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High demographic rates of the model epiphyte *Lobaria pulmonaria* in an oceanic hazelwood (western Scotland)

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ABSTRACT

The lichen *Lobaria pulmonaria* is a case-study species for research in forest ecology. Previous studies have emphasised both its niche specialism and slow growth with long generation times, explaining its occurrence on larger/older trees in forest stands with long temporal continuity. Contrastingly, *L. pulmonaria* is common among a broader range of habitats within an oceanic ('temperate rainforest') bioclimatic zone, and we investigate its population dynamics within this context to expand our understanding of the ecology of this model organism. The results indicated some of the highest growth rates and shortest generation times observed globally, with reproductive maturity achieved within c. 5–10 yr. This rapid growth to maturity and raised propagule density can explain the rapid colonisation of *L. pulmonaria* onto very young hazel stems. The work emphasises the viability of large populations of *L. pulmonaria* in western Scotland, underlining an International Responsibility for protection within a European context.

Introduction

The lichen epiphyte *Lobaria pulmonaria* (Fig 1A) is firmly established as a model organism in meta-population ecology and conservation biology (Scheidegger and Werth, 2009). The species is a dominant component of epiphyte communities in mixed broadleaf woodland in unpolluted environments of temperate Europe (Farmer et al., 1991; Scheidegger et al., 1998). It has a long-life-span (estimated to be 200 yr; Scheidegger et al., 1998) and has been described as a 'patch-tracking' organism (Snäll et al., 2005), colonising onto tree boles and persisting until tree mortality. Generation time is as yet uncertain (Scheidegger and Werth, 2009) though has been estimated to be at least c. 20 yr (Scheidegger et al., 1997) with higher rates of reproductive capacity occurring after c. 35 yr (Scheidegger and Goward, 2002).

Previous studies using both direct observation and molecular inference have suggested that *L. pulmonaria* is either dispersal-limited (Scheidegger, 1995; Gu et al., 2001; Walser et al., 2001), a habitat specialist (Werth et al., 2006; Otálora et al., 2011), or both (Öckinger et al., 2005; Jüriado et al., 2012), occurring preferentially on the sub-neutral bark

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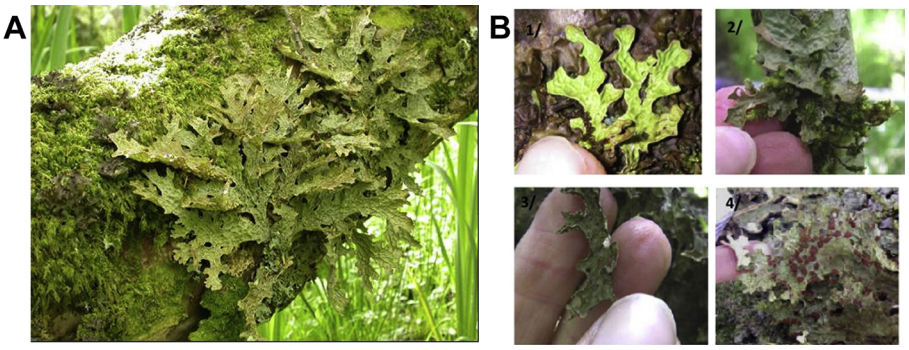

Fig 1 – (A). The foliose lichen *Lobaria pulmonaria*, a dominant species within the '*Lobarion*' community of lichen epiphytes (Barkman, 1958; Rose, 1988); (B). *Lobaria pulmonaria* life stages: (1) Juvenile *L. pulmonaria* thallus, which is small with closely adpressed lobes; (2) Mature thallus with developing larger and free lobes but without reproductive structures; (3) Mature thallus with isidia/soredia occurring on the lobes; and (4) Mature thallus with apothecia.

(Gauslaa, 1995; Rose, 1988) of larger/older trees (Gustafsson et al., 1992; Riiali et al., 2001) within ancient woodland stands (Rose, 1976, 1992; Scheidegger and Werth, 2009). Consequently, the species has been applied as a bioindicator for woodland continuity (Rose, 1976; Gauslaa, 1994; Kuusinen, 1996) and associated high biodiversity (Campbell and Fredeen, 2004; Nascimbene et al., 2010). Previous work on *L. pulmonaria* in Europe has, therefore, emphasised: (i) its longevity and slow reproductive maturity (ii) its niche specialism, and (iii) its dispersal limitation, which suggests that the species combines archetypal life-history traits of an organism expected to be threatened by anthropogenic change. For European forests, this includes the transition from old-growth to rapid rotation forestry and habitat fragmentation (Rose, 1992; Scheidegger et al., 2000; Scheidegger and Goward, 2002).

The majority of published research on the ecology of *L. pulmonaria* in Europe is focussed in relatively continental climatic regimes where it is often rare in the landscape; contrastingly, the species is common in oceanic environments, such as that occurring along the west coast of Scotland (Rose and Coppins, 1998). This difference in abundance possibly reflects an interaction between the macroclimate and an organisms' microhabitat specificity (Lisewski and Ellis, 2010), such that a species may become increasingly restricted to a limited suite of buffered microclimatic niches under sub-optimal macroclimatic conditions (Doering and Coxson, 2010), and therefore rarer. A further mechanism explaining the species' abundance in western Scotland might be faster growth rates within an oceanic climate (Eaton and Ellis, 2012). The onset of reproductive maturity is known to be related to thallus size with larger thalli being more likely to support reproductive structures than their smaller counterparts (Martinez et al., 2012). Therefore it is likely that populations exhibiting faster growth rates reach reproductive maturity more rapidly than those exhibiting slower growth rates (Høistad and Gjerde, 2011; MacDonald and Coxson, 2013). In turn this could lead to an increased colonisation pressure into sub-optimal habitats under source-sink dynamics (Pulliam, 1988), as has been previously invoked to explain the distribution of lichen epiphytes, including *L. pulmonaria* (Jüriado et al., 2012).

In this paper we estimate demographic rates for *L. pulmonaria* in a hazelwood (*Coryllus avellana*) in oceanic western Scotland. First, this provides new information in the population biology of this model organism, for a bioclimatic region in which it is relatively common, and which geopolitically is expected to have International Responsibility for the species' protection (Woods and Coppins, 2012). Second, demographic information used to interpret the dynamics of the species within the hazelwood system contrasts with situations in which *L. pulmonaria* has been shown to colonise slowly onto larger and older, mature and over-mature trees (Gustafsson et al., 1992; Hilmo et al., 2011; Öckinger et al., 2005). Individual hazel stems tend to be relatively short-lived with rapid turnover among stem microhabitats, though the hazel stools from which stems originate may themselves be persistent: we ask how it is possible for *L. pulmonaria* to persist in a woodland system with a rapid turnover of relatively short-lived microhabitat?

Methods

Study site

A single hazelwood (Fig 2) study site was located on the Morvern Peninsula of western Scotland (Fig 3). Historic

Fig 2 – An image of the interior of the hazelwood study site in Drimnin.