of the poor dispersal performance of the species. If the second hypothesis is correct, the effects of pure space and/or the abundance of mature thalli on the occurrence of juvenile thalli should overcome those of environmental factors, the juvenile thalli being in strict relation with the occurrence of mature thalli at the same site.

Methods

Seiophora villosa is a fruticose lichen with compressed-canaliculate laciniae, a hispid villose cinereous upper side, and a whitish, naked lower side. Apothecia are usually present, and are sub-apical, concave, and with red disks. In the Mediterranean basin this lichen is widespread, but not common, along the coasts of Spain, Portugal, Italy, the Greek islands, Israel and North Africa (Frödén and Lassen, 2004). In Italy, *S. villosa* has a western distribution along the peninsula (Nimis and Martellos, 2008), occurring in Tuscany, Latium, Campania, Sardinia and Sicily, where it grows on twigs of shrubs and trees (mainly *Juniperus* spp.) exposed to frequent humid maritime winds on sand dunes (Benesperi and Ravera, 2011).

The Duna Feniglia State Nature Reserve is a protected area encompassing Special Protection Area IT51A0028 (92/43 CEE Directive) in the coastal region of Southern Tuscany (Italy). Occupying an area of 474 ha, the reserve includes three main vegetational zones: a band overlooking the sea, consisting of typical coastal dune with psammophilous plants and a priority habitat with *Juniperus* spp. (Natura 2000 code 2250*), a central belt covered by Italian stone pine forest, and a narrower band with mixed pine-broadleaved species.

Preliminary observations of the survey area revealed a clustered distribution of the *S. villosa* population. We, therefore, applied strip adaptive cluster sampling (SACS), which in the case of non-homogeneous distribution of a target population gives better performance than the usual non-adaptive strategies (Pontius, 1997). SACS is based on two-level sampling, with a biased selection of sampling units. We randomly selected 15 primary units (strips) all along the dune system (Fig 1). Each strip was divided into secondary units, which were represented by 5×5 m square plots extending from the sea front to the back edge of the *Juniperus* shrubland across the dune. If *S. villosa* occurred in a secondary unit selected by the initial sample, we inspected every secondary unit in its neighborhood (Fig 2). Similarly, if *S. villosa* was found in a neighboring secondary unit, then every unit in that unit's neighborhood was inspected. This process continued until no additional secondary units hosting thalli were identified. The set of all such units in which *S. villosa* occurred was defined as the network associated with the initial sample. In this manner, we investigated a total of 92 secondary sampling units.

We visually counted both juvenile and mature thalli on each shrub and summed them per plot. Thalli that were < 3 cm in diameter and lacking apothecia were considered to be 'juvenile'. To control for the effect of thallus detectability, we carried out quality assurance procedures on a subset of plots, fixing the accuracy threshold at 80 % with respect to the count obtained by a control team.

For each plot, a set of environmental predictors potentially related to the establishment success of juvenile thalli was recorded in the field or obtained from cartographic data, including number of shrub species within the plot, average trunk circumference, total number of shrubs, distance of the plot from the sea, and the angle between the shrubland front and the main wind direction. We calculated pairwise dissimilarity matrices for geographic distance between plots

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