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## Multiple-scale environmental modulation of lichen reproduction

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### ABSTRACT

It is necessary to understand how environmental changes affect plant fitness to predict survival of a species, but this knowledge is scarce for lichens and complicated by their formation of sexual and asexual reproductive structures. Are the presence and number of reproductive structures in *Lobaria pulmonaria*, a threatened lichen, dependent on thallus size, and is their formation sequential? Does any size-dependence and sequential formation vary along a climate gradient? Generalized linear mixed models were used to explore the effect of environmental predictors on the size and presence/abundance of each reproductive structure and to determine the probability of a given-sized thallus to develop any reproductive structure. The largest individuals are more likely to develop reproductive structures, and the lichen uses a mixed strategy of early asexual reproduction and late sexual. Macro and microclimatic variables also influenced reproductive capacity. Relationships among climate conditions and lichen size and reproductive capacity can compromise the future viability of the species in the most southern populations of Europe.

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### Introduction

Having good estimates of fitness is a basic requisite for ecological studies at the species level (Young & Clarke 2000; Picó 2002; Milla *et al.* 2009). Understanding plant fitness responses to certain conditions is also critical when assessing the evolutionary impact of environmental heterogeneity, even more so for predicting the viability of the species (Jackson *et al.* 2006; Milla *et al.* 2009). In exploring this broad topic in detail for vascular plants, numerous researchers have developed a conceptual framework for explaining the relationships between size/age and reproduction (e.g., Harper & White 1974; Barot *et al.* 2002) and how the individual adjusts resource allocation between growth and

reproduction (Bazzaz & Reeckie 1985; Shipley & Dion 1992; Méndez 1999). Unfortunately, our knowledge on these critical issues for other biological groups is scarce and especially urgent in the case of certain groups such as lichenized fungi. Among the reasons that have been posed to explain this scarcity are the difficulties in obtaining good fitness estimates due to the 'supposed' great longevity of lichens and to the fact that the stages of their life cycle may not be completely known (Jackson *et al.* 2006). In this sense, we still need detailed demographic research for lichens, urgently for threatened lichen species (Scheidegger & Werth 2009).

Estimating the contribution of various components to the fitness of lichens is especially complex because lichens

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comprise two or more organisms and can reproduce sexually and asexually. Lichens are symbiotic associations between a mycobiont and one or more photobionts, mainly green algae and/or cyanobacteria (Friedl & Büdel 2008). As a consequence, reproduction in lichens is quite complex (Honegger 1998), being able to reproduce sexually, but also to form structures for asexual proliferation. Most lichens form apothecia with sexual fungal spores and symbiotic asexual reproductive structures of various sizes and shapes such as isidia or soredia (Büdel & Scheidegger 2008). The establishment of a new lichen association via sexual reproduction requires the germination of a mycobiont in a suitable microhabitat and rapid contact with a suitable photobiont (Honegger 1996; Seymour *et al.* 2005), which may be specialist or not (Otálora *et al.* 2010). Sexual reproduction seems especially suitable for long-distance dispersal, because spores are smaller than asexual propagules (Muñoz *et al.* 2004). On the other hand, asexual reproduction, which is genetically less variable (Williams 1975; Lawrey 1980), has the advantage of dispersing simultaneously from the photobiont and mycobiont and does not require relichenization (Seymour *et al.* 2005; Otálora *et al.* 2010).

Knowing when, where, and how these reproductive structures are developed during the life cycle of lichen species remains a priority. Only Denison (2003) has reported a full life cycle; following five individuals of *Lobaria pulmonaria* (L.) Willd. over a year, founding that apothecia emerge in late spring in this species. Several studies showed that some lichen species have thallus size-dependent survival probably because water retention capacity is higher in large thalli, allowing them to photosynthesize longer than smaller individuals (Hestmark 1997; Gauslaa & Solhaug 1998). Larger thalli could also be more efficient at forming sexual reproductive structures (Hestmark 1992; Ramstad & Hestmark 2001; Pringle *et al.* 2003). In addition, some studies have shown that some lichen species need to reach a critical mass/size before allocating resources to reproduction (Hestmark 1992; Clayden 1998; Ramstad & Hestmark 2001; Pringle *et al.* 2003), whereas others found the contrary (Jahns *et al.* 1978; Tretiach & Carpanelli 1992). Recently, Gauslaa (2006) showed that transplanted lobes of *L. pulmonaria* that had a greater amount of soredia/isidia had growth rates lower than those individuals with few or no asexual propagules, suggesting a trade-off between reproductive and vegetative growth allocation.

Most organisms can be found in a wide range of habitats or environmental conditions and, consequently, substantial intraspecific variation in vital processes such as fecundity should be expected as a reaction to this patchy heterogeneity. Study of the variation in vital processes from lichen to lichen between site/population conditions and particularly in reproductive parameters and structures, is interesting not only from an ecological perspective but also from an evolutionary perspective. Such variation is critical to understand the entire distribution of a species and how its demography adjusts to environmental conditions and, even more importantly, to predict changes in range limits in response to future climate change (Gaston 2003, 2009). Although many studies have been conducted on other groups of organisms to assess this possible relationship (Lennartsson & Oostermeijer 2001; Wilson *et al.* 2005; Giménez-Benavides *et al.* 2007; Marrero-Gómez *et al.* 2007), none have been done for lichens.

To our knowledge, size-dependence of lichen reproduction and between-site variation of reproductive traits have not been addressed together. However, a theoretical framework has been proposed for angiosperms (Freeman *et al.* 1980; Korpelainen 1998) on the basis of three models: (1) a patchy environment model (Freeman *et al.* 1980) in which sexual reproduction is mediated by stress conditions, (2) a size advantage model (Warner 1975) in which sexual reproduction is mediated by changes in size, and (3) a mixed model combining models 1 and 2.

To test these theoretical models in lichens, we have chosen as a model species the endangered epiphytic lichen *L. pulmonaria* because it is one of the best-known lichen species from an ecological point of view (Belinchón *et al.* 2009; Scheidegger & Werth 2009). This epiphytic species forms soredia and/or isidia (isidioid soredia, following Scheidegger (1995)) as asexual reproductive structures and occasionally forms apothecia as sexual reproductive structures (Belinchón *et al.* 2009; Scheidegger & Werth 2009). Recently, two studies have focused in different aspects related to factors influencing reproduction capacity in *L. pulmonaria*. Hilmo *et al.* (2011a) in a study about the population characteristics of epiphytic lichens in *Picea abies* plantations, found a correlation between thallus size and probability of reproduction in *L. pulmonaria*. Besides, Mykriukov *et al.* (2010) developed a study about the influence of certain ecological determinants on the reproduction of *L. pulmonaria* populations in the Urals. They found that total cover of *L. pulmonaria* and type of forest (coniferous or deciduous) influence the reproductive status of the populations.

The study of sexual reproduction in lichens is difficult because lichenized ascomycetes can be either homothallic or heterothallic species, depending on whether the haploid mycelium differentiates gametangia and gametes in the same thallus or on different thalli (Honegger & Scherrer 2008). Unfortunately, for most of lichen species, such information is lacking (Honegger & Scherrer 2008). So, with these difficulties our main goal is to know which are the most important factors determining lichen reproduction. We hypothesized those populations growing in more humid locations will have larger individuals and thus produce more reproductive structures, and that reproductive structures will develop in sequence, first asexual, then sexual. To test our hypothesis we determine different specific objectives: (1) to know when sexual or asexual structures are developed?; (2) to evaluate if there is any kind of hierarchy or sequence between the development of sexual and asexual structures; (3) to know which is the sizes structure of *L. pulmonaria* populations; (4) to evaluate if environmental conditions influence individual size and reproductive capacity.

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## Materials and methods

We selected 16 locations along a wide bioclimatic gradient that included two biogeographical regions (Atlantic and Mediterranean regions) in Spain (Fig 1; Table 1). Our goal was to include in the study *Lobaria pulmonaria* populations distributed along the Iberian Peninsula, trying to get the highest latitudinal gradient. Besides, populations included in the study had to

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