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Propagule size is not a good predictor for regional population subdivision or fine-scale spatial structure in lichenized fungi

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ABSTRACT

Propagule size has important consequences on the genetic structure of wind-dispersed species, as species with small propagules have higher capability of long-distance dispersal. Here, we studied reproductive modes and compared local and regional population structures in three Macaronesian lichenized fungi differing in propagule size. First, we quantified size distribution of propagules in each species. Second, genotype simulations based on microsatellite data were used to infer the reproductive mode. Third, using spatial analysis and population genetic approaches, we quantified the local and regional scale genetic structures of the fungal species. The three species differed in size distributions of propagules. The majority of populations exhibited clonal reproductive mode. Identical reproductive modes occurred often across species in the same sites, implying a possible relationship between reproductive mode and local site conditions. Contrary to expectation, at the local scale, the species exhibited similar patterns of spatial autocorrelation in genotypes. However, in agreement with the expectation based on propagule size, the species with highest frequency of small vegetative propagules (*L. pulmonaria*) exhibited lowest regional genetic differentiation. Nevertheless, altogether, our results show that propagule size is not a good predictor of population subdivision in lichenized fungi, neither at local nor regional spatial scale.

Introduction

Propagule size is an important factor affecting dispersal capacity in wind-dispersed plants. In plants, species with small seeds (i.e. low seed mass) are more efficient at dispersing over long distances than those with larger seeds, but establishment success is higher in species possessing large seeds (Morse & Schmitt 1985; Greene & Johnson 1993; Gravuer *et al.* 2003; Greene & Quesada 2005; Skarpaas *et al.* 2010; De Ryck *et al.* 2012). Hence, there is a tradeoff in propagule size, where high dispersal capability excludes high establishment success. Moreover, propagule size can have repercussions on population structure. Species with small, widely dispersing propagules would have less genetic differentiation between

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sites, as long as the small propagules are able to establish successfully. No effect of propagule size on population structure is expected if the establishment success of small propagules is low. Species may exhibit a size range in propagules, and effective dispersal rates may depend on the amount of small, lightweight propagules relative to heavier propagules.

The reproductive mode of a species has important consequences on its population subdivision (Hartl & Clark 1997). Lichenized fungi are interesting objects for population genetic studies because they form an obligate symbiosis with photosynthetic green-algae and/or cyanobacteria ('photobionts') and can reproduce either vegetatively with specialized clonal propagules or sexually with meiotic spores produced in apothecia (Büdel & Scheidegger 2008; Werth & Sork 2008; Scheidegger & Werth 2009). Some lichenized fungi have a mixed reproductive system with vegetative and sexual reproduction, as has been reported e.g. for the heterothallic lichenized fungus *Lobaria pulmonaria* (Dal Grande *et al.* 2012; Werth & Scheidegger 2012) and other species (Kroken & Taylor 2001; Högberg *et al.* 2002). Different mating systems are known for the haploid lichenized ascomycetes. For successful sexual reproduction, heterothallic species require a partner with compatible mating type (Scherrer *et al.* 2005; Seymour *et al.* 2005b; Scheidegger & Werth 2009; Singh *et al.* 2012). Heterothallism is thus analogous to obligate outcrossing in higher plants. For lichenized fungi, heterothallism is the most common mating system. However, some species were found to be homothallic, i.e. able to reproduce *via* selfing (Honegger *et al.* 2004; Seymour *et al.* 2005a; Honegger & Zippler 2007).

Here, we investigate the relationship between propagule size and genetic structure as well as reproductive mode in three codistributed species of lichenized fungi in Macaronesia, the Macaronesian endemics *Lobaria immixta* and *L. macaronesica*, and the widespread *L. pulmonaria*. These species can reproduce clonally and sexually but they differ in type and size distributions of clonal propagules.

We use a simulation approach to infer the reproductive mode of populations. Genotype simulations allow determining whether the number of multilocus genotypes (MLG) is consistent with a randomly mating population (Werth & Sork 2008; Werth & Scheidegger 2012). Compared with random mating, clonal reproduction leads to a reduction of the number of MLG in a sample. In fungal species sharing the same photobiont pool such as the species we studied (Dal Grande 2011), recombinant population structures in the same sites across species could either be the result of unknown favourable environmental factors (e.g. beneficial microclimate; high quality of microhabitats in a site) or of local availability of compatible photobionts.

First, we quantified the size distributions of vegetative propagules in each species to assess whether the species were likely to have different capabilities for long-distance dispersal. Second, we investigated the reproductive modes of the studied populations, as we were interested in evaluating whether reproductive modes were similar across species within the same site. To this end, we also evaluated whether sexual thalli occurred spatially aggregated, which would imply that beneficial environmental factors may trigger concerted fruiting across species. Third, we compared patterns of regional genetic differentiation across species. We hypothesized that the genetic differentiation among archipelagos would be lowest in the species with the smallest, putatively most far-dispersing clonal propagules. Fourth, we contrasted the fine-scale spatial autocorrelation in genotypes between species. We predicted that due to its small-sized and putatively far-dispersing clonal propagules, the extent of spatial autocorrelation in genotypes should be largest in the species with the highest fraction of small-sized propagules.

Material and methods

Study species, study area, and sampling

We investigated all species within *Lobaria* sect. *Lobaria* occurring in our study area: *Lobaria immixta* Vain., *Lobaria macaronesica* Cornejo & Scheid., and *Lobaria pulmonaria* (L.) Hoffm. These species are closely related (Cornejo & Scheidegger 2010). *Lobaria immixta* and *L. macaronesica* are sister species, and the widespread *L. pulmonaria* is their closest relative. While *L. pulmonaria* is widespread in Mediterranean to boreal parts of the Northern Hemisphere, with some occurrences in the Southern Hemisphere (Yoshimura 1971), *L. immixta* and *L. macaronesica* are Macaronesian endemics, with only one known occurrence on the Iberian Peninsula in an oceanic site with a high affinity to the Macaronesian flora (Burgaz & Martinez 1999; Cornejo & Scheidegger 2010; Werth *et al.* 2010, 2013b). The reasons for the discrepancy in distribution between the endemics and the widespread species are thus far unknown. It could be that the endemic species have a narrower ecological amplitude; on the Macaronesian islands, the endemics occur almost exclusively in the moistest sites (Laurisilva), while *L. pulmonaria* also occurs in the drier Canary Pine forest. Similar to what has been observed in Macaronesian endemic fungi of the genus *Nephroma*, *L. immixta* and *L. macaronesica* might represent neoendemics that arose after island formation (Sérusiaux *et al.* 2011), and if this was indeed the case, they would not have had equally much time to expand their distribution as *L. pulmonaria*. The three species of *Lobaria* are all associated with the same primary photobiont, the green alga *Dictyochloropsis reticulata* (Dal Grande 2011). They form large, foliose lichens inhabiting trunks and branches of trees in moist forests of the study area where they are associated with the Lobarion community (Rose 1988; Gauslaa 1995; Schumm 2008). According to our field observations from Macaronesia, all three species frequently form fruiting bodies (apothecia), the structures where microscopically small fungal ascospores are produced. The three fungi frequently cooccurred in the Lobarion community on the same host trees (phorophytes), which led to equal spatial sampling across species, a prerequisite to compare fine-scale spatial autocorrelation. The three taxa are recognized morphologically based on their clonal, symbiotic propagules: globose as well as cylindrical, secondarily developed structures (soredia) in *L. pulmonaria*; larger coralloid branched or unbranched structures (isidia) in *L. macaronesica*; and flat marginal protuberances (phyllidia) in *L. immixta* (see Fig 4 in Cornejo & Scheidegger 2010).