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Achieving Landscape-scale Conservation for Scotland's Rainforest Epiphytes

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PhD Thesis

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Abstract

Within the UK, the continuing biodiversity crisis has led to a policy driven shift in the conservation sector; moving away from localized site scale conservation to a landscape-scale. This approach encourages fragmented habitat patches to be integrated into a much larger habitat network. Epiphytic lichens provide an ideal model system for studying the effectiveness of conservation initiatives within fragmented habitats, due to their metapopulation structures whereby individual trees within woodlands (and woodland stands within wooded landscapes), represent isolated habitat patches.

Old-growth woodland in particular provides suitable habitat to a suite of lichens known as the *Lobarion* community, which are declining throughout Europe. Regeneration within these old growth areas, though essential for future habitat persistence, causes shading and ultimately leads to local extinctions of shade intolerant lichen epiphytes. A landscape scale conservation strategy that relies on habitat permeability to balance colonisation of post-regeneration woodland patches with extinctions in ageing woodland patches elsewhere in the landscape has been proposed as a management strategy to meet the needs of both lichen epiphytes and their woodland habitat. The unique conditions found in western Scotland, combining a relative abundance of high quality old growth habitat (in a European context) coupled with robust populations of some members of the *Lobarion* community, could provide an ideal opportunity to test such a management strategy.

In this thesis, the plausibility of landscape-scale conservation as a management strategy for epiphytic lichens is explored, using a suite of nine target epiphytes of contrasting ecological traits set within Glen Creran, a temperate rainforest on the west coast of Scotland:

1. The habitat requirements of nine target epiphytes were identified and predictions of species distribution made over an entire glen using a species distribution modelling (SDM) approach. The SDM's were found to apply more generally within the wider biogeographic area for five of the nine species, providing an evidence base for future conservation plans in Scotland's rainforest zone.

2. A novel method to determine dispersal distance in lichen epiphytes was developed, combining a mechanized propagule trap with molecular techniques. This methodological advance allowed the first direct comparative study of lichen epiphytes in a natural context.

3. An agent based model was developed combining the results of 1. and 2. above to investigate the effect of habitat connectivity on colonisation in six contrasting lichen epiphytes, enabling inferences of species response to landscape-scale conservation scenarios within the study system to be made.

Document contents

Papers

This thesis is based on the following papers which are referred to in the main body of the text:

I. Eaton, S., Ellis, C., Genney, D., Thompson, R., Yahr, R. and Haydon, D.T. 2018. Adding small species to the big picture: Species distribution modelling in an age of landscape-scale conservation. Biological Conservation, 217, pp.251-258. DOI https://doi.org/10.1016/j.biocon.2017.11.012

II. Eaton, S., Ellis, C. J. and Yahr, R. 2018. How Many? Spore emission experiments in four species characteristic of old-growth woodlands. The Lichenologist. Accepted for publication.

III. Eaton, S., Zuniga, C., Czyzewski, J., Ellis, C.J., Genney, D., Haydon, D., Mirzai, N. and Yahr, R., 2018. A method for the direct detection of airborne dispersal in lichens. Molecular Ecology Resources. Published on-line. DOI: 10.1111/1755-0998.12731

IV. Eaton, S., Yahr, R., Haydon, D.T., Genney, D. and Ellis, C. J. An inter-specific study of dispersal in lichen epiphytes. Manuscript.

V. Eaton, S., Genney, D., Yahr, R., Haydon, D. and Ellis, C. J. Agent-based modelling for old-growth woodland dependent species: a simulation for lichen conservation. Manuscript.

The contribution to the papers included in this thesis was as follows:

I. CE, DH, DG, RY, RT and SE conceived the ideas and designed the methodology, SE collected the data, SE analysed the data with support and guidance from CE and DH, SE led writing of the manuscript with support and guidance from CE and DH. All authors contributed critically to the drafts.

II. SE and RY conceived the ideas and designed the methodology, SE collected and analysed the data, SE led writing of the manuscript with support and guidance from RY and CE. All authors contributed critically to the drafts.

III. SE, CE, RY, DH and DG conceived the initial ideas for this project. NM, JC and SE designed the propagule traps, JC built the propagule traps, CZ designed the species-specific primers with support and guidance from SE and RY, SE optimized the DNA extraction and nested PCR protocol with support and guidance from RY, SE conducted sensitivity, specificity and proof of concept tests with support and guidance from RY and CE. SE led the writing of the manuscript with support and guidance from RY and CE. All authors contributed critically to the drafts.

IV. SE, CE, DH, DG and RY conceived the ideas and designed the methodology, SE collected the data, SE analysed the data with support and guidance from CE, RY and DH, SE led writing of the manuscript with support and guidance from CE and DH. All authors contributed critically to the drafts.

V. SE, CE and DG conceived the ideas and designed the methodology, SE designed and built the model, SE ran the simulations and analysed the data with support and guidance from CE and DH, SE led writing of the manuscript with support and guidance from CE and DH. All authors contributed critically to the drafts.

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Front cover image: Sally Eaton: taken from the south-western shore of Loch Creran looking down into Glen Creran.

Authors Declaration

I declare that, except where explicit reference is made to the contribution of others, that this dissertation is the result of my own work and has not been submitted for any other degree
at the University of Glasgow or any other institution.

Printed Name:

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Signature:

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List of Abbreviations:

ASN	Ancient Semi-Natural (Woodland)
AUC	Area Under the (Receiver Operating) Curve
CT	Classification Tree
GAM	Generalised Additive Model
GLM	Generalised Linear Model
GLMM	Generalised Linear Mixed Model
HM	High Management
LD	Long Distance
LDD	Long Distance Dispersal
LM	Low Management
LSC	Landscape-scale Conservation
NPMR	Non-Parametric Multiplicative Regression
NWSS	Native Woodland Survey of Scotland
RW	Regenerating Woodland
SD	Short Distance
SDD	Shot Distance Dispersal
SDM	Species Distribution Model
SLCS	Small/Less Charismatic Species
SSSI	Site of Special Scientific Interest
SW	Source Woodland
TSS	True Skill Statistic

Chapter 1. Introduction

In this chapter I will first introduce my study system; lichens within the epiphytic habitat, and explore processes and patterns of importance to the conservation of these fascinating organisms. Second, I will introduce the concept of landscape-scale conservation, and explore how it may offer a conservation solution for lichen epiphytes found within a temperate rainforest landscape of western Scotland.

1.1. Lichen epiphytes

1.1.1 What are lichens?

There are around 28,000 species of lichens worldwide, found on every continent in a variety of habitats from sea shores to mountain tops, from deserts to tropical rainforests (Galloway 2008). They are the dominant organisms in around 8% of the world's land area and they play important roles in many terrestrial ecosystems. Supporting services provided by lichens include soil formation, rock decomposition and nutrient cycling; regulating services include water regulation and erosion prevention; provisioning services include their use as food stuffs, as medicines, or dyes; and cultural services include bioindication, inspiration for art and design, and use as educational tools. In addition, they provide food, habitat, camouflage and nesting material to numerous other organisms.

Lichens are stable, self-supporting associations of a fungal partner, the mycobiont, and a photosynthesising partner, the photobiont (Kirk et al 2008). The mycobiont and photobiont live together in a symbiosis whereby the fungal partner provides the main structure of the organism and produces chemicals which protect both partners from environmental stress (such as UV rays and desiccation), whereas the photobiont produces sugars through the process of photosynthesis (which are assimilated by the mycobiont). Most lichenologists view the symbiosis as a mutualistic relationship, whereby mycobiont and photobiont both receive benefit, though there are some lichenologists who perceive the symbiosis as being in the mycobiont's favour, and thus represent a form of controlled parasitism (Ahmadjian 1993).

Though lichens are comprised of more than one species, they are named after the mycobiont, which in 99% of cases is an ascomycete fungus (Lücking et al 2016). The photosynthetic partner of the lichen may comprise a green alga, or a cyanobacterium, or in the case of some species e.g. *Lobaria pulmonaria*, both an alga and a cyanobacterium. More recent research has demonstrated that there are more than the two (or three) partners living together within the lichen symbiosis however, with bacteria apparently omnipresent (Grube et al 2015) and basidiomycete yeasts being found in the cortex of many common lichens (Spribille et al 2016).

1.1.2 Life history traits

The life cycle of an epiphytic lichen comprises several stages as demonstrated in Figure 1, each of which will be discussed in turn below.

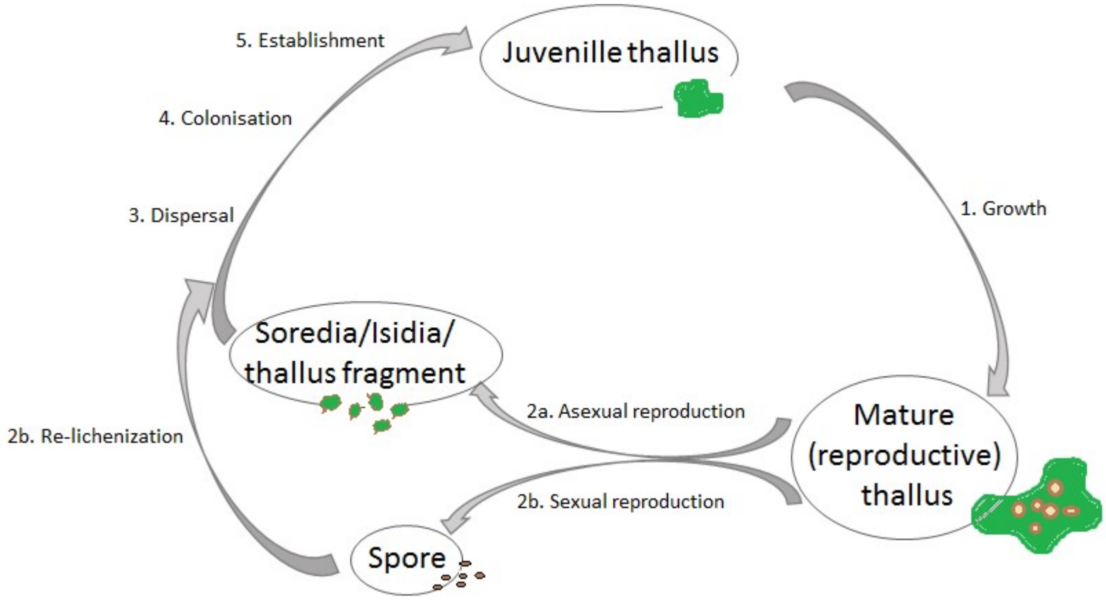

Figure 1. The lichen life-cycle

Stage one of the lichen life cycle sees a juvenile thallus grow into a mature thallus. The time taken for a thallus to reach reproductive maturity is both species- and environment-specific. For example, in the relatively cold dry climate of continental Europe, *Lobaria pulmonaria* has been reported to take around 20 years to reach reproductive maturity (Scheidegger et al 1997), whereas in the milder wetter conditions of western Europe it has been estimated to take as little as 5 years (Eaton & Ellis 2014).

Stage 2 of the life cycle comprises the reproductive stage, which occurs as a result of asexual reproduction, sexual reproduction, or both. Asexual reproduction occurs in a process by which packages of the mycobiont and photobiont are released together. These packages, known as soredia or isidia, are produced in a variety of ways (from the thallus surface, edge or underside), and take on a variety of shapes and sizes. These propagules are not actively discharged and rely on external factors such as air movement, a passing invertebrate or rain splash, to detach them from their parent thallus. The vast majority of lichen epiphytes reproduce sexually however (Purvis et al 1992), and thus produce spores which represent the mycobiont component of the symbiosis only. Spores are produced from reproductive structures found on the surface of the thallus called apothecia or perithecia. The full details of sexual reproductio1n in lichens are not yet fully understood, though it is thought to involve the fusion of a spermatium (a mobile gamete) with a trichogyne (a receptive hypha) (Culberson et al 1988, Honegger 1984, Sanders 2014, Zoller et al 1999,). Some species are able to 'self', that is to successfully fuse a spermatium and trichiogyne from a single thallus, whereas others are self-incompatible (Honegger et al 2004, Honegger & Zippler 2007). Under suitable conditions the spores are ejected from asci into the atmosphere, where they may be picked up by a wind current or alternative dispersal vector. After being deposited however, before a spore can go on to establish in its new habitat, it must find an appropriate algal partner in a process known as lichenization. Lichenization is a critical part of the life cycle given that, one; most lichen fungi cannot survive for very long without their photobiont partner (Ahmadjian 1993) and two; the mycobiont shows very strong selectivity for particular photobionts (Beck et al 2002, Rikkinen et al 2002, Stenroos et al 2006, Summerfield *et al.*, 2002, Yahr et al, 2004). Many photobiont species are found in free-living populations as well as within lichen symbioses (Nash 1996), allowing developing spores to lichenize with free-living photobiont cells. Many cyanolichens (lichens whose photobiont partner is a cyanobacterium rather than a green algae) share a pool of cyanobacteria which are found in both a free-living and lichenized form (O'Brien et al 2013). These species are thought to lichenize through a community process (known as the core-fringe hypothesis (Rikkinen et al 2002) including facilitation (Belinchòn et al 2015, Fedrowitz et al 2012)), whereby asexual propagules (containing the required cyanobacterial photobiont) of more common species first arrive onto an uncolonized tree, and only once these asexual species have established (along with the required cyanobacteria) are the sexual species able to colonise. The rarer sexual species thus sequester the photobionts from the asexual propagules of prior colonists.

Stage 3, 4 and 5 of the lifecycle comprise dispersal, colonisation and establishment and allow the reproductive propagule to develop into a juvenile thallus. Note, throughout this document, the collective term 'propagules' is used when referring to sexual spores, asexual soredia/isidia, or both. The respective costs and benefits of the different propagule types appear to predispose them to different ecological responses; asexual propagules are larger and heavier than their sexual counterparts and as a result are thought to be less capable of dispersing relatively longer distances (Seaward 2008). Sexual spores on the other hand, being small and light, are thought to be better adapted to long distance dispersal, though having arrived in an area of suitable habitat they are restricted in their establishment by the need to find a suitable photosynthetic partner.

Dispersal, colonisation and establishment are discussed in detail in Section 2.2.1 of this thesis.

1.1.3 The epiphytic habit

Epiphytes are species that grow on living plants, largely trees. By growing on another plant, epiphytes are able to escape the competition for space and light found at the ground level in wooded habitats. All epiphytes are photosynthetic and are thus able to produce their own food. They come in the form of vascular plants, algae, bryophytes and lichens. Water and nutrients are gathered from rainwater and humid air, and in this way they rely on the substrate for little more than structural support. The epiphytic habitat plays to a lichen's evolutionary adaptation; being poikilohydric organisms, lichens are able to withstand the prolonged dry periods often experienced above ground, rehydrating when water becomes available.

Considering the large surface area of a tree compared to its basal area, and the fact that 30% of the world's land area is covered by woodlands and forests (NASA 2012), it becomes clear that epiphytes have an extensive amount of habitat space available to them. When you consider that a single tree has been found to support 173 species of lichen epiphytes (Aptroot 2001) the biodiversity potential of the epiphyte habitat becomes apparent.

1.1.4 Habitat specificity

Within the epiphytic habitat some lichens are more patchily distributed than others; some species appear to occur relatively frequently, on a wide variety of tree species and in a wide variety of situations (in this document, such species will be referred to as habitat generalists), whilst others appear to be extremely restricted in where they are found (here referred to as habitat specialists). This range of specificity in the epiphytic habit exhibited by different lichen species can be attributed to their tolerance of particular conditions, particularly those associated with the bark environment, such as pH (Bates, 1992, Gauslaa, 1995, Jüriado et al., 2009, Kuusinen, 1996, Lewis & Ellis, 2010), roughness (Bates, 1992, Fritz et al., 2009, Ranius et al., 2008), and light availability (Gauslaa & Solhaug 1996, McCune et al., 2000, Williams & Sillett, 2007). In general, trees of different species and age present differing bark habitats, for example the bark of a mature *Fraxinus excelsior* is likely to be courser in texture and higher in pH than that of a young *Betula pendula*. As a result, it is unsurprising that lichen communities would be associated with different tree species (e.g. Esseen 1981, Jüriado et al., 2003, Kuusinen, 1996, Nascimbene et al., 2009) and ages (Brunialti et al., 2010). There are few reports of epiphytic lichens being restricted to a unique tree species, and they are more frequently found on a particular group of trees e.g. *Lobaria amplissima* is chiefly found on *Fraxinus excelsior, Ulmus sp., Acer pseudoplatanus* and *Quercus sp.* in Britain (Smith et al 2010), or on trees of a certain age e.g. *Lobaria pulmonaria* is more commonly found on larger/older trees (Gu et al 2001, Gustafsson 1992, Johansson & Ehrlén 2003). Several studies have shown the importance of tree species and size in controlling epiphyte community dynamics (e.g. Ellis et al 2015), however statistical descriptions of the precise habitat requirements of individual species, leading to predictions of species presence-absence, are not currently available.

1.1.5 The 'old-growth' habitat and the Lobarion

A dependence on older/larger trees is particularly important for certain species, such as those forming what is known as the *Lobarion* community. This is a climax community of epiphytes which are thought to have once been found on mature trees in post-glacial woodlands and forests throughout Europe (Rose 1988). Today the community is more restricted in its distribution (as a result of air pollution and intensive habitat management), and is now considered an indicator of ancient woodland sites with a long ecological continuity (Gauslaa 1995, Kuusinen 1996, McCune 1993, Rose 1976, 1988, 1992). The precise reason for the dependence of these species on 'old-growth' conditions is not yet understood (Scheidegger & Werth 2009), though may be explained by metapopulation processes such as extinction and colonisation (as discussed in Section 2.2.1) which restrict the species to long-lived substrates. The lichen element of this community comprises foliose cyanobacterial lichens including the genera *Lobaria* (Schreber) Hoffm., *Pannaria* Delise, *Nephroma* Ach., and *Degelia* Arv. & Galloway, which are the subject of investigations in this thesis.

1.2 Patterns and Processes of Importance to the Conservation of Lichen Epiphytes

The term metapopulation has been used to describe a "population of populations" (Levins 1969). This nested structure is strongly exhibited by lichen epiphytes, with multiple isolated patches of colonised habitat at two scales 1) trees within a woodland, or 2) woodland stands within a landscape. Lichen epiphytes are thus ideal for study in a metapopulation framework (Hedenås et al 2003, Snäll et al 2003).

Metapopulation theory has become an important tool in conservation planning, as it enables predictions to be made about how the abundance of a species may respond to a change in their wider habitat across the landscape. The most basic spatially structured metapopulation model (Levins 1969) assumes all local populations to be equally connected, making it possible to estimate the rate of change in habitat-patch occupancy, given the difference between the rate of colonization and the rate of extinction. The spatially realistic metapopulation model (Hanski 2001) extends the Levins model to include the effects of patch area (or quality), and connectivity, making it particularly pertinent in modelling the dynamics of organisms whose life cycles are closely linked to that of its habitat (Snäll et al 2003). At a basic level, lichen epiphytes need to be able to colonise a sufficient number of establishing/unoccupied trees, in order to balance those lost through tree fall events.

1.2.1 Population processes in lichen epiphytes

Factors affecting colonisation (including dispersal and establishment) and extinction in lichen epiphytes are discussed in more detail below.

❖ *Colonisation*

According to metapopulation theory, the probability that a habitat patch (such as a tree) will be colonised is dependent on the number of immigrants arriving per unit time (Hanski & Gaggiotti 2004). Colonisation rates of epiphytic lichens however cannot be estimated *in situ*; propagules are microscopic and for several months after deposition there would be no evidence of colonisation to be seen by the naked eye. When it is not possible to measure the number of immigrants into a population, colonisation probability can be calculated as a product of habitat-specific variables (such as spatial pattern of patches, patch size and patch quality which are discussed in Section 2.2.2), and species-specific variables (such as the dispersal ability of the species and survivorship of immigrants, which are discussed below) (Hanski 1999). These species-specific processes can be translated into dispersal and establishment ability in the case of lichen epiphytes.

- Dispersal

Dispersal ability is known to be an important trait influencing the connectivity of patches within metapopulations (Hansson 1991), and therefore species persistence in a changing landscape (e.g. Johst 2002). Being sessile organisms, dispersal is a fundamental process to lichens (Bailey 1976); propagules must successfully disperse to uncolonized habitat patches if long term population persistence is to be secured.

For lichen propagules to successfully disperse, they must undergo four processes; emission, take off, movement across a hostile matrix, and deposition (Clobert 2012, Ingold 1971). These processes are known to be affected by atmospheric conditions such as wind speed, temperature, atmospheric pressure, air turbulence and precipitation (Armstrong 1987, Bailey 1976, Hirst et al 1967, Kuparinen 2006). Despite numerous studies of dispersal in lichens there seems little agreement concerning their overall dispersal ability; for example, Armstrong (1994) found lichen propagules to disperse just

80cm from their parent thallus, suggesting dispersal limitation, whereas Harmata & Olech (1991) found them to be present many hundreds of kilometres from any potential source, suggesting an unlimited dispersal ability. The lack of consensus about lichen dispersal ability could be related to a variety of factors:

1/ the atmospheric and topographic conditions present in the various study systems, which range from sheltered boreal ravines of northern Europe (Hilmo et al 2012), exposed frozen tundra of Antarctica (Marshall 1996), and the open seas of the Atlantic Ocean (Harmata & Olech 1991);

2/ the range of methods that have been employed to make estimates; from fitting empirical models to patterns of propagule deposition (Werth et al 2006a), optimizing parameters in metapopulation models (Johansson et al 2012, Ruete et al 2014, Snäll et al 2005), monitoring change in species distribution through time (Belinchòn et al 2017, Fedrowitz et al 2012, Tapper 1976), to inferring dispersal ability from extant populations, such as in relation to spatial genetic structure (Buschbom 2007, Dal Grande et al 2012, Jones 2015) or distribution patterns (Belinchòn et al 2011, Boudreault et al 2012, Dettki et al 2000).

3/ the type of data used; some studies base their dispersal estimates on the distribution of established lichen thalli (leading to indirect dispersal estimates) and others on the distribution of propagules (leading to direct dispersal estimates). Direct dispersal comprises the emission, take off, movement and deposition of all propagules, whereas indirect dispersal only considers these processes in the small fraction of such events that result in a successful colonisation. Indirect dispersal estimates are therefore more likely to over- or under-estimate dispersal due to other factors affecting the spatial distribution of established thalli, such as the current and historic distribution of habitat patches (Ellis & Coppins 2007), whereas direct estimates of dispersal may result in over-estimates of colonisation ability and population resilience as establishment processes (which may severely limit population size and distribution) are not taken into account.

The dispersal ability of a particular species may be described by the number of propagules arriving into an unoccupied habitat-patch. Both distance (from a potential source) and abundance (number of propagules produced by the source) will affect this metric. First, the distance that airborne propagules will travel is thought to be related to physical properties of size, shape and weight (Ingold 1971, Kuparinen 2006) as well as environmental factors such as wind speed and topography. Lichen epiphytes are known to produce propagules of greatly varying physical properties, from small light spores to larger heavier soredia, isidia and thallus fragments. However, despite these differences there is much debate over the extent to which propagule size affects dispersal ability, e.g. some studies show sexual species to be more limited in their distribution than asexual species (Otálora et al 2013), others that asexual species are more limited than sexual species (Johansson et al 2012, Ruete et al 2014), while some conclude that propagule size makes no difference at all (Leger and Forister 2009, Schei et al 2012, Werth et al 2014). Second, the abundance of emigrants moving from colonised patches will be determined by the abundance of reproductive thalli within the colonised patch of habitat, as well as the fecundity of the species/individuals present. Although studies have shown that colonisation probability is linked to species abundance within a patch (Belinchòn et al 2017, Fedrowitz et al 2012), the degree to which fecundity will affect colonisation is unknown. Indeed, studies of fecundity in lichen epiphytes are lacking (though see Armstrong 1991, Crittenden et al 1995, Sangvichien et al 2011), and therefore the importance of this variable (and particularly the magnitude of species-specific differences) is not well understood.

- Establishment

Establishment refers to the period of time after a propagule has landed on a substrate, before it has developed key attachment organs or organised itself structurally to form a stratified thallus (Scheidegger & Werth 2009). Some species may take several months to establish e.g. *Sticta sylvatica* and *Lobaria pulmonaria* (Scheidegger 1995, Zoller et al 2000), and mortality rates are expected to be high in this precarious stage of the lifecycle (Scheidegger et al 1995). The importance of the establishment phase in controlling lichen epiphyte dynamics has been demonstrated in experimental studies where individual thalli or propagules are artificially introduced to a substrate, and are shown to increase the colonisation rates (Belinchòn et al 2017, Hilmo et al 2011). Therefore, the establishment phase of lichen epiphyte dynamics has been linked to a population "bottleneck" in isolated habitat patches (Gjerde et al 2012), in which a small proportion of dispersed propagules manage to successfully establish.

Mortality associated with this phase of the lichen life cycle may be separated into stochastic and deterministic factors:

Stochastic variables include the risk of detachment from the substrate (Hilmo & Saastad 2001, Scheidegger 1995) as a result of propagules being unable to secure themselves. Competition from other epiphytes is thought likely to cause propagule mortality, as are the effects of grazing by slugs and snails (Asplund & Gaaslaa 2008, Scheidegger 1995, Zoller et al 2000). A cross-species study of sexual spore emission and germination (in artificial conditions) found that around 62% of all emitted spores failed to germinate or to sustain their growth (Crittenden et al 1995), suggesting that even having landed in a suitable habitat, there is still a high cost associated with sexual reproduction. Sexual spores may also be compromised as a result of photobiont limitation, whereby lichenization cannot occur due to an absence of the required photobiont at the site of settlement (Belinchòn et al 2015, Werth et al 2007). Although the likelihood that a fungal spore will settle close to an available photobiont may seem remote, the degree to which re-lichenization acts as a limiting factor in the establishment phase is as yet unclear.

Deterministic variables on the other hand are related to the presence of particular conditions at the settlement site. These 'microsite factors' (Scheidegger & Werth 2009) comprise nested tree-level variables such as bark pH, light levels and topography (as set out in section 2.1.4). The magnitude of the establishment costs associated with microsite requirements will depend on the niche specificity of the target species, whereby habitat generalists are expected to suffer lower costs than habitat specialists, due to breadth of tolerance of microsite conditions (however the extent to which the establishment niche differs from the niche of an established thallus is not yet clear).

❖ *Extinction*

Metapopulation theory predicts that local extinctions occur as a result of demographic or environmental stochasticity (Hanski 1999). This is because most metapopulation models assume that the dynamics of the target species are faster than that of their patches however, resulting in purely stochastic extinction rates which are not related to deterministic changes of the habitats themselves. In the case of species whose dynamics are slower than those of their habitat, patch dynamics e.g. succession, also need to be accounted for in determining extinction rates (Thomas & Hanski 1997). In extreme cases, stochastic extinctions appear negligible as species dynamics are much slower than that of their patches, leading to extinction rates that are seemingly wholly deterministic (Snäll et al 2003). As epiphytes are long lived and exhibit metapopulation processes that often occur over a slower timescale than that of their host, they are thought to fall into the category in which stochastic extinctions can be discounted and are referred to thus as "patch tracking" metapopulations (Snäll et al. 2003). Individual trees are thought to carry local populations that exist until tree death (Snäll et al 2005). This has been shown to be the case in a large proportion (32 of 39) of documented losses of *Lobaria* from repeated surveys across more than 3500 trees (Belinchòn 2017). When considering extinction in lichen epiphytes, it is important to take their slow metapopulation dynamics into account. As they are expected to react slowly to any changes within their environment, they can remain in a woodland long after the environment has been altered. This lag time causes an extinction debt (Tilman et al 1994), which has been found to be an important parameter in explaining current distributions of lichens in wooded landscapes (Johansson et al 2013, Ellis & Coppins 2007).

The slow dynamics of lichen epiphytes has led to theory that their extinction rates are largely deterministic, dependent entirely on that of their hosts (Johansson et al 2012). Although many studies support this theory (e.g. Belinchòn et al 2017, Johansson et al 2012, Ruete et al 2014), the risk of underestimating the extinction rate, and thus overestimating population size, has also been emphasised (e.g. Belinchòn et al 2017). Stochastic extinction maybe an important variable to include when explaining epiphyte population dynamics (Fedrowitz et al 2012). Indeed, stochastic extinction events may be caused by a variety of factors, from a change in the woodland environment, for example in pollution levels (Hawksworth & Rose, 1970), light levels (Kiraly et al 2013), or climate (Ellis & Coppins 2007), or as a result of tree disease (Ellis et al 2012), a change in management (Rose 1992), or even as a result of more localised effects such as branch snapping, bark peeling or cattle rubbing (Eaton 2014).

1.2.2 Spatial pattern and metapopulation process in lichen epiphytes

The spatial pattern of habitat within a landscape is known to be an important driver of metapopulation processes. Theoretically, colonisation rates in patches that are close to occupied patches are higher than those of more isolated patches, and extinction rates of smaller patches are higher than those of larger patches (Hanski 1999, MacArthur & Wilson 1967). Although there are few empirical colonisation/extinction rate studies in lichen epiphytes (as a result of their slow metapopulation dynamics), there is evidence of these patterns at two spatial scales; 1/ that of individual trees within a woodland, and 2/ that of woodland stands within a landscape.

First, at the individual tree level, colonisation rates have been found to be higher when the density of suitable habitat-providing-trees is higher (Johansson et al 2012) suggesting dispersal limitation as an important factor explaining species distributions; and, extinction rates on individual trees may be explained by tree diameter (with small trees harbouring higher extinction rates than larger trees, Fedrowitz et al 2012), supported by evidence that larger trees support a higher abundance of the target species than smaller trees (Öckinger & Nilsson 2010).

Second, at the woodland stand level, the colonisation rates of five epiphytic lichens were found to decrease with increasing fragmentation of woodland stands within a landscape (Ruete et al 2014). There is currently no evidence directly linking the size of a woodland patch to extinction rate; however, in the same study, Öckinger & Nilsson 2010 found that populations in 13% of colonised woodland stands went extinct over a 10 year study period. Although the extinction risk could not be explained by basal tree area, it was linked to the number of colonised trees within a stand (with stands harbouring fewer colonised trees being more likely to suffer extinction than those harbouring larger populations).

1.2.3 Predicting spatial pattern

The ability to describe and predict spatial patterns of species distribution is essential in enabling informed decision making in biodiversity management and conservation practice (Hortal et al. 2004; Martínez et al. 2006; Seoane et al. 2005), and providing the evidence base on which conservation decisions can be made. In the case of small and cryptic species such as lichen epiphytes, species distribution data is often unavailable as the surveying methods required are too intensive to be applied at a high resolution over large areas (Britton et al 2013, Vanderpoorten et al 2005). As a result, existing datasets are often patchy (Rondinini et al 2006), unreliable (Britton et al 2014), and/or often concentrated on specific areas such as nature reserves, or are coarse-grained (Hartley et al 2004), such as standard 10km mapping schemes (e.g. Seaward 1995).

Species distribution modelling is a method commonly used to predict the distribution of higher plants and animals using environmental predictor variables. This method has also been successfully used to predict the distribution of lichens (e.g. Bollinger et al 2007, Martínez et al 2006), though at relatively coarse resolutions relative to their habitat requirements; the reliance of lichens on micro-environmental niches such as wound tracks on a trunk (Gauslaa et al 2007), makes it difficult to correlate between micro-scale factors and environmental predictor data (which are largely only available at a coarse scale, for factors such as vegetation type, altitude or climate).

The potential to develop finer resolution models for lichen epiphytes in Scotland has been recently improved through a vast body of digital woodland data that have been made available as the Native Woodland Survey Scotland (NWSS, Grieve 2011). Despite the availability of this digital dataset, at present there are no published predictive distribution models for epiphyte species which have used this resource. If such models can be shown to be accurate, the resulting landscape projections could be used as powerful conservation planning tools. For this to happen, a number of challenges must be overcome. First, a suite of environmental variables must be identified, which not only capture the species niche requirements but are also available in the digital dataset (here the NWSS). Second, different modelling methods have been found to produce differing predictions (Pearson et al 2006, Thuiller et al 2003), making the method choice for SDM a critical consideration. Third, the extent to which a model may be used predictively in the wider landscape (outside the region in which the explanatory data was gathered) is critical and can be highly variable (Randin et al 2006). Testing of the applicability of the model in the wider landscape prior to application is therefore an essential step. These challenges are all explored in this thesis.

1.3 What is landscape-scale conservation?

Continuing declines in biodiversity (Butchart et al 2010) during a time of extreme habitat fragmentation (Sala et al 2000) and unprecedented environmental change (Rockström et al 2009), have led to a revolution in the UK's approach to nature conservation (Lawton 2010, TEEB 2010, UKNEA 2011); a previous focus on protecting species and habitats (Franklin 1993) has given way to ambitions of protecting entire ecosystems (Worboys 2010, CBD 2004) and ecological networks (Scottish Government 2015). As a result, conservation management is increasingly being applied, both strategically (e.g. DEFRA 2011, Scottish Government 2013, 2015) and practically (Adams 2012, Adams 2014), at the landscape-scale under various guises. These include rewilding (Navarro and Pereira 2012), the creation of ecological networks (Boitani et al 2007, Jongman 1995, Opdam et al 2006, Scottish Government 2015), and landscape restoration (Holl et al 2003). For simplicity, the term landscape-scale conservation (LSC) will be used here to represent all landscape-scale approaches to conservation planning and practice (Bourn & Bulman 2005, Kautz al 2006, Mac Nally & Horrocks 2000, Merckx et al 2009, Pressey & Bottrill 2009).

Landscape-scale conservation has been variously defined, from an "action that covers a large spatial scale, usually addressing a range of ecosystem processes, conservation objectives and land uses" (DEFRA 2011) to "coordinated conservation and management of habitats for a range of species across a large natural area, often made up of a network of sites" (Bourne & Bullman 2005). Though the definitions may be diverse, the basic premise is that ecosystem functions can be maintained whilst increasing the persistence of species by addressing land management issues across large spatial areas (Bennett & Mulongoy 2006, Bennett & Wit 2001, Jongman & Pungetti 2004, Lawton 2010).

Through LSC, a dynamic yet sustainable trajectory is sought (Haines-Young 2000), which allows for change both at the species and habitat level within a landscape. In the case of habitats, it is hoped that sites of nature conservation value (which are largely small and isolated in the UK (Marren 2002)), will be connected to form larger ecological networks (Opdam et al 1995), thus reducing the current pressure on local sites to provide multiple benefits. In the case of species, particularly rare/endangered species, it is hoped that reducing habitat fragmentation (thought to be one of the greatest threats to endangered species and biodiversity in general (Ehrlich 1988, Kurki et al., 2000, Wilcove et al 1998, Wilson 1992), will allow local extinction events to be balanced by colonisations elsewhere in a region (Opdam et al 2006), thus accepting that populations and their habitats are dynamic entities.

From an ecological perspective, the basic principle that piecemeal, isolated habitat patches harbour reduced biodiversity (MacArthur & Wilson 1967) and a reduced capacity for resilience during periods of environmental change (Travis 2003) underpins the rationale of the landscape-scale approach. Although theoretically LSC serves well as a conceptual framework for species conservation (Fahrig 2003, Fischer & Lindenmayer 2007), there is a need for an improved scientific evidence base to enable confident practical application (Boitani et al 2007, Watts et al 2016).

Criticism of the LSC approach includes the neglect of traditional site-scale actions (see Watts et al 2016) which for many years have been the backbone of biodiversity conservation (Franklin 1993). The commonly cited mantra “bigger, better, more, joined” (e.g. Lawton 2010) brings together the importance of retaining both site -scale conservation actions (bigger, better) whilst incorporating landscape-scale actions (more, connected). The importance of size (bigger), habitat quality (better), patch number (more) and/or landscape matrix e.g. stepping stone habitats, corridors etc. (joined) for species conservation is hotly debated however (e.g. see Doerr et al 2011 v’s Fahrig 2013). Current conservation practices for lichen epiphytes focus mainly on site scale actions and the potential for landscape scale actions (the focus of this thesis) is yet largely untested.

A second criticism of LSC theory is related to the lack of evidence underpinning the approach; as connectivity/fragmentation are scale- and target-dependent phenomena (Crooks & Sanjayan 2006), the perceived connectivity/fragmentation of a resource within a landscape will be species-dependent (Lord & Norton 1990). Despite the fact that species-specific measures of connectivity may be limited in scope (Boitani et al 2007), several LSC programs are either being planned (e.g. the National Ecological Network in Scotland (Scottish Government 2015)) or are being executed e.g. the “Futurescapes” of the Royal Society for the Protection of Birds, and the “Living Landscapes” of the Wildlife Trusts (Adams et al. 2014, Macgregor et al 2012). The current interest and momentum around LSC programs, coupled with the lack of basic understanding on how individual species perceive landscapes, creates an urgency for research into species-specific connectivity measures to enable functional network design (Van Teeffelen et al 2012).

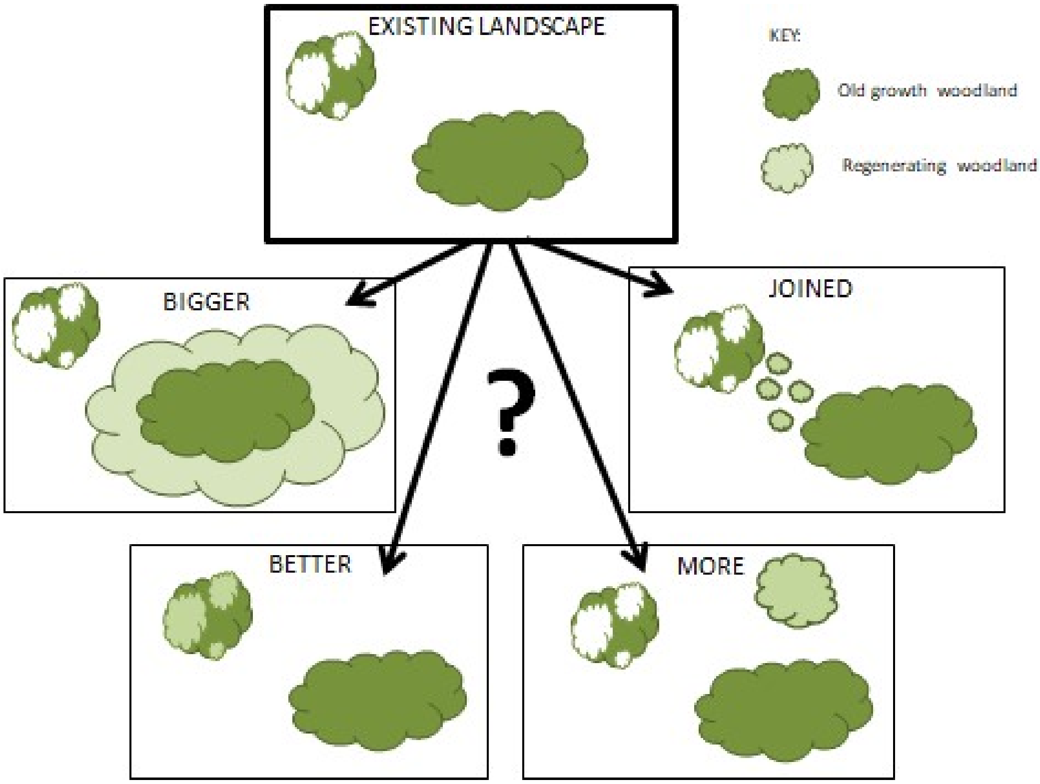

Figure 2. Bigger, better, more, joined.

1.4 Woodland conservation in the UK

The loss and degradation of forests is considered to be a major contributing factor to the current global extinction crisis (Ceballos & Ehrlich 2002, Thomas et al 2004). Within the UK, patches of woodland exist as remnants of a historically extensive habitat; in the post glacial era, around 75% of the land is thought to have been covered by woodland, reduced to just 5% at the beginning of the 20th century as a result of anthropogenic intervention (Rackham 1986). More recently, this number rose to around 11% (Forestry Commission, 2003) largely due to afforestation (principally comprising exotic conifers). These fluctuations in land-use have resulted in just 4% of all UK woodlands being of ancient semi-natural (ASN) origin. These areas hold the highest biodiversity value of any of our woodlands (Peterken, 1993), though the nature conservation value of these habitats is supressed by their fragmented nature, with a large proportion of ASN existing in small isolated pockets.

Today, the importance of a landscape-scale approach to woodland conservation is widely acknowledged (e.g. Humphrey et al. 2003) in terms of combating the negative effects of fragmentation (through creation of forest networks), aiding species migration under climate change (Harrison et al. 2001, Peterken 2002) and optimising structural diversity through landscape wide co-ordinated management (Latham 2000). Despite this, the current protected woodland network remains a product of 20th century conservation objectives, where the main focus was on mapping habitats, recognising rare species, and ensuring their protection through legal documentation (such as the Wildlife and Countryside Act 1981) and designation (such as Sites of Special Scientific Interest) (Marren 2002).

The overall aim of native woodland management for biodiversity is to increase or maintain high levels of habitat heterogeneity (Fuller & Warren 1996, Harmer et al. 2010) largely by ensuring a variety of successional stages exist at any one point in time. Managing isolated woodland sites in this way can lead to management conflicts however, particularly within designated sites where multiple species of conservation concern may be present. By increasing connectivity of woodland habitats within a landscape, a variety of successional stages are able to co-exist within the same framework of management, thus reducing conflicts of interest between multiple species and habitats, and reducing spatial and temporal trade-offs (Cordingley et al 2016). In the context of woodland conservation, addressing problems at a landscape-scale has the potential to benefit multiple features of nature conservation value simultaneously.

1.4.1 Temperate rainforests

Temperate rainforests are restricted to highly disjunct and isolated regions (DellaSala 2011, Rhind, 2003, Timdal et al 2006), and are arguably equally or even more threatened than their tropical counterparts (DellaSala 2011). Within Europe, temperate rainforests may be found wherever native semi-natural forest occurs within the Atlantic-oceanic climate zone (as described by Alaback (1991): annual precipitation greater than 1400mm, with 10% of the annual precipitation falling during summer, and a mean July isotherm less than 16^{o}C). Many of these forests have been destroyed or degraded throughout history (Hannah et al 1995), leaving fragmentary remnants a conservation priority e.g. the oceanic facies of the EU Annex 1 habitat, 'old sessile oakwood' (McLeod et al 2005).

1.4.2 A Scottish perspective

In Scotland, multiple anthropogenic effects on the landscape e.g. conversion of woodland to plantation forestry, heather moorland or grazed pasture (Hobbs 2009) have resulted in just 1% of the land area now supporting ancient semi-natural woodland (SNH 2016). Despite this, of the European countries, Scotland has among the best remaining examples of temperate rainforest ecosystems; the ancient semi natural woodlands along the west coast of Scotland (remnants of a post glacial forest mosaic) provide internationally-important examples of European temperate rainforest (Ellis et al 2015), despite lying within a heavily human-modified landscape (Birks 1988).

The lichen epiphytes of temperate rainforests are one of the most important and diverse components of their biodiversity (DellaSala 2011). In central Europe however, this characteristic diversity has been lost from many woodlands as a result of pollution, habitat loss and changes in management (Hawksworth & Rose 1970, Van Herk et al 2003). In contrast, temperate rainforests in Scotland benefit from a long historical continuity (Walker & Kirby 1987) and low levels of air pollution (NEGTAP, 2001), and as a result populations of many notable communities which are declining elsewhere in Europe e.g. *Lobarion* (Hallingbäck & Martinsson 1987), continue to thrive. The *Lobarion* community (Rose 1988) is highly characteristic of the temperate rainforests and populations in Scotland are important from both a national and international perspective; in some cases over 10% of the global population of a lichen epiphyte is held in Scotland with an international responsibility towards the species' protection (Woods & Coppins 2012).

Current threats to temperate rainforests and their associated epiphytic lichens in Scotland include; overgrazing, under-grazing, habitat loss and fragmentation, invasive species e.g. *Rhododendron ponticum*, tree disease e.g. *Chalara fraxinea,* and climate change (Ellis & Eaton 2016, Ellis et al 2013, Thompson & Coppins 2015). The importance of grazing levels to epiphytic lichen populations may be exemplified by considering the importance of grazed forests/pasture parkland to lichen epiphytes, particularly those of the *Lobarion* community (Rose 1992, Douglas et al 2010). The dependence of this community on these conditions may be partially explained by a requirement for relatively high levels of light (Gustafsson & Erikson 1995, Kiraly et al 2013, Ranius et al 2008, Rose 1992) which are created and maintained by grazing which in turn prevents shade-inducing woodland regeneration. As a result of this light dependency, woodland regeneration is linked to loss of lichen epiphyte diversity, and is therefore often discouraged in woodlands of high lichen epiphyte value (Coppins 2003).

1.4.3 Case Study of Glen Creran and Glasdrum National Nature Reserve

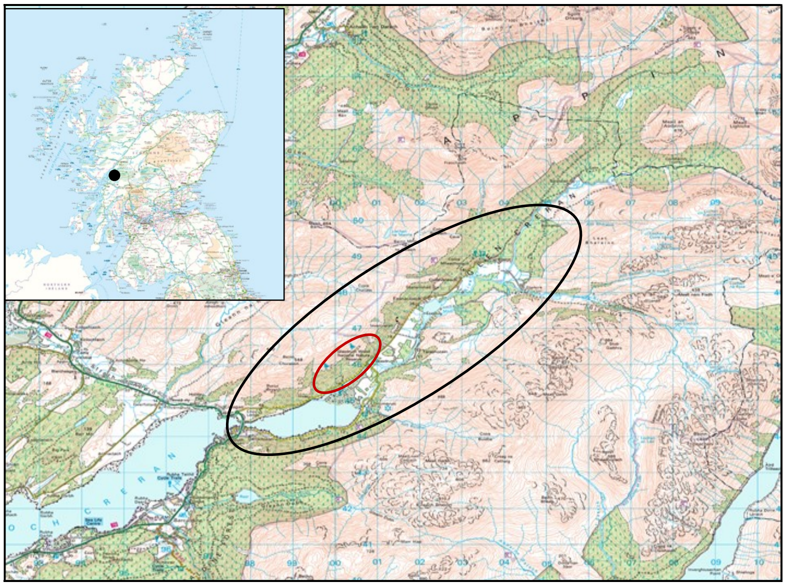

Figure 3. Glen Creran, showing the approximate location of the SSSI (black outline) and the Glasdrum NNR (red outline). Inset map shows the approximate location of Glen Creran in relation to Scotland. © *Crown Copyright and Database Right (2017) OS (Digimap Licence).*

Glen Creran is a wooded valley lying within the temperate rainforest bioclimatic zone on the west coast of Scotland (see Figure 3). The glen has been designated as a Site of Special Scientific Interest (SSSI) due to the nature conservation value of the woodland itself, as well as the bryophyte, butterfly and lichen assemblages within. The Lobarion community of lichens in particular has been described as "exceptional", and "probably among the best in Europe" (Sanderson 2005).

Within the wider SSSI is the Glasdrum National Nature Reserve (NNR), which is of importance to rare epiphytic lichens e.g. *Nephroma parile*, and butterflies e.g. pearl-bordered fritillary *Boloria euphrosyne*. Both of these groups (epiphytic lichens and butterflies) require well-lit conditions within woodland habitats, as provided by a gladed woodland structure that includes areas of veteran ash-trees within a pasture parkland setting. If the future of this aging habitat is to be secured, grazing pressure must be reduced to allow for woodland regeneration. However, this regeneration is likely to lead to a reduction in the light levels within the woodland as young trees and shrubs develop, thus making the habitat less suitable for the very species for which it is designated and for which the regeneration is necessary. This represents a paradox at the heart of woodland management.

1.5 The Landscape Approach and Lichen Epiphytes

Landscape-scale conservation is a conceivable solution for conserving lichen epiphytes within woodland systems (Ellis 2012, Scheidegger & Werth 2009) as it would allow areas of woodland regeneration and lichen importance to co-exist in separate though dynamic woodland stands within the landscape. Such a strategy relies on increased landscape permeability, allowing dispersal and colonisation to offset local extinctions. The holistic nature of this approach has led to it being proposed as a management strategy for lichen epiphytes (Scheidegger & Werth 2009).

The ability of species to persist within such a network is dependent on species-specific traits, such as habitat specificity and dispersal ability (Vos et al 2001), as well as habitat factors such as the spatial distribution of available habitat. It is thought that species with a wide ecological tolerance that are able to disperse freely through the landscape, will respond better to a landscape-scale approach to conservation, than those with a narrow ecological tolerance and a poor dispersal ability (see Figure 4 below).

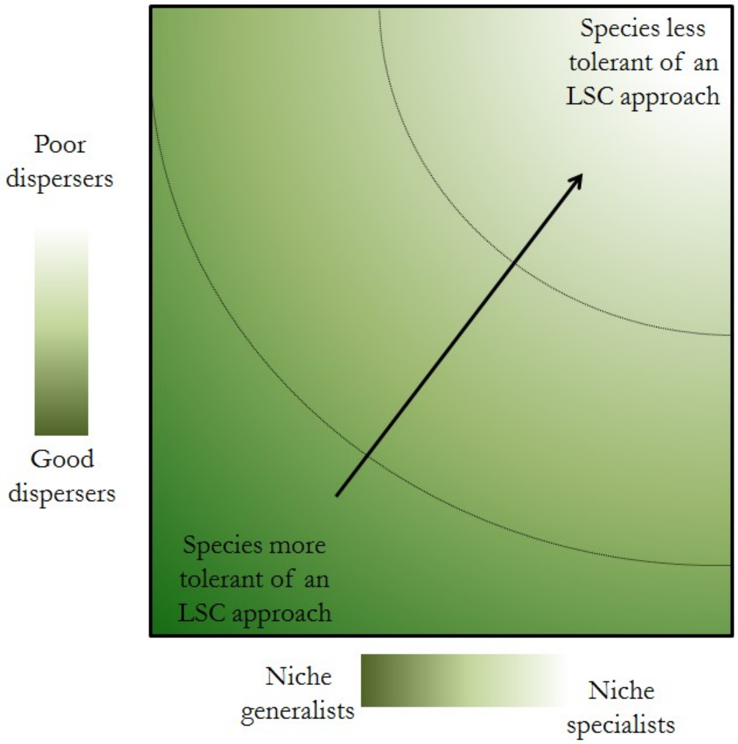

Figure 4 – Species tolerance to landscape-scale conservation will depend on their dispersal ability and habitat specificity.

The type of species-specific data concerning the dynamics and distribution of lichen epiphytes is largely unknown, however (Coppins 2003). Accordingly, lichen epiphytes have often being neglected from large scale conservation planning (Scheidegger & Storfer 2015). In order to predict how lichen epiphytes might respond to LSC scenarios, information on habitat requirements, spatial distribution and dispersal ability are required.

Chapter 2. Project aims

The aim of this project was to identify the extent to which a landscape-scale metapopulation conservation strategy could be used to conserve lichen epiphytes within temperate rainforests of Scotland. The unique conditions found in western Scotland, combining a relative abundance of high quality temperate rainforest habitat (in a European context) coupled with robust populations for many members of the *Lobarion* community; provide an ideal opportunity to test such an approach.

Here we predict the response of lichen epiphytes to landscape-scale approaches applied to the conservation of their temperate rainforest habitat. In order to do this, information on i) habitat requirements, ii) spatial distribution, iii) patterns of productivity and iii) dispersal ability is required. Although patterns of mortality are also important in making predictions about future populations, as lichen epiphytes are known to follow patch tracking dynamic mortality will be explained by that of their hosts (and therefore through an understanding of i) habitat requirements).

There are five specific project objectives (in most cases developed by or in consultation with Scottish Natural Heritage (SNH) staff):

1. To quantify the habitat requirements of a suite of target epiphyte species which are characteristic of Scotland's west-coast temperate rainforest, focussing on epiphytes with contrasting ecological traits in terms of habitat specialization, and reproductive mode (see Table 1);
2. To map suitable habitat space for the target species over an entire landscape (Glen Creran, the case study site);
3. To test the extent to which the habitat descriptions may be applied in the wider biogeographic region;
4. To explore patterns of productivity in the study species;
5. To describe and quantify the dispersal ability of the target lichen epiphytes; and
6. To combine data on (a) habitat requirements (1., above), (b) species distribution (2., above) and (c) dispersal ability (4., above), in order to explore contrasting landscape scenarios of habitat connectivity/isolation specific to the Glen Creran study system.

A total of nine epiphytic lichens of contrasting habitat specificity and dispersal ability were identified as target species. Habitat specificity (assigned through expert opinion) is used as a proxy for species abundance in the landscape, while dispersal ability is presumed to correlate with reproductive mode. Species were selected for field sampling according to three criteria: (i) their ability to be identified under field conditions using morphological characters, (ii) their contrasting habitat specialism, and (iii) contrasting dispersal modes (see Table 1).

Species	**Conservation evaluation**	**Habitat description**	**Niche specialism**	**Reproductive mode**
Parmelia saxatilis	-	Numerous substrates, from the coast to the mountain summits, often abundant.	Generalist	Asexual
Graphis scripta	LC	On moderately shaded smooth bark of a wide range of trees.	Generalist	Sexual
Lobaria pulmonaria	LC, SBL, IR	On broadleaved trees, low scrub, *Calluna* and mossy rocks. Locally abundant in Scotland	Specialist	Both (though predominantly asexual)
Pectenia cyanoloma	LC, IR	On mossy broadleaved trees and rocks in open relict woodlands and on coastal rocks.	Specialist	Sexual
Pectenia atlantica	LC, IR	On shaded mossy broadleaved trees in cool sheltered humid woodlands, rarely on mossy rocks.	Specialist	Asexual
Pannaria conoplea	LC, SBL, IR	On mossy bark of broad leaved trees, rarely rocks in humid sheltered woodlands.	Specialist	Asexual
Pannaria rubiginosa	LC, SBL, IR	On mossy broadleaved trees, rarely on rocks in humid sheltered woods.	Specialist	Sexual
Nephroma parile	LC	On bark and mosses, characteristic of old woodlands.	Super-specialist	Asexual
Nephroma laevigatum	LC, SBL, IR	Primarily on bark in mossy humid communities in markedly oceanic habitats in relict woodlands.	Super-specialist	Sexual

Table 1 – Conservation evaluation (LC = Red List (Least Concern), SBL = Scottish Biodiversity List species, IR = International responsibility species) taken from Woods & Coppins (2012), habitat description (Smith et al 2009), and *a priori* assigned niche specialism of epiphytic lichens included in this study.

Chapter 3. Discussion

In this chapter I discuss the individual findings of this study in the broader context of the project aim; to identify the extent to which a landscape-scale metapopulation conservation strategy could be used to conserve lichen epiphytes in temperate rainforests of Scotland.

First, I will summarise the main findings of the study as they relate to the five specific project objectives (for details the reader may refer to the discussion contained within each individual Paper). Second, drawing on these findings I will conduct a more general discussion on the circumstances in which a landscape approach may be successful in the case of lichen epiphyte conservation. And finally, I will look to the future and consider what may lie ahead in the field of landscape-scale conservation studies for lichen epiphytes.

3.1 Landscape-scale conservation (LSC) studies for lichen epiphytes –main findings of this study

OBJECTIVE 1. To quantify the habitat requirements of a suite of target epiphyte species, which are characteristic of Scotland's west-coast temperate rainforest.

The habitat requirements of the nine target epiphytes were identified using Generalised Additive Modelling (GAM, see Paper I). Tree species and size were identified as optimum predictors for all nine epiphytes, with *Nephroma* species models also including canopy gap as an explanatory variable. The results of the modelling agreed with prior expectations (based on field observations; for example, that *L. pulmonaria* is found more commonly on older/larger trees, and on trees that tend towards more basic bark such as *Fraxinus excelsior* and *Corylus avellana*) as well as published material (Angelstam 1999, Ellis et al 2015, Gustaffsson & Eriksson 1995, Johansson et al 2009, Kiraly et al 2013, Uliczka & Mezaka et al 2012). Niche specificity categories assigned a *priori* were also found to be correct, the niche generalists were found to be tolerant of a wider range of substrates according to the GAMs, than the niche specialists.

OBJECTIVE 2. To map suitable habitat space for the target species within the case study site, and for unprotected woodlands in the surrounding landscape matrix.

The success of tree species and size as predictor variables enabled predictions of species distribution to be made over the entire landscape of the study area of Glen Creran using an species distribution modelling approach (SDM, see Paper I). This was made possible by the availability of digital environmental data in the form of the Native Woodland Survey of Scotland (Grieve 2011). Data on tree species composition, maturity, density etc. enabled predictions of habitat suitability/availability to be made at the resolution of individual trees across the landscape. It is envisaged that these maps will be used as a basis for future conservation planning for epiphytes within Glen Creran.

For the sake of the SDM exercise, the lichen epiphytes under study were assumed to be in equilibrium with the wooded environment within Glen Creran, with factors such as historic management practices and dispersal limitation assumed to have no bearing on current distribution patters. This assumption was made due to: 1/ the long historic continuity and stable nature of the woodland within Glen Creran (being an area of 'ancient' woodland that is known to have been present in the landscape for at least 260 years) and 2/ the relatively fast population dynamics of the Lobarion community on the west coast of Scotland (Eaton and Ellis 2012) as compared to those in continental Europe. Combined, these conditions increase the chance that habitat occupancy (a result of colonisation and extinction events) corresponds directly with habitat availability.

The population dynamics exhibited by lichen epiphytes (whereby sub-optimal habitat may be occupied as a result of patch tracking dynamics and optimal habitat may remain vacant as a result of slow colonisation rates) make assumptions about equilibrium more difficult to accept however, even within ancient woodland sites on the west coast Scotland. To accommodate such population anomalies, a large training dataset was used to build the SDM's, comprising 600 trees collected from an area of over 15km in length and 3km in width, taking in diverse woodland types (comprising a variety of woodland composition, maturity and density), land ownership and management history (as confirmed through searches of historic letters and documents relating to the site held in the National Library of Scotland). Under the assumption that the majority of the epiphyte population is in equilibrium with its environment, including such diversity in the training dataset enabled suitable habitat for the target species to be identified (even when a portion of the suboptimal habitat was occupied and/or a portion of the suitable habitat was empty), by combining the probabilistic nature of the SDM predictions with a sensitivity and specificity optimising threshold.

OBJECTIVE 3. To test the extent to which the habitat descriptions may be applied in the wider biogeographic region.

Predictions of species presence/absence were assessed for accuracy in ten ancient woodland sites in the wider temperate rainforest biogeographic region (see Paper I). The statistical descriptions of suitable habitat were found to be accurate within the wider biogeographic area for five of the nine species. The species whose habitat descriptions did not apply more widely were those of the habitat generalists (*G. scripta* and *P. saxatilis*) and the super-specialists (*N. parile* and *N. laevigatum*). In the case of the habitat generalists it was argued that the range of habitats tolerated by these species was not entirely present within the training site (Glen Creran). Novel suitable habitat space was thus encountered and found to be occupied within the test sites, causing poor overall prediction accuracy. In the case of the niche super-specialists, model accuracy was thought to be explained by a statistical artefact, linked to the low probabilities of presence predicted by the models. The habitat specialists (*L. pulmonaria, P. conoplea, P. rubiginosa, P. cyanoloma* and *P. atlantica*) were found to transfer to new sites with an acceptable level of accuracy, indicating that these SDM's are more generally valuable as a conservation tool.

Model accuracy was found to be poor in two sites in particular (Knapdale and Glen Trool). It is possible that populations of lichen epiphytes are not at equilibrium with their environment at these two sites, perhaps due to historic management practices or mass population effects increasing colonisation of suboptimal habitats. As stated in Objective 2 above, an assumption of population equilibrium in Glen Creran was made in for the SDM exercise, which does not account for occupancy anomalies such as extinction debts, local population size, mass effects, habitat configuration (isolation/fragmentation) etc, the cause and extent of which may differ from one place to another e.g. as a result of historic and current management practices as well as successional dynamics and wider environmental issues such as pollution levels. This issue becomes apparent when transferring SDMs developed in one landscape to another.

The probabilistic nature of SDM predictions mitigates for occupancy anomalies to a certain extent, whereby an optimal habitat patch may have a 60% occupancy rate within a landscape, for example as a result of isolation linked dispersal limitation. This advantage is lost when probabilistic SDM predictions are translated into useful maps of species presence however, as a threshold must be applied to the predictions, thus removing tolerance for these anomalies. Applying landscape specific thresholds to SDM predictions may be a solution to this particular problem. Alternatively, forces driving occupancy anomalies such as historic management, woodland type and pollution data may be incorporated into SDMs as explanatory variables (though this depends on such data being available).

OBJECTIVE 4. To explore patterns of productivity in the study species.

The number of spores emitted over a 72hr period was investigated in all of the sexually reproducing study species (*L. pulmonaria*, *N. laevigatum*, *P. rubiginosa* and *P.*

cyanoloma). Variability in spore production was found between species, with *L. pulmonaria* and *N. laevigatum* producing over 1000 spores over a 72hr period and *P. cyanaoloma* and *P. rubiginosa* producing fewer than 100, however no relationship could be found between the number of colonised trees in the landscape and productivity, suggesting that dispersal, establishment or habitat availability are more important in limiting population size.

OBJECTIVE 5. To describe the dispersal ability of contrasting lichen epiphytes

A novel method to determine dispersal distance in lichen epiphytes was developed, combining a mechanized propagule trap with molecular techniques (see Paper III), and enabling a single asexual propagule (soredium or isidium), or as few as 10 spores, to be detected in an atmospheric sample. This methodological advance allowed the first direct comparative study of lichen epiphyte dispersal in a natural context (see Paper IV); the study demonstrated high inter-specific variability in dispersal pattern, with *P. saxatilis* yielding positive results in 80% of the 198 trapping events, *L. pulmonaria* 79%, *N. laevigatum* 62%, *P. rubiginosa* 31%, *P. conoplea* 24%, *Pectenia sp*. 23%, and *N. parile* 9%.

Overall, reproductive mode, distance and aspect were all found to be important dispersal determinants over short distances from a propagule source (up to 20m), with most species also exhibiting measurable dispersal at 200m. In order to account for these findings, a two tier structure to the dispersal process is proposed (with support from previous studies e.g. Gjerde et al (2015), Johansson et al (2012) and Ruete et al (2014)); whereby propagules dispersing over short distances (within a woodland stand) are subject to a different set of dispersal constraints than those which are affected by trajectory altering wind gusts and ultimately disperse over longer distances (between woodland stands).

OBJECTIVE 6. To combine data on (a) habitat requirements (1., above), (b) species distribution (2., above) and (c) dispersal ability (5., above), to explore contrasting landscape scenarios of habitat connectivity/isolation.

An agent based model combined the results on habitat requirements and species distribution from Paper I, with dispersal metrics from Paper IV, to investigate the effect of habitat connectivity in six contrasting species; two habitat super-specialists (the sexual *N. laevigatum,* and the asexual *N. parile*) and four habitat specialists (the asexual *Pannaria conoplea* and *Pectenia atlantica;* the sexual *Pannaria rubiginosa;* and *L. pulmonaria* which is capable of both sexual and asexual reproduction). This enabled comparisons to be made among species with contrasting ecological traits.

As expected, variability in the magnitude and temporal scale of colonisation was found amongst the target species, e.g. under a 0m isolation scenario, first colonisation events ranged from 5 years in the sexual/asexual habitat specialist *L. pulmonaria* to 45 years in the asexual habitat super-specialist *N. parile*. The colonisation patterns demonstrated by the model were ecologically plausible and consistent with the scientific literature, creating confidence in model output. As a result, general inferences about landscape-scale woodland management for lichen epiphytes could be determined from model predictions (see Paper V) e.g. in order to increase chances of sustained colonisation of a regenerating woodland patch, it should be located at a distance less than 100m from the nearest propagule source; when this is not possible (distance > 100m), the greatest improvement in colonisation will be effected through improved management of the regenerating woodland stand, e.g. selective thinning to create a *Fraxinus excelsior*, *Quercus* sp. and *Corylus avellana* dominant woodland composition. However, caution must be applied prior to further testing of the model, particularly in spatially realistic woodland environments.

4.2 Landscape-scale conservation studies for lichen epiphytes – can it work?

Whether an LSC approach will enable long term preservation of a particular species in a given landscape will depend on 1/ the population dynamics of the given species (particularly spatial and temporal scales of colonisation and extinction) as well as 2/ the dynamics and distribution of their habitat within the landscape in question. As the population dynamics of epiphytic lichens are known to follow patch tracking, rather than classical, metapopulation dynamics however (whereby colonisations are distance dependent and local extinctions are caused by deterministic habitat patch destruction), they are heavily dependent on 1) species dispersal ability and 2) the distribution and dynamics of their habitat, (both of which were the subject of study in this thesis). These patch tracking dynamics, coupled with slow colonisation process can makes them difficult to study using standard metapopulation models (such as the incidence function model), which often require assumptions about the population to be made e.g. that the population is in equilibrium with its environment.

Agent or individual based models on the other hand are more flexible in their approach and do not require the same assumptions to be made. For the epiphyte woodland system they are particularly good at making predictions about populations in novel environments e.g. regenerating woodlands (Grimm and Railsback 2005) where equilibrium dynamics are not expected (as they may be in more established/ancient woodland), as assumptions about equilibrium do not have to be made.

We can a definition of LSC management for lichen epiphytes; the presence of spatially/temporally separate, though ecologically connected, dynamic woodland stands, whereby areas of regenerating woodland and stands of lichen importance (largely old-growth woodland) are both present in the landscape at any one point in time. This scenario requires that colonisation of regenerating woodland stands offsets local extinctions of lichen epiphytes occurring in areas undergoing regeneration. In order to successfully manage this trade-off and design a conservation strategy in which landscape-scale processes maintain viable (patch tracking) meta-populations, it is necessary to understand the spatial and temporal scales over which populations are operating.

This leads to two questions. First, since the spatial and temporal scales at which landscape-scale processes operate are thought to be species specific, related to ecological characters such as habitat specificity and dispersal ability (Vos et al 2001), are we able to predict species response from general ecological traits, or must data be generated for individual species? Second, over what spatial and temporal scale does the landscape process of colonisation operate in our study system?

In answer to the first question, reproductive mode (sexual or asexual) was investigated (Paper 4 and 5) by testing its importance to the landscape-scale process of dispersal. Unsurprisingly, propagule deposition probabilities were found to be higher in sexual than asexual species. However, what was particularly surprising was that in a metapopulation model, colonisation did not follow an equivalent pattern; sexual species were not found to colonise trees in a greater abundance and faster than their asexual counter-parts (for example, the asexual *P. conoplea* was often one of the first species to colonise the regenerating woodland, where as the sexual *P. rubiginosa* was one of the last). Processes operating at finer spatial scales (the environmental conditions at the scale of individual trees) appear to be just as important as dispersal in determining colonisation. For example, the *Nephroma* species, being the most selective of species in habitat preference, were also found to be the least effective colonisers of all the target species regardless of their reproductive mode. This suggests that although landscape-scale processes (such as dispersal) are important, finer scale processes (such as tree growth and epiphyte niche specificity) are just as important when making predictions about the spatial and temporal scales of species response to LSC scenarios. Thus, ecological traits can predict landscape scale processes, but smaller scale factors (such as species' habitat preferences) must also be considered when making predictions about the species response to LSC scenarios. In the case of the lichen epiphyte/woodland study system, agent based models provide a particularly good platform for incorporating these multi-scale effects; whilst programmed behaviours (such as dispersal) may operate over large scales, individual agents may operate at fine-scales (such as those of individual trees), and when combined, these processes are able to create emergent patterns (such as colonisation trends).

The second question asked is what spatial and temporal scales does the landscape-scale process of colonisation operate over in my study system? The spatial scale of colonisation was found to be larger than expected because of a considerable propagule rain, detected even at long distances from propagule sources (over 200m), and suggesting that woodland patches can be considered connected even at distance. However, despite propagule rain into isolated sites, colonisation events were much reduced for sites out-with the local propagule deposition range (50m from a propagule source). For example, the maximum number of trees colonised by each of the target species at a 0m isolation distance ranged from 2 to 34, compared to just 1 to 3 at 250m. This reduction is most likely due to the high establishment costs suffered during the colonisation/establishment process, which results in the majority of successful dispersal events ending in establishment failure. Many successful dispersal events are therefore required in order to create a single colonisation, as evidenced in isolated sites, where, although propagules continue to arrive, incoming propagule pressure is much reduced resulting in fewer successful colonisations.

Temporal scales of colonisation in a regenerating woodland stand are heavily dependent on the age-suitability relationships of the tree species, and according to the suitability thresholds identified in the SDM exercise (Paper I), many tree species did not become suitable for colonisation until they were over 100 years old e.g. *Quercus sp*. took between 75 and 150 years to become a suitable habitat (target species dependent). Temporal scales of colonisation were also found to be dependent on spatial scales of isolation, for example first colonisations ranged from 2 to 33 years in a regenerating stand at 0m from a colonised woodland (species dependent), and from 9 to 188 years in a stand 250m from a colonised woodland.

These findings suggest that landscape-scale conservation plans for lichen epiphytes need to cover long (circa. 100 year) time periods. This strategy is required to plan for a) stands of regenerating woodland maturing into suitable habitat for the target epiphytes and b) successful dispersal events occurring and effecting colonisation (particularly for rarer species i.e. the niche super-specialists). With an ability to plan over such long-time scales, large scale LSC scenarios could be used to conserve species by utilising a less intensive management style than is currently implemented, including for rare species i.e. niche super-specialists. The importance of retaining stands of open structured old-growth woodland is emphasised however, and only when woodland stands of various successional stages are established in the landscape would it become possible to relax the management intensity of existing old growth stands. If practical restrictions prevent such long-term planning, then the principles of LSC (ensuring the existence of both regenerating woodland stands and stands of lichen importance (largely old-growth) within a single landscape at any one point in time) must occur over much smaller spatial scales. In this instance, work to apply the LSC principles to existing stands of old growth woodland (see Figure 5A and 4B), should create a smaller scale mosaic of dynamic woodland stands (with no more than 50m between woodland stands) in which landscape-scale processes such as colonisation may operate at faster time scales. These small-scale mosaics could be expanded over time through modular addition within each subsequent management plan. Alternatively, translocations could be used to ensure colonisation of newly created woodland stands by rarer species (the niche super-specialists), whilst allowing niche specialists and generalists to undergo natural colonisation. Both these approaches would deliver results more quickly, in terms of securing colonisation of the regenerating woodland by the full range of target epiphytes.

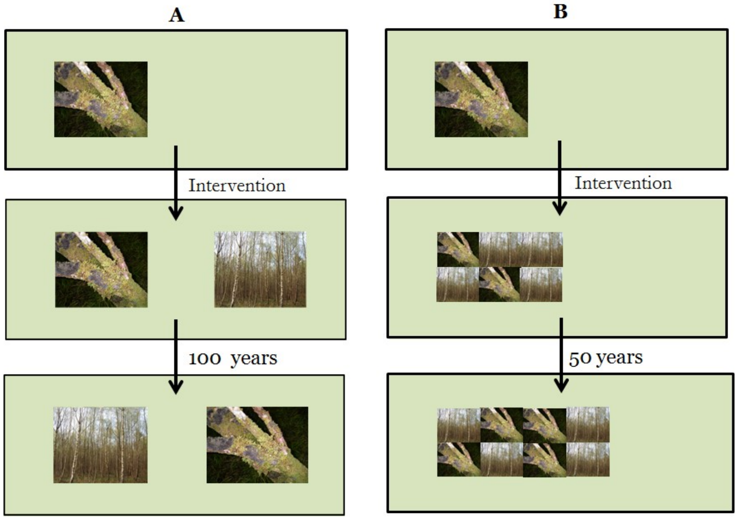

Figure 5. Management recommendations where  = old growth woodland stand, and  = regenerating woodland stand. Figure 5A: assuming that management plans could cover a 100-year period, the traditional LSC principles could be applied over large spatial scales whereby young woodland is placed elsewhere in the landscape. This woodland eventually matures and provides the old growth conditions required by the target epiphytes. Figure 5B: assuming that management plans can only be secured over

shorter time frames, regenerating woodland stands should be placed as near to the extant old growth woodland as possible (less than 100m) and the woodland managed in such a way as to create a smaller spatial scale mosaic of stand ages.

3.3 Landscape-scale conservation studies for lichen epiphytes – what lies ahead.

Although this thesis has advanced lichen epiphyte ecology and conservation, it also points to future studies;

- In particular, the subject would benefit from an empirical dataset of colonisation dynamics in a real world LSC scenario, against which metapopulation models could be calibrated. Plantation on Ancient Woodland Sites (PAWS) which are undergoing restoration to native woodland offer an opportunity to monitor lichen colonisation rates within the temperate rainforest belt. Such data would provide a detailed understanding of the temporal scale of colonisation and would ultimately enable fine tuning of model parameters.
- The development of mechanistic spore traps and molecular methods to enable direct dispersal studies opens up a host of further questions that this technology could be used to explore. In particular, work exploring the generality of the propagule deposition metrics demonstrated by this study, including results derived from choice of source tree or a different landscape? Particularly given the suggestion that topography may play an important factor in propagule dispersal (Paper IV). As the SDM's for the niche specialist species were found to be applicable out-with Glen Creran, having the same level of spatial confidence in transferability of a dispersal metric would greatly enhance the value of the metapopulation models, the predictions from which could then be applied over a much wider geographic area. An interesting line of investigation would involve modelling the existing trap data as a mixture of contributions from multiple colonised trees in the vicinity including those out-with the existing 20m radius (rather than the single focal tree from which all SDD propagules are assumed to have been emitted from here), and as a mixture of two different kernels (to include 'background' propagule deposition as well that from recorded trees).
- There is an especially interesting question to be asked of the point at which short distance dispersal becomes negligible. Here a distance of 50m from the propagule source (a colonised tree) was assumed, however the exact cut-off distance, and whether this distance is variable amongst species could now be explored by setting spore traps at distances between 20m and 100m and

investigating the point at which dispersal becomes similar to that found in long distance traps.

- Another topic which has yet received very little attention is the extent to which the size of the propagule source affects dispersal/propagule deposition metrics. It seems highly likely that a tree that has many reproductive thalli will produce a larger propagule 'cloud' than one with fewer/less productive thalli, however the extent to which this affects dispersal/colonisation is yet unknown. A qPCR approach, rather than the presence/absence approach employed here, could be used to address this question.
- The importance of source size to dispersal/propagule deposition metrics was particularly apparent in the development of the metapopulation model. Here, it was assumed that once colonised, all trees had equal dispersal weights, regardless of the number of thalli on the tree or the reproductive capacity of the thallus (which is likely linked to thallus age). In the same way, epiphyte extinction was also assumed to be independent of the number of thalli inhabiting a tree, with all thalli present being considered a functional individual. These assumptions did not allow room for within-tree extinctions and colonisations, and therefore the sensitivity of model output to this level of detail is yet unknown; though (given some empirical data on the subject) this level of detail could theoretically be built into the metapopulation model.
- There is much scope for the methods developed in this thesis to be used to explore similar issues in other cryptic species of conservation concern. For example, in light of data from the NWSS making high resolution species distribution modelling possible, suitable habitat/species distributions of other tree dependent species could be produced for the study system e.g. for bryophytes, non-lichenised fungi and butterflies. In addition, the development of the dispersal methods demonstrated in this thesis could be used to further our knowledge of dispersal in other species of conservation concern, such as ferns and bryophytes, as well as rare vascular plants.
- One of the most exciting avenues for further study is the need for improved estimates of establishment costs in the target species. Though the idea of the regeneration niche is an old concept (Grubb 1977), there is still very little evidence on the subject (but see Belinchòn et al 2017 and Scheidegger 1995 who both investigated establishment costs in *L. pulmonaria*). An artificial seeding experiment as part of a translocation study would be an excellent opportunity to

gather such data. A better understanding of factors limiting the establishment process could be used to manipulate population dynamics through increasing colonisation rates. The importance of studying establishment costs in a variety of species exhibiting a range of ecological traits (rather than just *L. pulmonaria*) is emphasised.

- Given time constraints to the PhD, the metapopulation modelling work focused on the practical demands that were required by the funder – Scottish Natural Heritage, and a wish to provide some very practical conservation advice for the study system. However the datasets produced along the way provide a platform for future work. This could see a move from simulation to analytical methods that pursue greater generality in the modelling approach, or larger landscape-scale models of woodland succession could be used to look beyond the short-term transients and at longer term equilibrium metapopulation structure and composition.
- Although translocation is proposed here as a solution to landscape-scale conservation scenarios, where timeframes and/or spatial scales cannot account for population processes, particularly of rare species, there is very little evidence/advice on the best way to go about such as procedure. There is therefore much work to be done in developing a methodology for the translocation of rare lichen epiphytes species, with investigations exploring methods such as propagule paints, and the attachment of thallus fragments, or larger thallus pieces.
- Finally, the widely divergent outcomes demonstrated by different species under scenarios of LSC shows the importance of expanding work from its current focus on the model species *L. pulmonaria,* to include species exhibiting a wider range of ecological traits. This is particularly important in making predictions about species' responses to change, as *L. pulmonaria* appears to be relatively resilient, and predictions based on this species alone could underestimate impacts on lichen epiphyte populations.

Chapter 4. Concluding remarks

The original idea for this PhD emerged during a day out in an old-growth woodland on the west coast of Scotland, when a conservation manager asked a group of lichenologists ‘what would the impact be on the lichen epiphyte population of these woods, if we were to put a fence up around a small part of it to allow some regeneration?’. The answers from the lichenologists were spectacularly mixed, from predictions of outright disaster to some uncertain reassurance all would be well; it all seemed to depend on how lichens moved around in wooded landscapes, how far and how quickly, to which we had few answers.

Looking to the future, I hope that the findings of the PhD will enable more confident answers to that innocent question, but so much more has been discovered in the process. For example; SDM’s have been used to produce maps of species distribution, which can now be used in conservation planning; a novel method for detecting airborne propagules of lichen epiphytes has been designed allowing us to better understand propagule movements, and as a result the first comparative study of direct dispersal in lichen epiphytes in a natural context has been achieved; a metapopulation model has been developed that allows LSC scenarios to be explored in the study system, making it possible to answer questions such as that posed above, and providing a powerful evidence base for other decision makers asking similar questions. In addition, the project has opened the door to a wealth of further work that will help us to gain greater resolution in this exciting area of practical ecological research. Overall, I hope that the work completed over the past few years will improve the chances of survival of these beautiful and fascinating species in an increasingly uncertain world.

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Paper II

How many? Spore emission experiments in four species characteristic of old-growth woodlands.

Eaton, S., Ellis, C.J., and Yahr, R.

Short Communication - accepted for publication in The Lichenologist

Introduction

With 90% of lichens found in Great Britain and Ireland producing ascospores (Purvis et al., 1992), quantification of spore emission is an interesting subject in its own right. However, it is of particular interest when considering population dynamics of lichen epiphytes characteristic of old-growth woodlands, which are often restricted in their population size (Rose 1976, Goward 1995, Sillet et al 2000, Snall et al 2005, Scheidegger).

Although several studies have considered the potential for limited ascospore movement (i.e. restricted dispersal distance) to limit species abundance (e.g. Werth 2006, Walser 2004), the extent to which propagule abundance (fecundity) may act as a factor controlling population size is rarely explicitly and independently considered, despite being an important factor determining the number of potential colonization events that may occur. Here the question is asked; do species which produce a greater number of spores occupy a greater number of trees in a landscape?

The number of spores emitted by different species of sexually reproducing lichens has been studied previously and found to vary greatly, from *Lecanora conizaeoides*, which emitted c. 20,000 spores in a 24hr period (Bailey and Garrett 1968), to *Caloplaca aurantia*, which emitted just 27 spores in a 3 hr period (Garrett 1971). Variation in observed patterns of discharge for in-situ experiments has been linked to seasonality (Pyatt 1969, Clayden 1977), or to conditions of rainfall, temperature and humidity (Kofler and Bouzon 1960, Pyatt 1969, Scott 1959, Ostrofsky and Denison 1980, Sangvichien et al 2011). In contrast, in ex-situ experiments, variation has been linked to differences in the treatment of thalli after collection (Crittenden et al. 1995), the time/season of collection (Yoshimura et al 2002), and the length of time between collection and discharge (Crittenden et al. 1995, Sangvichien et al. 2011). Such factors have made it difficult to draw cross-species comparisons of fecundity, particularly when the information originates from different studies.

In order to explore species fecundity among species, a large cross-species spore discharge experiment was conducted on tropical species of Thailand (Sangvichien et al 2011), finding considerable variation in spore discharge between species. However, even within this single study, variability in the freshness of samples and season of collection, coupled with low sample sizes, meant that robust cross-species comparisons could not be made.

Here, the number of spores emitted by four different epiphytic lichen species (*Lobaria pulmonaria, Nephroma laevigatum, Pannaria rubiginosa,* and *Pectenia cyanoloma* was investigated in such a way as to enable cross species comparisons of fecundity. These results were then compared to species abundance data, in order to determine whether there is any relationship between fecundity and population size. In addition, experiments were conducted to investigate whether a relationship could be found between the size of an apothecium and the number of spores produced.

Method

Nine thalli of each target species were collected from Glen Creran SSSI in Argyll (Lat: 56.545293N Long: 5.254924W). Care was taken to ensure that the thalli collected provided good examples of the given species, being healthy (free from necrosis/obvious infection) and morphologically typical. The thalli collected were also selected based on the presence of mature apothecia (determined by their size and colour). A single thallus of each species was taken from each collection location within the SSSI, with a minimum of 30m between collection points.

Thalli were carefully removed from their respective trees and transferred to a paper packet, for transport back to the herbarium in Edinburgh. Upon arrival, thalli were air dried in their packets (over a 48hr period), and transferred to the refrigerator for storage at 4^{o}C.

After 5 days, the thalli were removed and allowed to come to room temperature, after which, an individual mature apothecium was removed from each thallus using a clean scalpel blade.

Spores were then extracted from their apothecia using a method adapted from Yoshimura et al 2002. The apothecia of each species were transferred to a muslin bag and secured (by folding over the top of the bag and fastening it with paper clips), and left in a 250ml beaker of water under a running tap for ca. 4hrs. Apothecia from each bag were then immediately transferred to 90mm petri-dishes. Three apothecia were assigned to each dish, attached (in a single line) to the inside of the upper lid, using petroleum jelly. A microscope slide was attached to the lower lid using balls of putty, ensuring that the distance between the apothecial surface and the slide was c.10mm. Prior to attachment, the approximate location of each apothecium in relation to the slide was delimited using permanent marker. The dishes were then sealed with Parafilm and left on a window ledge for 72 hrs. Earlier experimentation found that optimum spore discharge occurred with multiple wetting/drying cycles of the apothecia. Therefore, after each 24hr period, a water droplet was pipetted onto each apothecium, and the dishes re-sealed.

At the end of the 72hr period, the slides were transferred to a compound microscope for spore counting. The previously applied apothecial location marks were used to locate the three ‘centers of emission’, around which spores were most likely to be found. The spores clustered around each of the ‘centers of emission’ were counted at x100 or x400 magnification. Since clusters of spores were discrete and non-overlapping on the slides, the total number of spores emitted per apothecium could be counted, and the overall mean number of spores per species calculated.

The mean number of spores emitted per species was then compared in an exploratory analysis to species abundance in the landscape of the collection sites (Glen Creran). Species abundance was estimated from a lichen survey conducted in 2014, in which 600 trees were surveyed for the presence/absence of the target species. For further details see Eaton et al 2017 (in preparation).

The number of spores emitted per species was also compared to apothecium size. Mean apothecium size per species was estimated from herbarium material, and the 5 most recent specimens of each species (containing apothecia) were selected. The 5 largest apothecia per specimen were measured using a dissecting microscope fitted with an eyepiece reticle. The longest length and perpendicular width of each apothecium were used to calculate the elliptical area ($A = \pi \times \frac{length}{2} \times \frac{width}{2}$).

In addition, the area of each of the *L. pulmonaria* apothecia used in the investigation were also measured in this way. After these initial investigations, the experiment was repeated on further apothecia from other *L. pulmonaria* thalli (also collected in the same way) and under less typical apothecia (i.e. exceptionally large or small) than those selected for spore counts.

Results

A total of 36 apothecia from 4 different species were investigated to estimate fecundity as the total number of spores produced using a standardized method. Variability in spore emittance was found both within and among the different species as shown in Figure 1, with *Lobaria pulmonaria* and *Nephroma laevigatum* in general emitting more spores than *Pectenia cyanoloma* or *Pannaria rubiginosa*. The mean number of spores ranged from 42 in *P. cyanoloma* to 107 in *P. rubiginosa*, 1,099 in *N. laevigatum* and 1,754 in *L. pulmonaria*. An ANOVA test showed that there was a significant difference in the number of spores emitted by the different species (p = 7.93 E-09).

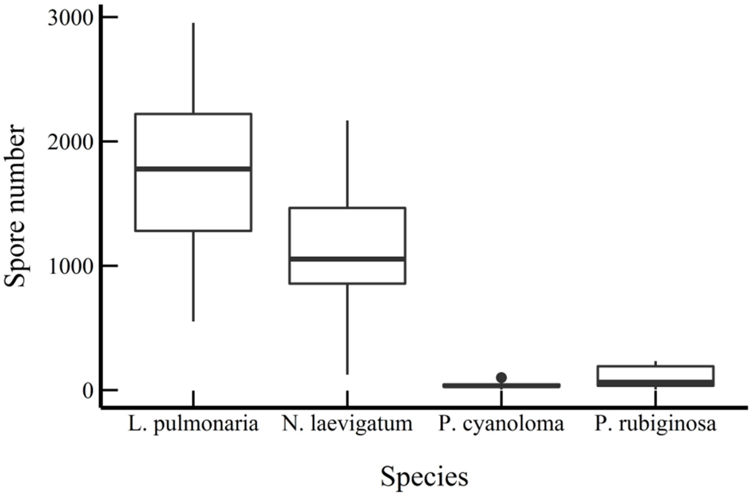

Figure 1: Boxplots showing the number of spores emitted per species. Centre lines show the medians; box limits indicate the 25th and 75th percentiles; whiskers extend 1.5 times the interquartile range from the 25th and 75th percentiles, and outliers are represented by dots.

No relationship could be found between the mean number of spores emitted by a species and its abundance in the landscape (Figure 2A). Although species that appear limited in the number of spores they produce consistently occupied around 10% of all trees surveyed, those with higher apparent fecundity were more variable in their abundances, with *N. laevigatum* occupying just 3% of trees and *L. pulmonaria* occupying over 15%.

As may be expected, a positive relationship ($R^2 = 0.69$) was found between the size of *L. pulmonaria* apothecia and the number of ascospores produced over a 72hr period. What is perhaps more interesting is that this relationship may also hold amongst species (see Figures 2B and 3).

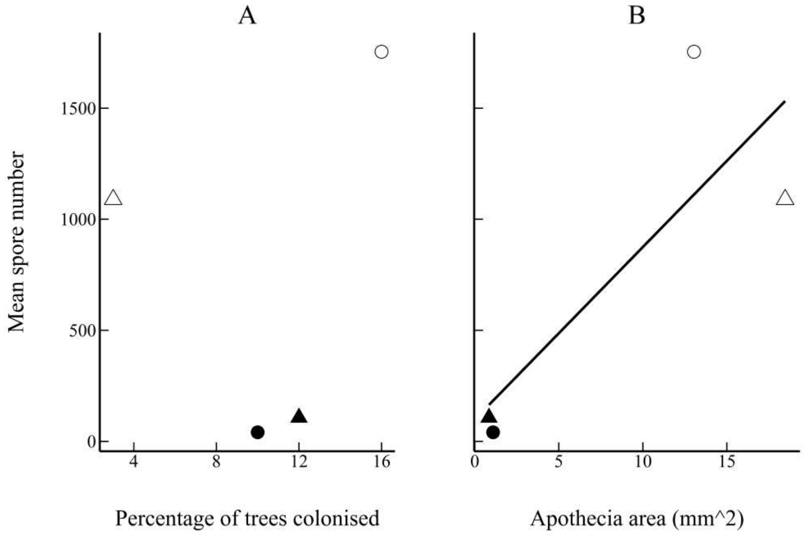

Figure 2. Mean (n=9) number of spores produced per species v's A) the proportion of surveyed trees colonised and B) the mean size of five largest apothecia. Each species is represented by a different symbol: filled circle = *P. cyanoloma,* filled triangle = *P. rubiginosa*, Empty circle = *L. pulmonaria* and empty triangle = *N. laevigatum*. SE values are not shown as they are less than the value of symbols in two of the species. Relationship between apothecia area and number of spores produced ($y = 77.61x + 98.90$, $R^2 = 0.68$) was non significant ($p>0.1$).

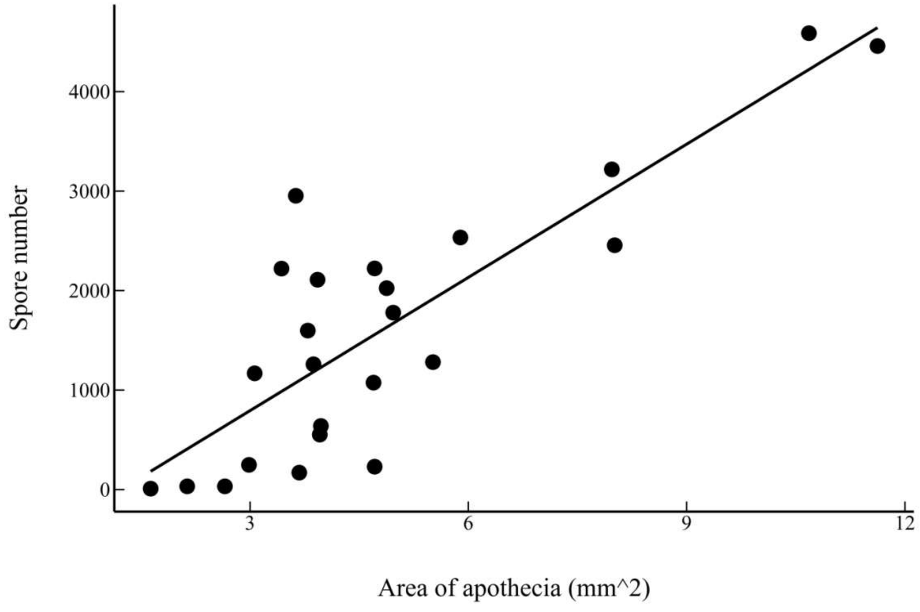

Figure 3. Number of spores produced by individual L. pulmonaria apothecia v's apothecia size. The number of spores produced could be predicted by apothecia area ($y = 446x - 546$), R2 = 0.69, $p<0.001$).

Discussion

Fecundity refers to the potential reproductive output of an individual or population (Rockwood 2015) and is an important factor in the regulation of population size (Begon et al 1996). This study was carried out to enable comparisons of fecundity to be made between four species of lichen epiphyte collected from a landscape in western Scotland. The species *Lobaria pulmonaria* and *Nephroma laevigatum* were found to produce significantly more spores than *Pectenia cyanoloma* or *Pannaria rubiginosa*.

There appears to be no relationship between the number of trees colonized by a species and the number of spores it is capable of discharging; the species most limited in its distribution (*N. laevigatum*) was found to produce similar spore numbers to the most abundant species (*L. pulmonaria*). The results of this study therefore suggest that fecundity alone will not account for differences in species distribution/abundance, pointing to effects such as dispersal distance and/or habitat constraints in limiting occurrence.

It should be noted that, the spore counts observed are based on a very small sample of individuals collected from a single wooded location, possibly representing a single population, and therefore the conclusions are limited. As a final caveat, a study of germination efficiency (therefore giving the number of viable spores) may help clarify many of the findings presented here, particularly as the counts do not necessarily represent actively discharged spores, being from a downward spore deposition method. Further study is recommended if we are to fully understand limits imposed by reproduction in the population dynamics of sexually reproducing lichen epiphytes. Further studies could include:

- A cross-species study of the number of viable spores produced by a species and their distribution (utilizing germination experiments such as those of Sangvichien et al 2011 and Crittenden 1995),
- A larger cross-species study of the mean number and size of apothecia on a thallus, and the mean number of spores discharged by a species,
- A larger-scale repeat of this study incorporating a greater range of species of lichen epiphytes from a wider population pool.

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Paper IV

An inter-specific study of dispersal in lichen epiphytes

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Abstract

Dispersal is important in explaining species distribution/abundance and response to environmental change. However, direct estimates of dispersal are scarce, particularly in passive dispersers such as plants and fungi, for which dispersal is often indirectly inferred. Different inferential methods are built on contrasting assumptions. Those that infer dispersal from spatial pattern for example must account for limits to establishment as well as colonisation, and may be sensitive to spatial and historic landscape context. Inference has therefore produced diverse and often contradictory estimates for the dispersal of an equivalent species, making any such values difficult to apply more generally.

In this study, a single direct method (propagule trapping with molecular detection) was used to investigate dispersal ability of six contrasting lichen epiphytes. These species are passively dispersed by microscopic propagules (making direct measurements of dispersal a technical challenge) and they represent an ecological guild that is threatened by forest fragmentation and isolation (so that direct measurement of dispersal is key to informing conservation strategy). Dispersal was measured for species occurring in temperate rainforests of western Scotland. Traps were deployed at both short (up to 20m) and long (up to 200m) distances from propagule sources, and samples were tested for the presence of the target species, representing both sexually and asexually reproducing modes.

This is the first direct comparative study of lichen epiphytes in a natural context. We found that reproductive mode, distance decay and aspect were all important dispersal determinants over short distances from a propagule source. Most species also exhibited measurable dispersal at 200m, with the logistic function (with a floor > 0) providing a better fit to the data in five of six species, than the exponential function. A two tier structure to the dispersal process is strongly supported; whereby propagules dispersing over short distances (within a woodland stand) are subject to a different set of dispersal determinants than those dispersing over longer distances (between woodland stands).

Keywords: abundance, asexual, connectivity, dispersal determinants, general linear mixed model, long distance dispersal, propagules, sexual, short distance dispersal, spores.

Introduction

Dispersal is a fundamental process enabling population and metapopulation persistence (Hanski 1999; Levins 1969) and is therefore central to species conservation. The quantification of dispersal is increasingly important to conservation planning, because improving functional connectivity is a goal for managing fragmented landscapes (Calabrese & Fagan 2004; Jongman & Pungetti 2004). However understanding when sufficient connectivity has been achieved is extremely difficult. For mobile organisms, dispersal can be directly measured using mark-recapture methods (Turchin and Thoeny 1993). However, particularly for sessile organisms such as plants and fungi, dispersal is often inferred indirectly rather than directly measured. This poses problems, since inferential methods are subject to contrasting assumptions sensitive to spatial and historic landscape context. In this paper we use a direct method for measuring dispersal in sessile organisms (lichen epiphytes) which avoids these issues.

The importance of dispersal for epiphytic lichens is related to their role as patch tracking organisms (Snäll et al 2005); they must disperse between trees before the death of their host to secure short-term population continuity, and between woodland patches within the landscape to secure long-term population persistence. They are thus severely threatened by intensification of forest management, or forest loss and fragmentation; however, the direct detection of their propagules presents a technical challenge (largely due to their microscopic size). To sidestep technical issues, inferential methods for lichen epiphytes have employed a wide range of different approaches: optimizing parameters in metapopulation models (Johansson et al 2012; Ruete et al 2014; Snäll et al 2005), monitoring change in species distribution through time (Belinchon et al 2017; Fedrowitz et al 2012; Tapper 1976), inferring dispersal ability from extant populations, using spatial genetic structure (Buschbom 2007; Dal Grande et al 2012, Jones et al 2015) or occurrence patterns (Boudreault et al 2012; Dettki et al 2000). However, the results of inferential studies have been highly contrasting; even for the same species (e.g. *Lobaria pulmonaria*) these studies have indicated distance decay and local spatial genetic structure over short distances (Dal Grande et al 2012; Jüriado et al 2011), while also inferring effective long-distance dispersal (Hilmo et al 2012; Otálora et al 2015; Wagner et al 2006; Werth et al 2007).

One of the broad assumptions in dispersal studies is that propagule type will strongly affect dispersal limits. Lichens may have sexual propagules (comprising small, light fungal spores), and/or asexual propagules (comprising larger heavier arrangements of fungal hyphae plus a photobiont; such as in soredia, isidia and thallus fragments). Physical differences between the two propagule types are thought to lead to contrasting effects of gravity and impaction, with larger propagules being more likely to deposit under the influence of gravity (Gregory 1961), or impact onto a surface (Solomon 2003), than smaller propagules. This is consistent with many studies suggesting that asexual propagules will be more limited in their dispersal ability (as concluded by Armstrong 1987; Cassie & Piercey-Normore 2008; Heinken 1999; Jüriado et al 2011; Snäll et al 2005; Tapper 1976; Walser et al 2001; Werth et al 2006b,) than sexual species (as shown by Alors et al 2017; Buschbom 2007; Geml et al 2010; Lättman et al 2009; Lindblom and Ekman 2006; Otálora et al 2010). Although these findings are plausible, other inferential methods have shown conflicting results; indicating that spores may be restricted in their dispersal ability (Favero-Longo et al 2014; Jones et al 2015), with asexual propagules easily capable of long distance dispersal (e.g. Harmata & Olech 1991; Johansson & Ehrlen 2003; Otálora 2010, 2013; Werth et al 2006a). However, the approaches used by these studies may confound the process of dispersal per se, with establishment, which depends on the re-association of sexual propagules (fungal spores) with a compatible photobiont partner, representing an unquantified but limiting stage in lichen distribution/abundance patterns. Again, this underscores the importance of direct measurement of dispersal, as a process distinct from that inferred by patterns dependent on prior establishment.

Many dispersal studies assume that the majority of propagules settle within a short distance of their source (Clobert 2012). As a result, dispersal kernels are often estimated by fitting continuous distributions (such as exponential curves) to short range dispersal data, leaving long distance dispersal to be inferred on the basis of extrapolation. However, in the case of wind dispersed species, propagules travelling outside of their short distance dispersal (SDD) range (known as the "escape fraction", Sesartic and Dallafior 2011) may become affected by trajectory altering wind gusts (known as uplifting events, Nathan et al 2002) which are no longer subject to the same dispersal decay rate as that of SDD propagules. If the escape fraction from all local sources is thus combined, an independent, 'background' propagule supply (Gjerde 2015; Johansson et al. 2012) is formed, contributing to long distance dispersal (LDD) at the regional scale. As a result, dispersal models with fat tails or a floor > 0, have been found to provide a better fit to dispersal data in the case of wind dispersed species (Austerlitz et al 2004; Devaux et al 2007; Klein et al 2006; Schurr et al 2008).

Although LDD has been shown to be important in describing lichen epiphyte distribution patterns (e.g. Gjerde et al 2015), there are no direct studies of dispersal in a natural setting that would allow comparisons to be made for contrasting species, i.e. with different reproductive and dispersal-modes.

Here, the contribution of dispersing propagules to both short (representing connectivity between trees) and long (representing connectivity between woodland stands) distance dispersal is explored for sexually and asexually reproducing lichen epiphytes. Using measures of direct dispersal in six contrasting epiphytic lichens, we test the following hypotheses:

i) Reproductive mode will be an important determinant of dispersal; asexually reproducing species (with larger propagules) will be more limited in their dispersal ability than sexually reproducing species (with smaller propagules);

ii) Time will be an important determinant of dispersal; the probability of propagule capture will increase with time-period over which trapping occurred;

iii) Wind will be an important determinant of dispersal; the probability of propagule capture will be affected by wind direction, with a higher detection rate recorded downwind (to the east) of the propagule source;

iv) Distance will be an important determinant of dispersal; probability of propagule capture will diminish with distance from the propagule source.

Method

Data collection

Propagule trapping was carried out in Glen Creran, located in Argyll on the west coast of Scotland (latitude 56.56548, longitude -5.23387). An area of birch woodland (*Betula sp.),* with only occasional oak (*Quercus sp.*) and willow (*Salix sp.*) was selected as the study site (Fig. 1B), and which included a single mature hazel tree (*Corylus avellana)* colonized by the target epiphytic lichens: the sexual *Nephroma laevigatum* and *Pannaria rubiginosa*, *the* asexual *Nephroma parile, Pannaria conoplea* and *Pectenia atlantica,* and *Lobaria pulmonaria*. Although *L. pulmonaria* is capable of reproducing sexually and asexually, because sexually reproducing *L. pulmonaria* thalli were present on the focal tree, it is treated as a sexually reproducing species in this study. The birch woodland (devoid of target epiphytes) extended for at least 50m (and up to 200m) around the focal hazel in all aspects, before transitioning into ash/oak woodland, where occasional trees colonized by the target epiphytes were found. This sampling setup assumes that propagule contributions from trees out-with the focal tree are equal regardless of their distance to the traps.

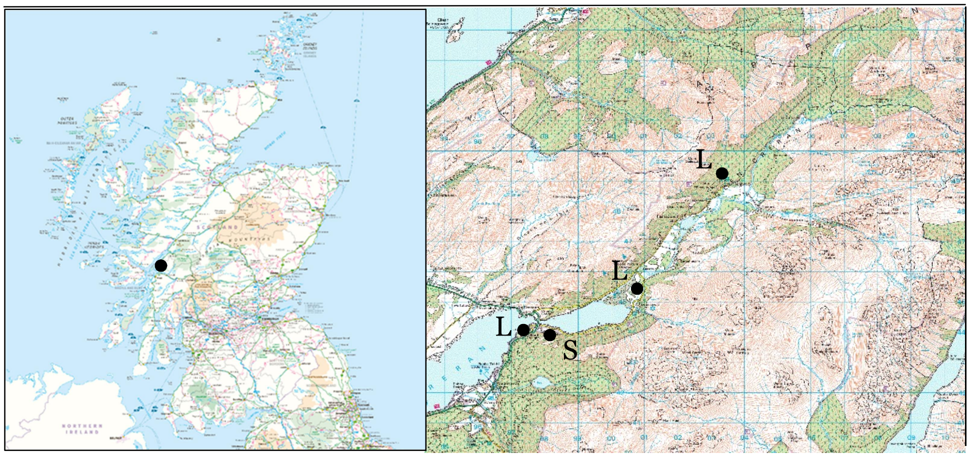

Figure 1. Map on left shows location of Glen Creran in relation to Scotland, map on right shows approximate locations of the three long distance propagule trap sites (L) and the short distance trap sites (S) © Crown Copyright and Database Right [2017]. Ordnance Survey (Digimap Licence).

Automated propagule traps (as described in Eaton et al 2017a) were positioned around the focal hazel, along north, east, south and west aspects, at distances of 1m, 2m, 5m, 10m and 20m. The traps were erected on poles at 1m height above the ground. Prior to their use, the trap sampling arms were sterilized (autoclaved) and sealed until arrival at the trapping locations. The front facing side of 1.5cm^2 sampling arms (two per trap) were covered with a thin layer of sampling medium (petroleum jelly, approx. 0.1g). Experimental trapping was carried out between 1st October and 31st October 2015. The traps were deployed over three different time-periods; 24hrs, 36hrs and 60hrs. The traps were run intermittently (3 min on, 3 min off) over the 36hr and 60hr periods, to extend the battery life. Each different time-period was repeated over 3 separate occasions, to give a possible total of 9 experimental replicates per distance and aspect (combined over the different time-periods).

In addition, three traps were deployed in the wider landscape at sites remote (around 200m) from any woodland (see Figure 1), to trap propagules that represented long distance dispersal. These traps were positioned at the mouth of the glen on an area of coastal shingle, midway up the glen in an area of grazing marsh, and at the head of the glen in an area of recently cleared plantation woodland. The traps were run over the same experimental time-periods as described above, to give a total of 9 possible long distance replicates per location.

At the end of each time-period, the sampling medium was transferred from the pair of collecting arms directly into extraction tubes at the trap site, using a sterilized scalpel. Trapping was then repeated using a new pair of sterilized sampling arms. In this way, a total of 198 samples were collected.

The samples from the traps were subject to DNA extraction and nested PCR as described in Eaton et al. (2017a). Additional negative controls were added to the sample pipeline (every 20 samples), comprising sampling medium which had been applied in the laboratory to a pair of sterilized sampling arms, and then transferred (without experimental trapping) to an extraction tube.

Note that the species-specific primers in the case of *P. atlantica* are not sensitive to this species alone but to *P. cyanoloma* also (a species which was present in the wider landscape). Therefore, therefore although only *P. atlantica* was present on the focal tree the presence of *P. cyanoloma* propagules in the air mass could not be ruled out, and results for the target species *P. atlantica* are here referred to as *Pectenia sp.*

Analysis 1. General linear mixed model

In order to identify determinants of dispersal, the SDD data (taken at distances of 1m, 2m, 5m, 10m and 20m from the focal hazel tree) were analysed using general linear mixed models (GLMM) with a binomial distribution (logit link function; logistic regression). The LDD results were omitted from this analysis as the exact source of captured propagules in the LDD traps was unknown (other than being > 200m away).

We constructed the most plausibly complex model to explain the molecular pattern of propagule presence-absence using five explanatory variables - time-period over which trapping occurred, distance of traps from the focal hazel tree, reproductive mode, propagule size and trap aspect – with the three replicates and six species treated as random effects, using the R package lme4 (Bates et al 2015). The models were optimized by backwards selection and the significance of fixed effects assessed using likelihood ratio tests (LRTs), using a significance threshold of $P<0.05$ (Crawley 2007; Zuur et al. 2009).

Residual deviance of the final models was tested using chi-square to examine model fit.

Analysis 2. Non-linear regression

In order to identify whether a decay model with a floor of zero, or one with a floor > 0 (representing background propagule deposition) best represents the dispersal data, two non-linear regression models were compared using the Levenberg Marquardt method employed in CurveExpert Professional 2.6 (Hyams, D. 2017). This program fits nonlinear equations to the data, subsequently ranking the data according to r^2-values.

Dispersal probabilities per distance were calculated by combining presence-absence data among the experimental trap aspects and time-periods, thus producing three mean 'probability of detection' data points for each replicate (at distances of 1m, 2m, 5m, 10m, 20m and 200m). These three data points were then used to produce a mean and standard deviation of 'probability of detection' per distance for each species. Standard deviations were used to weight each of the data points in the curve fitting.

Two non-linear regression models were trialled; an exponential model:

$y = ae^{\alpha x}$

where 'a' represents the starting value on the y axis and 'α' the (negative) dispersal decay parameter, and the logistic model:

$y = b/(1+ae^{\alpha x})$

where 'b' is the background dispersal rate, 'a' represents a shift on the x axis and 'α' is the dispersal parameter.

The coefficient of determination (r^2) and sum of squares were computed for each of the model fits, and an F-test used to compare the sum of squares of the two models to determine whether the more complex logistic model was preferred over the simpler exponential model.

Results

Raw data

There was high inter-specific variability in the propagule trapping (see Appendix 1 and 2); *L. pulmonaria* yielded positive results in 79% of the 198 trapping events, *N. laevigatum* 62%, *P. rubiginosa* 31%, *P. conoplea* 24%, *Pectenia sp*. 23%, and *N. parile* 9%. There appeared to be a general decline in positive trappings with distance; 47% at 1m, 46% at 2m, 37% at 5m, 33% at 10m, 36% at 20m, and 27% in the LDD traps, with only a very small aspect signature such that 46% of trappings were to the east of the focal tree (downwind), 43% to the west (upwind), 38% to the north, and 34% to the south.

Statistical comparison of propagule presence-absence with explanatory factors (aspect, distance, time, reproductive mode and propagule size), revealed that distance, aspect and reproductive mode were significant effects ($p<0.05$) determining propagule deposition over short distances (up to 20m) from their source (see Table 1). The random effects of species and replicate had variances of 0.86 and 0.09 respectively. The residual deviance in the final model was not found to be significant (residual deviance = 1009, residual degrees freedom = 1012, p = 0.51).

Effect	ChiSq (-2LL)	DF	p-value	Estimate
Distance	7.56	4	0.006	-0.03
Reproductive Mode	5.32	1	0.021	2.26 (Sexual)
Aspect	10.09	3	0.018	-0.43 (N), -0.66 (S), -0.21 (W)

Table 1. Significant fixed effects identified through LRT's

Testing for existence of long-range dispersal

A visual inspection of the nonlinear regression curves (see Figure 2) suggested that both the logistic and exponential curves provided a similar fit to the data in most species (apart from *Pectenia sp.*), particularly over distances of up to 20m. Unusually, the shape of the exponential curve in the case of *N. parile* showed an increase with distance rather than a decrease; however there was wide variation among the *N. parile* LDD data points making the exact shape of the curve in this species highly uncertain.

According to r^2 (see Table 2), the logistic curve provided a better fit to the observed data in five species (all except for *N. parile*). For these five species, F-tests ($p < 0.05$) showed that the more complex logistic model was not a statistically better fit than the simpler exponential model however (*L. pulmonaria* (F=7.00 p=0.07), *Pectenia sp.* (F=1.84 p=0.26), *P. conoplea* (F=4.37 p=0.1275) and *N. laevigatum* (F=0.1001 p=0.77)) apart from in the case of *P. rubiginosa* (F=13.75 p=0.03).

	Exponential				Logistic				
	a	α	r^2	Sum of Squares	a	b	α	r^2	Sum of Squares
L pulmonaria	0.906	-0.005	0.32	0.06	-0.431	0.526	-0.010	0.79	0.02
N laevigatum	0.740	-0.002	0.67	0.01	-0.999	0.001	0.000	0.68	0.01
N parile	0.049	0.006	0.57	0.01	803660.303	54693.896	-0.025	0	0.04
P conoplea	0.256	0.000	0	0.02	-0.964	0.257	1.156	0.59	0.01
P rubiginosa	0.501	-0.073	0.86	0.02	-0.862	0.075	0.024	0.98	0
Pectenia sp.	0.229	-0.007	0.39	0.04	-0.809	0.068	0.020	0.62	0.03

Table 2. Results and parameters of exponential and logistic curves

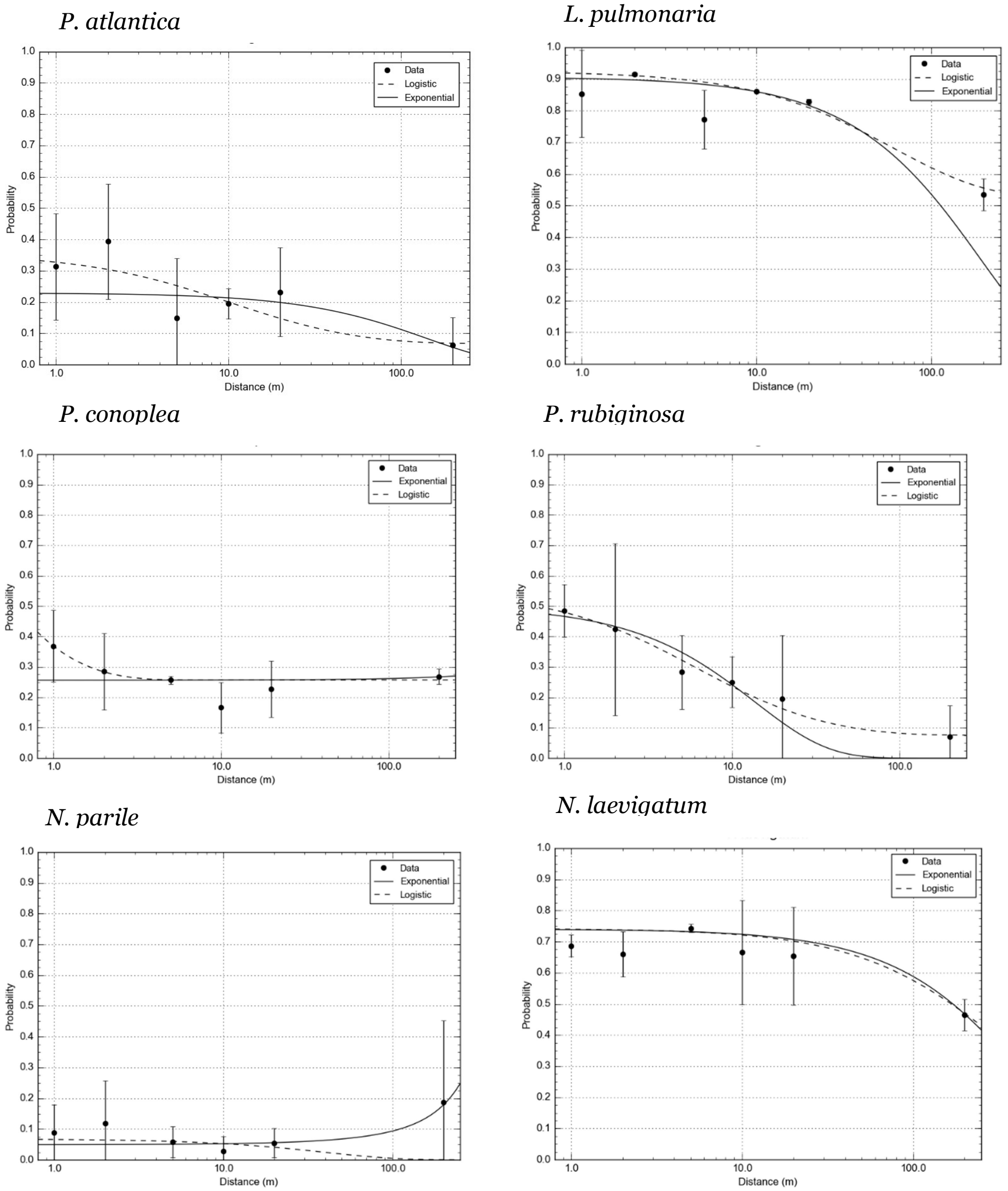

Figure 2. Pooled probability of detections (mean and SD) with fitted exponential and logistic curves. Note left column = asexual species and right column = sexual species.

Discussion

This study set out to explore the determinants of dispersal for six contrasting lichen epiphytes. We found that reproductive mode, distance and aspect were all important factors affecting dispersal over short distances from the propagule source. When long distance data was also considered, most species exhibited measurable dispersal at 200m, with the logistic function providing a better fit to the data than the exponential function in most species, supporting the importance of long distance dispersal in explaining lichen epiphyte distribution patterns. Each of the hypotheses set out in the introduction will be considered in turn below:

i) Reproductive mode as a determinant of dispersal;

The sexual species (*N. laevigatum*, *L. pulmonaria* and *P. rubiginosa*) were caught more frequently in the traps than asexual species (*Pectenia atlantica*, *P. conoplea* and *N. parile)*. These results may be explained by the greater abundance of propagules produced by sexually reproducing species as compared to asexual species; a single apothecium may produce over 1000 spores in a 72 hr period (Eaton et al 2017b), whereas an asexual species is thought to produce far fewer propagules (e.g. Wagner et al 2006 estimate a maximum annual soredia production in a single *L. pulmonaria* thallus to be 200).

Combined with the frequency of capture data, the results from GLMM highlighted that asexual species are more limited in their dispersal ability than sexual species. Although other studies have suggested this to be the case, we believe ours is the first direct comparative study of both sexual and asexual species for the same study system. Interestingly, propagule size was not found to be a significant determinant of dispersal when reproductive mode was included as a factor, suggesting that reproductive mode might be used as a proxy for propagule size when making generalisations about short distance dispersal among lichen epiphytes.

ii) Time as a determinant of dispersal;

The lack of significance of time-period over which trapping occurred may be an artefact if we assume that the trapping medium became saturated with non-target material in less than 24hrs. This seems likely given that during trapping experiments woodland ferns were sporulating. The abundance of fern spores was observed by the discoloration of the trapping medium.

iii) Wind as a determinant of dispersal;

Aspect was found to be a significant determinant of dispersal although it was expected that most deposition would occur downwind of the propagule traps (to the east), the raw data showed weak evidence for this, with traps lying to the east or west of the source securing positive trappings in almost equal numbers. Traps to the north or south of the source tree demonstrated considerably fewer positive trappings however. As these traps were set either up-slope (in the case of the southern traps) or down-slope (in the case of the northern traps) of the source tree, this suggests that topography may have more of an influence on propagule movement than prevailing wind direction. The importance of topography to dispersal in plants and non-lichenized fungi has been evidenced previously (e.g. Allen et al 1989; Tackenberg 2003). The weak wind direction signature may therefore be explained by topography related air turbulence within the canopy, creating local air currents (which are known to strongly affect particle dispersal (Kuparinen et al 2007)) and masking wind aspect signatures over short distances. The fact that lower wind speeds are found in/under woodland canopies than in open landscapes (Kaimal & Finnigan 1994) may thus reduce the impact of prevailing wind direction within the epiphytic environment.

iv) Distance as a determinant of dispersal;

Over short distances (up to 20m from the propagule source), distance decay was found to be an important determinant of dispersal, supported by other studies for epiphytic lichens that have demonstrated a distance decay effect over similarly short spatial scales (Walser et al 2001, Gu et al 2001). The distance over which SDD may be assumed to operate is limited here by the experimental setup, whereby the area of woodland devoid of the focal species had a radius of just 50m (from the focal tree) in places, therefore making the maximum SDD distance of 20m rather arbitrary. However, the scale of the study is in line with previous findings; measurements of propagule deposition made by Walser et al 2001 for the focal species *L. pulmonaria* found a steeply declining dispersal signature with only limited evidence of dispersal at 50m, consistent with the mean 35m dispersal distance found by Öckinger et al 2005.

At long distances however (around 200m from the propagule source), most species continued to exhibit measurable dispersal, supporting the importance of long distance dispersal in explaining lichen epiphyte distribution patterns (Gjerde et al 2012; Hilmo et al 2012; Johansson et al 2012; Ronnas et al 2017; Ruete et al 2014; Werth et al 2007). In addition, a logistic dispersal function (with a floor > 0) appeared to provide a better fit to the dispersal data (albeit marginally) than the exponential decline function, again supporting the presence of an independent 'background' propagule supply (Gjerde 2015;

Johansson et al 2012). Only in *N. parile* did the exponential model provide a better fit to the data; however the wide variation among the LDD data points for this species made the exact shape of the curve highly uncertain. Both models provided a similar level of fit in *N. laevigatum*. The lack of significance of the logistic model as the preferred fit may be compromised by the single long distance data point included in the analysis.

These contrasting results (the importance of distance decay in explaining propagule deposition over short distances, and the existence of measurable dispersal over long distances), indicate a two-tier structure to the dispersal process; whereby propagules dispersing over short distances (within a woodland stand) are subject to a different set of dispersal constraints than those dispersing over longer distances (between woodland stands). Such a tiered or composite structure to the dispersal process has been acknowledged previously (Clark et al 1998, Higgins & Richardson 1999), and separate local and regional contributions to dispersal have since been found to describe lichen epiphyte colonisation patterns (Gjerde et al 2015). This composite dispersal pattern can explain seemingly conflicting evidence for dispersal limitation over short distances (Dal Grande et al 2012; Jüriado et al 2011; Walser et al 2001) and unlimited dispersal ability over long-distances (Hilmo et al 2012; Otálora et al 2015; Walser 2004; Wagner et al 2006; Werth et al 2007) for the model epiphyte species *L. pulmonaria*.

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Author Contributions:

SE, CE, DH, DG and RY conceived the ideas and designed the methodology, SE collected the data, SE analysed the data with support and guidance from CE, RY and DH, SE led writing of the manuscript with support and guidance from CE and DH. All authors contributed critically to the drafts.

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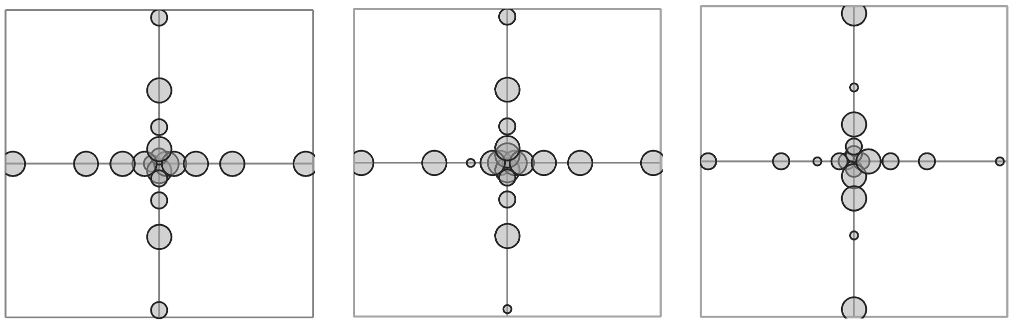
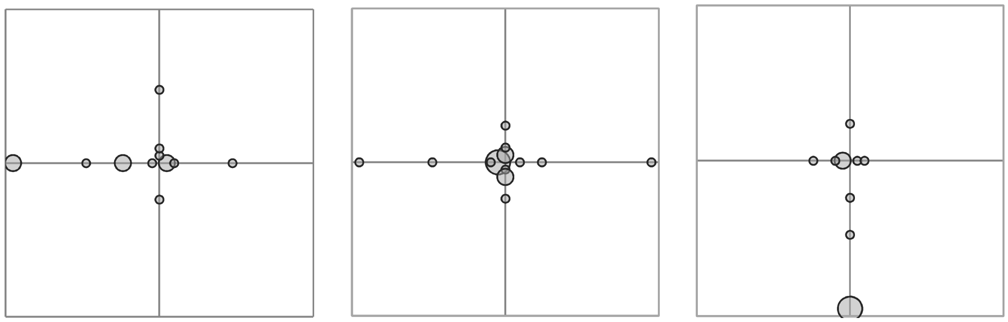
Appendix 1 Frequency of positive SDD propagule trap result within the 20m x 20m trapping area along N, E, S, W axes; size of bubble represents frequency of positive result from 1 (smallest) to 3 (largest).

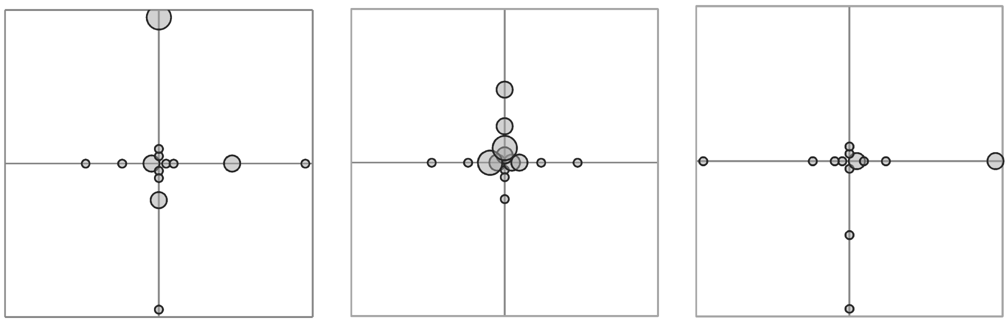
1 day results 3 day results 5 day results



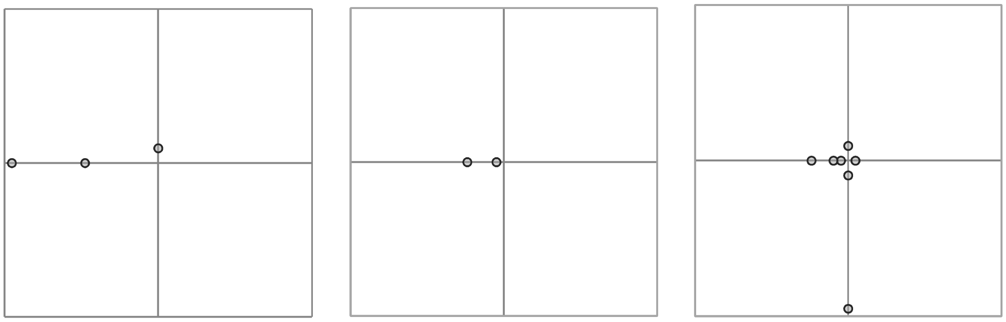
A. *Lobaria pulmonaria*



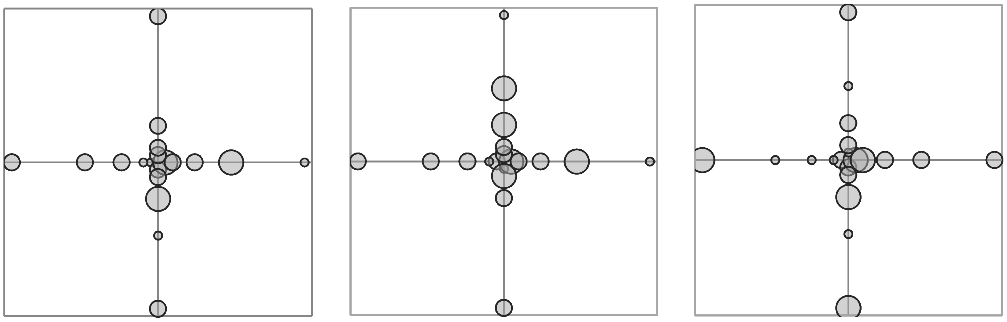
B. *Pannaria conoplea*



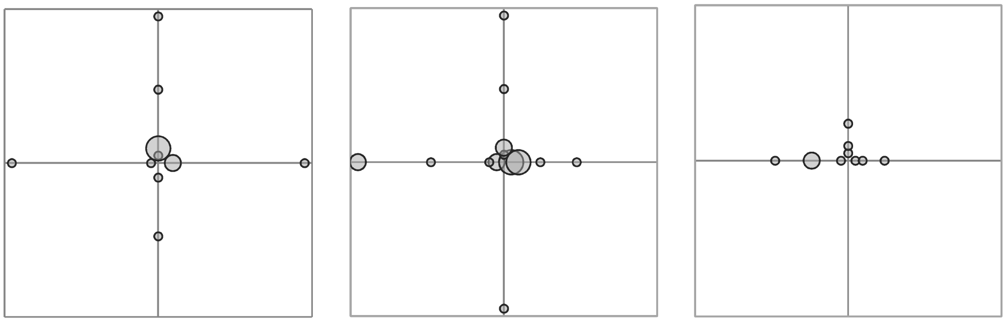
C. *Pannaria rubiginosa*



D. *Nephroma parile*

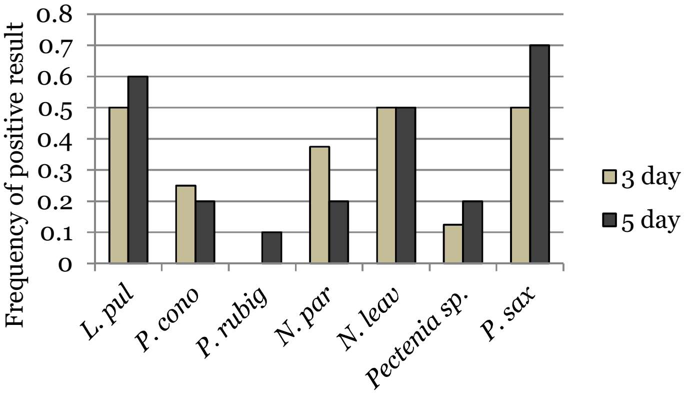


E. *Nephroma laevigatum*



F. *Pectenia sp.*

Appendix 2 Frequency of a positive PCR result, from the 3 and 5 day long distance spore trap trials.



Paper V

Agent-based modelling for old-growth dependent species: a simulation for lichen conservation

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Abstract

Conservation planning is increasingly carried out at the landscape-scale, enabling population processes (such as dispersal and colonisation) to occur in increasingly fragmented landscapes. These processes are vital to ensure a species' resilience during periods of environmental change. However, the spatial and temporal scale over which these processes operate is unknown for many species, restricting the application of landscape-scale conservation.

Here, an agent based model was used to explore spatially explicit landscape-scale conservation scenarios for 'old-growth' dependent lichen epiphytes. Scales of connectivity were investigated in a hypothetical landscape as proof-of-concept, using empirically determined biological parameters: (i) size/age-linked suitability predictions of five lichen epiphytes for trees, coupled with (ii) species-specific estimates of dispersal. Specifically, we explore the spatial and temporal scale over which colonisation occurs for regenerating woodlands under scenarios of increasing isolation distance, for different landscape matrices and under contrasting woodland management regimes.

We demonstrate that the agent based model is able to simulate ecologically plausible behaviour in the target species, allowing it to be applied to explore spatially realistic conservation proposals. As a result, the following general principles of landscape-scale management for lichen epiphytes are supported: 1. In order to increase chances of sustained colonisation of a regenerating woodland patch, it should be cited within 100m of a propagule source; 2. When this is not possible (distance > 100m), the greatest improvement in conservation outcome will be effected through managed habitat quality of the regenerating woodland; 3. Smaller improvements can be realised through increased landscape connectivity, however when improving connectivity is the only option, scattered trees provide the best strategy as opposed to lines or blocks of trees. We also caution that monitoring would ideally occur over many decades, with colonisation of some species not to be expected for around 50 years under optimum scenarios.

Keywords: colonisation, connectivity, landscape-scale conservation, management, metapopulation

Introduction

Practical conservation management is increasingly applied at the landscape-scale (Adams 2014) reflecting a transition to the ecosystem-approach in conservation policy and planning (e.g. Watson and Albon 2011). Although landscape-scale processes are thought to be essential to species persistence during periods of environmental change (Van Teeffelen et al 2012), the spatial and temporal scales over which these processes operate is difficult to measure and are unknown for many species (Clobert 2001, Lindenmayer and Franklin 2002, Tischendorf & Fahrig 2000).

Management of woodland ecosystems considerably influences the presence and abundance of dependent species, through control of tree species composition, stand structure and density (Harmer et al 2010). Epiphytic bryophytes and lichens in particular are some of the most sensitive species to management-induced change within woodlands (Király et al 2013), and for some epiphytic species slow colonisation and shade intolerance (Gustafsson & Erikson 1995, Király et al 2013, Ranius et al 2008) explains a reliance on old-growth conditions (Gu et al 2001, Kuusinen 1996, Rose 1992). In the past, traditionally managed woodlands have been surrogates for the persistence of these old-growth epiphytes (Rose 1992), with timber/wood harvesting or grazing reducing shade whilst also preventing natural regeneration (McDonnell 2014). Conservation management that continues to prevent shading may reduce population extinction for internationally important old-growth epiphytes, however it also prevents the woodland from undergoing evolutionary adaptation or community succession; as old trees die and are not replaced, the temporal continuity of the woodland, as well as the epiphyte populations within, ultimately become threatened (Coppins 2003, Kirby et al 1995).

The landscape-scale approach presents an opportunity to consider conservation of old-growth dependent epiphytes over larger areas. Allowing some areas of woodland to undergo periods of regeneration ensures that woodland continuity, and therefore future old growth conditions are secured, while extant epiphyte populations are maintained within protected (non-regenerated) patches of old-growth as sources of propagules for future colonisation into regenerated patches. Despite the clear rationale for this approach (Scheidegger & Werth 2009), the spatial and temporal scale over which many epiphyte populations and their habitat patches function is largely unknown (Coppins 2003), and so the landscape approach is as yet unworkable.

In the case of sessile species such as epiphytes, isolated patches of suitable habitat are connected by dispersal events, creating a metapopulation structure (Levins 1969).

Theory predicts that more connected patches of habitat will have a higher probability of colonisation (Hanski 1999) and a lower probability of extinction (Brown and Kodric-Brown 1977). In more general terms, colonisation is dependent on dispersal ability and niche specificity of the focal species, as well as the spatial pattern and condition of habitat patches, whereas extinction is dependent on stochastic and/or deterministic events affecting the habitat patches (e.g. succession) or the species directly (independently of the habitat patch, e.g. age related mortality, low population size). However, in the case of epiphytes, these metapopulation processes may be interpreted at two spatial scales; at the local scale where individual trees act as patches, or at a landscape-scale, where isolated woodland stands act as patches. At the landscape-scale, colonisation and extinction are both expected to be dependent on patch (woodland stand) size, in addition to the quality of the habitat, and the isolation/connectedness of woodland stands in the landscape (Hanski 1999, Fleishman et al 2002, Moilanen & Hanski, 1998, Snäll et al 2005a). At the local level however, patch dynamics are more temporally dynamic (Jonsson et al 2008, Snäll et al 2003), with colonisation dependent on the age of the tree (larger/older trees are known to provide a more suitable habitat for many old-growth epiphytes (Gu et al. 2001, Gustafsson et al 1992, Öckinger et al. 2005)), whereas extinction is largely deterministic (Belinchón et al 2017, Johansson et al 2012, Ruete et al 2014), being dependent on tree death (Snäll et al 2003). In order to fully understand population dynamics of epiphytes at the landscape-scale, it is important to embed both tree level dynamics within dynamics operating at a larger landscape-scale (Holt 1992, Löbel et al 2006).

A further challenge to metapopulation studies is to move away from investigations of static landscapes, where patches of unvarying quality are permanently present in the landscape, towards a more dynamic system (Johst et al 2011). Although a growing body of work has considered the impact of management scenarios and landscape connectivity on epiphyte metapopulation dynamics (e.g. Belinchón et al 2009, 2017, Fedrowitz et al 2012, Gjerde et al 2015, Johansson et al 2012, 2013, Johansson & Ehlren 2003, Löbel et al 2006, Snäll et al 2005b, Wagner et al 2006), to date dynamic processes occurring at both the local (tree) and landscape (woodland stand) scales have not been modelled simultaneously (though see Snäll et al 2014). Complex agent based models enable such multi-scale dynamics to be investigated, by reconstructing the effect of landscape pattern on detailed biological processes (Wiens et al 1993) and allowing the more precise predictions of species response to landscape-scale conservation scenarios (Ruete et al 2014).

Here, an agent based model was designed to enable spatially explicit scenarios of landscape-scale conservation to be tested, using a temporally dynamic system that coupled size/age suitability predictions for trees (Eaton et al 2017a) with species-specific estimates of dispersal range (Eaton et al 2017b). Specifically, we test the extent to which i) isolation distance, ii) woodland management and iii) tree configuration in the surrounding landscape matrix affect the colonisation of a regenerating woodland by five old-growth lichen epiphytes, namely; *Nephroma parile, N. laevigatum*, *Pannaria conoplea, P. rubiginosa* and *Lobaria pulmonaria*.

Method

Study System

The temperate rainforest bioclimatic zone is globally-restricted, and where suitable climate occurs over the European landmass, the associated biodiversity has suffered from either (i) extensive deforestation (Timdal et al 2006), or (ii) high-levels of pollution which negatively impact the characteristic epiphytes (Mitchell et al 2005). Western Scotland has pockets of ancient woodland in a relatively clean-air environment, and retains among the best examples of rainforest epiphytic diversity (Ellis et al 2015), as well as large populations of species that are declining elsewhere in Europe e.g. *Lobaria pulmonaria*, creating an international responsibility for their conservation (Woods & Coppins 2012). As a specific case study, Glasdrum National Nature Reserve located in Glen Creran (a wooded valley lying on the west coast of Scotland) is currently managed to maintain old growth conditions in order to preserve its rich and internationally important lichen diversity (McDonnell 2014).

Scotland's native woodlands have been mapped, structurally characterised and digitised within the Native Woodland Survey of Scotland (NWSS: Grieve 2011). Data from the NWSS were used to stratify 181 individual woodland polygons occurring within Glen Creran, according to habitat type, canopy cover and habitat maturity. Each of these polygons was assigned to one of 30 unique woodland 'types', and this well characterised landscape formed the basis for detailed investigations to quantify the probability of lichen epiphyte occurrence on tree species of different size and age (see Eaton et al 2017a), and for the same species, their dispersal distances measured using direct molecular detection of propagules (see Eaton et al. 2017b). During the field survey of 600 trees, randomly stratified within the Glen Creran polygons (Eaton et al 2017a), *Nephroma parile* and *N. laevigatum* were found to be a relatively rare, being present on just 1% and 2% of the surveyed trees respectively, whereas *L. pulmonaria, P. conoplea* and *P. rubiginosa* and were more abundant, being found on 16%, 28% and 12% of the surveyed trees respectively.

Agent Based Model

An agent based model of the temperate rainforest/epiphyte system was simulated using NetLogo version 6.0 (Wilensky 1999). An artificial wooded area 100m * 50m in size was created and populated with 1200 randomly positioned trees to simulate a source woodland (SW) exhibiting old growth conditions. Each simulated tree was assigned a species (one of *Alnus glutinosa, Betula pendula, Corylus avellana, Fraxinus excelsior, Ilex aquifolium, Pinus sylvestris, Quercus sp.,* and *Salix sp.*), age/size and presence/absence of the old-growth epiphytes (*Lobaria pulmonaria, Nephroma parile, N. laevigatum*, *Pannaria conoplea and P. rubiginosa*), in such a way as to reflect empirically determined age/size distributions and observed epiphyte colonization frequencies collected during the field survey (see Study System above). In addition, an experimental block of 30m x 30m regenerating woodland (RW) was also created, comprising 250 sapling birch trees, which were devoid of the target epiphytes. The position of the RW in relation to the SW was subject to a user set parameter (see Figure 1 for model setup and Netlogo GUI and Figure 2 for user-set-up commands).

At each time step of the model, dispersal events occurred (see the Dispersal Sub-model for details), offering un-colonized trees in both the SW and the RW an opportunity of colonisation (see the Colonisation Sub-model for details). As spore discharge in lichens has been strongly linked with rainfall events (Denison 1980, Favero-Longo et al 2014, Ostrofsky & Pyatt 1973), the number of days where rainfall > 1mm (estimated to be c. 200 days per year using Met Office Climate Averages for the Glen Creran area, 1971-2000) was used to estimate the number of time steps in a given year when dispersal events may occur. Within each year, some trees died and others established, and all extant trees aged by 1 year (see the Tree dynamics Sub-model below for details). Species-specific variables used in the dispersal and colonisation sub-models are set out in Table 1 below.

Species	Local propagule deposition probability	Background propagule deposition probability	Dispersal weighting factor	Stochastic death rate (annual)
L. pulmonaria	0.85	0.55	1.5 E-5	0.03
P. conoplea	0.30	0.25	4.0 E-5	0.03
P. rubiginosa	0.36	0.11	1.25 E-5	0.03
N. laevigatum	0.64	0.44	5.0 E-5	0.03
N. parile	0.10	0.09	5.0 E-4	0.03

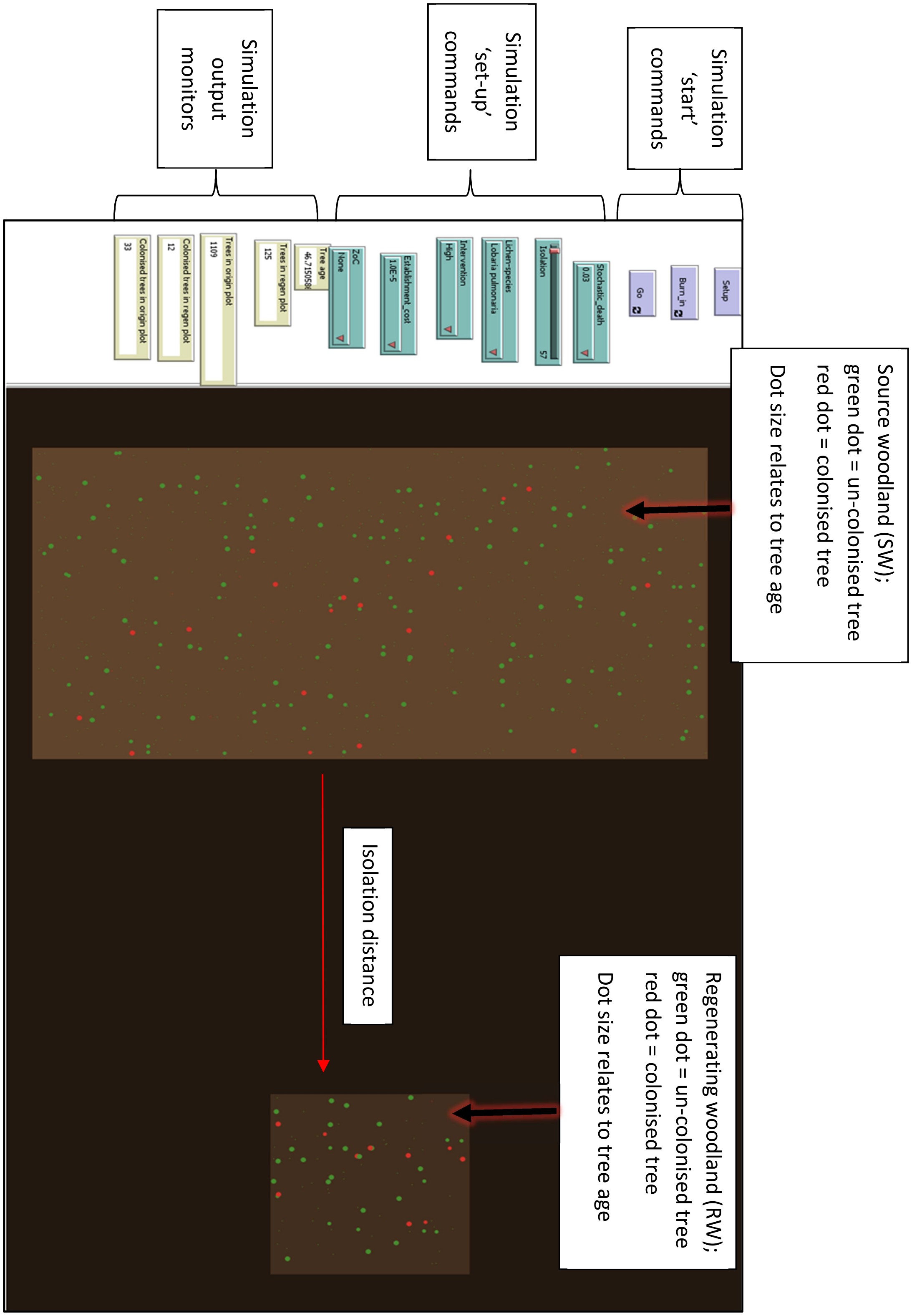
Table 1. Species specific variables used in the dispersal and colonisation sub-models.

Sub-model 1 - Dispersal

For the purpose of the simulations all lichen epiphytes of a single species inhabiting the same tree were considered a functional individual (Scheidegger & Goward 2002, Scheidegger & Werth 2009) and as a result, the dispersal sub-model assumed density independence at the tree level; once a tree become colonised it maintained a uniform dispersal output till death - the dispersal output was not increased e.g. as a result of further colonisation events onto a single tree, nor decreased e.g. as a result of damage/necrosis to some thalli inhabiting a tree, over time.

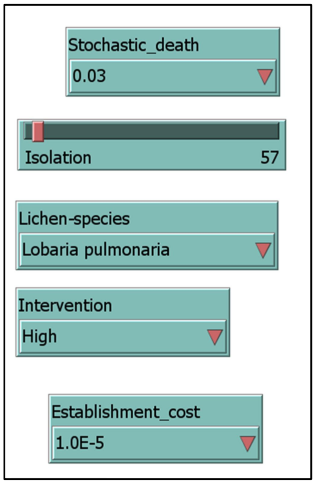
Species-specific dispersal metrics were based on the results of dispersal experiments (Eaton et al 2017b) which determined propagule deposition in the target species followed a two-tier structure; with local (or within-woodland) dispersal and background (or long-distance) dispersal characterised as two separate probabilities (as summarised in Table 1).

Though this earlier study found distance to be an important determinant of probability of propagule deposition over short distances (up to 20m), the actual decay rates were small and therefore a single short distance dispersal probability was used for analytical simplicity ('local propagule deposition' probability, see Table 1), calculated from the mean of propagule deposition probabilities estimated over short distances (1 to 20m) by Eaton et al 2017b. The maximum distance over which the local dispersal probability was assumed to operate was 50m, consistent with the dispersal gradient found by Walser et al 2001.



Stochastic_death: 0.03
Isolation: 57
Lichen-species: Lobaria pulmonaria
Intervention: High
Establishment_cost: 1.0E-5
ZoC: None
Tree age: 46.715058
Trees in regen plot: 125
Trees in origin plot: 1109
Colonised trees in regen plot: 12
Colonised trees in origin plot: 33

Figure 1. The Netlogo GUI.



Stochastic_death
0.03

Isolation 57

Lichen-species
Lobaria pulmonaria

Intervention
High

Establishment_cost
1.0E-5

Figure 2. Simulation set-up commands (user defined) including the stochastic death rate, isolation distance (between SW and RW), the lichen species under study, intervention (high management, low management), establishment costs/dispersal weighting factor.

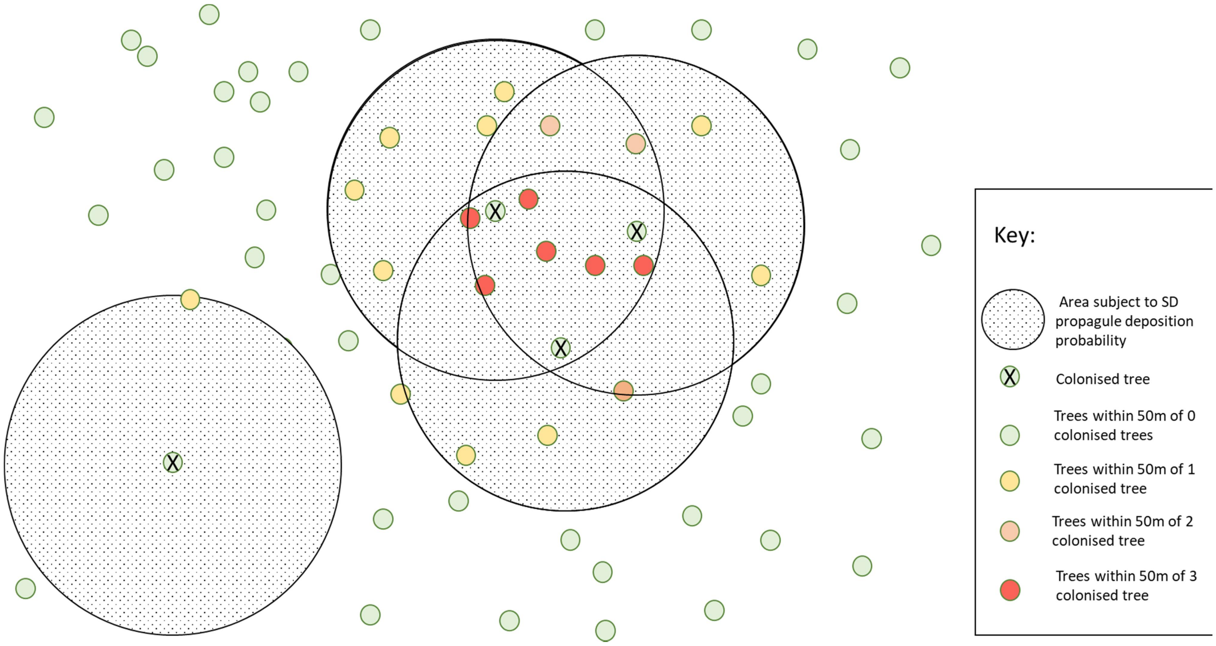


Figure 3. Propagule rain onto uncolonized trees

At each time step, daily dispersal events were simulated; each un-colonised tree within 50m of a colonised tree was assigned the 'local propagule deposition' probability (Eaton et al 2017b). Un-colonised trees within 50m of multiple colonised trees were assigned cumulative local propagule deposition probabilities to reflect the number propagule sources in the surrounding area. In addition, all un-colonised trees within the model out-with this area were assigned a 'background propagule deposition' probability (Eaton et al 2017b). This background probability incorporates the dispersal of propagules travelling over long distances (Gjerde et al 2015, Johansson et al. 2012). Figure 3 demonstrates how propagule deposition was assigned according proximity to colonised trees.

Sub-model 2 – Colonisation

The probability of colonisation of an un-colonised tree was determined by the total probability of propagule deposition (as set out in Dispersal Sub-model), weighted by an establishment cost (dispersal weighting factor, as discussed below), and combined with the habitat suitability of the tree as follows:

$$\text{Probability of colonisation} = \left(\text{total propagule deposition probability} \times \text{dispersal weighting factor} \right) \times \text{habitat suitability}$$

Equation 1 – used to determine probability of colonisation

Un-colonised trees were deemed to be ‘colonised’ if this probability was larger than a randomly generated number (between 0 and 1). The mechanics of this sub-model are documented in Figure 4 below. Dispersal weighting factors (representing the process of establishment) were assigned to each lichen species in order to account for the high rates of juvenile mortality suffered during the establishment phase among lichen epiphytes (Scheidegger 1995). As the values for propagule deposition used here were calculated from direct dispersal patterns (see Eaton et al 2017b), they do not take these establishment costs into account. Establishment costs are required to account for; non-viable spores (Crittenden et al 1995 found 70% of lichen spores did not successfully germinate in isolation experiments), wash-off and herbivory (Scheidegger 1995 found over 90% of asexual propagules perished during the first 20 months in a transplant experiment), and photobiont limitation for sexual propagules (see Belinchón et al 2015, Werth et al 2007). These dispersal weighting factors were parameterised for each lichen species by testing a range of values and selecting that which produced an equilibrium population size over a period of 50 years. The equilibrium population size equalled that for a field observed number of colonised trees from an empirical dataset collected in Glen Creran. During the 50 year period the trees did not age (therefore their suitability as habitat remained constant), although trees (and therefore their dependent lichen populations) were subject to an annual mortality rate of 0.02 (see Sub-model 3 - Tree dynamics, and Figure 5) in addition to the 0.03 stochastic extinction rate applied to the lichen epiphyte populations (see Sub-model 4 - Stochastic death, and Figure 5).

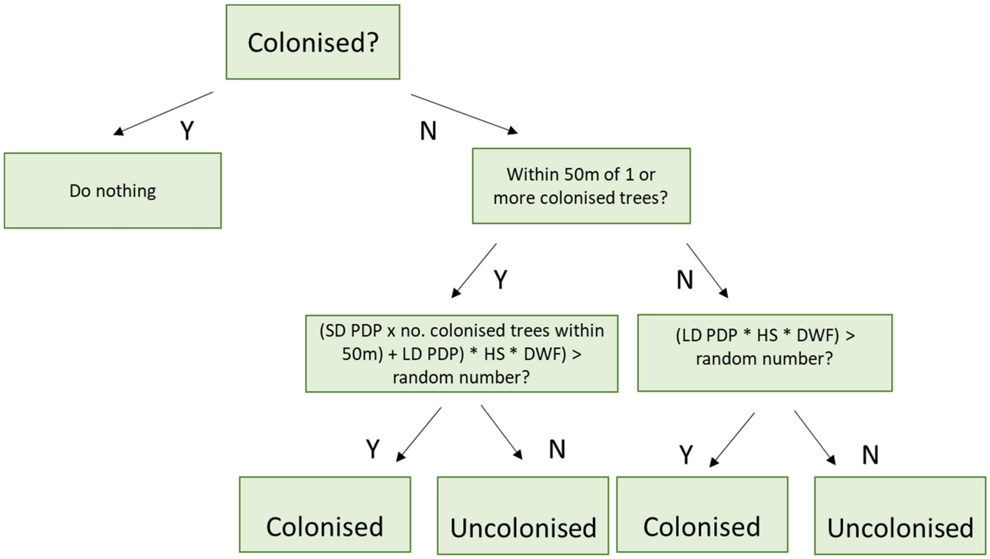


Figure 4. The tree colonisation sub-model. SD PDP = short distance propagule deposition probability, LD PDP = Long distance propagule deposition probability, HS = habitat sutiability, DWF = dispersal weighting factor.

The habitat suitability parameter of trees within the model was determined from the results of a species distribution modelling (SDM) exercise within Glen Creran (Eaton et al 2017a) and which found trees became more suitable as they got larger, though subject to tree-species-specific relationships. Particular tree species e.g. *Fraxinus excelsior* (Ash), *Corylus avellana* (Hazel), *Quercus sp.* (Oak) were found to provide optimum conditions for most of the target species. The relationship between tree size and probability of presence for each of the lichen epiphyte-tree species combinations was estimated from SDM predictions onto trees aged 1 to 500 (using the predict function of 'mgcv' (type = response) in R), with tree age converted to an estimate of size (girth) using species-specific relationships sampled for Scotland (Ellis et al 2015). These relationships between tree size and probability of presence were then fitted with polynomials (to give an $R^2 > 0.99$). Thus, trees became more or less suitable for a particular lichen species on an annual basis (as demonstrated in Eaton et al 2017a). In addition to tree species and size/age, trees adjacent to gaps in the tree canopy were found to provide more/less suitable conditions than those under closed-canopy conditions in the case of *N. laevigatum* and *N. parile*. This factor was incorporated into the model by identifying canopy gaps as open (tree-less) areas of at least 2m x 2m in size.

After becoming colonised, trees were subject to a 10-year delay period before becoming a propagule source thus simulating a juvenile development phase for western Scotland (Eaton & Ellis 2014).

Sub-model 3 - Tree dynamics

Each year, two percent of trees in the SW were randomly removed from the landscape to approximate average mortality rates in mixed deciduous woodlands (Drobyshev et al 2009). In addition, all tree species had a species-specific maximum-tree-age, whereby trees reaching their maximum age were removed from the model (see Figure 5 for mechanism of local extinctions). These maximum-tree-ages were approximated from dendrochronological studies of the Glen Creran study site (Ellis et al 2016, Mulchany 2014) and ranged from 300 years in *Betula pendula* to 500 years in *Quercus sp.*, *Fraxinus excelsior* and *Pinus sylvestris*. Any colonised trees removed from the model represented deterministic lichen extinction events. To ensure woodland continuity during the simulation, the same number of trees was introduced into the woodland blocks as were removed, on an annual basis. Introduced trees were given an age of 0, were assigned to keep the tree species proportions in the SW approximately constant and were devoid of target epiphytes. The habitat suitability of each tree for the target epiphytes species was re-calculated annually (see the Colonisation Sub-model).

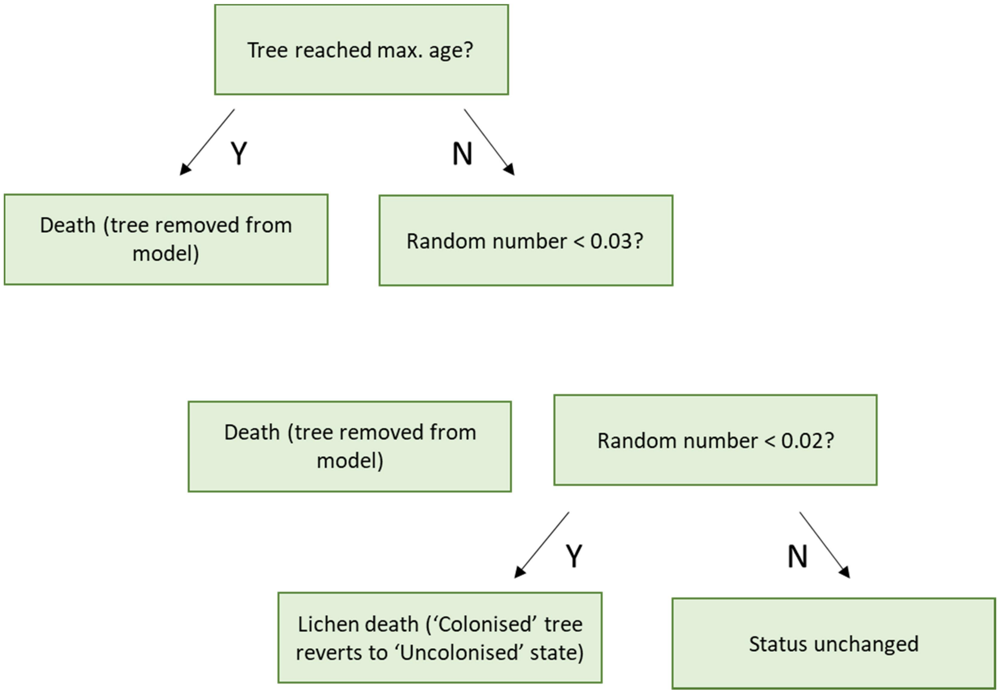


Figure 5. Local extinction model (deterministic = tree death, stochastic = a colonised tree reverts to uncolonized status).

Sub-model 4 - Stochastic death

Although mortality of epiphytic lichens may be largely deterministic (Belinchón et al 2017, Johansson et al 2012, Ruete et al 2014), the risk of underestimating the mortality rate in simulation experiments, and thus overestimating ultimate population sizes, has also been emphasised (e.g. Belinchón et al 2017). A study of colonisation and local-extinction from trees in the focal species carried out over a 13 year period in Finland found relatively high stochastic mortality rates of 0.33 in *Lobaria pulmonaria*, 0.31 in *Nephroma parile* and 0.2 in *Nephroma laevigatum* (Fedrowitz et al 2012), while numerous opportunities for stochastic loss of lichen epiphytes in temperate rainforests have been observed and described (Eaton 2014). Thus, an annual mortality rate of 0.03 was applied to the focal species here, in both the SW and the RW (see Figure 5 above).

Simulations

A total of 18 scenarios were explored per lichen species, each of which was replicated ten times using the BehaviourSpace tool in Netlogo (see Table 2 below). The number of colonised trees present in the RW was reported each year for a total of 200 years.

Simulation	Isolation distance	Management	Connectivity
1	0m	Low	None
2	25m	Low	None
3	50m	Low	None
4	100m	Low	None
5	250m	Low	None
6	500m	Low	None
7	0m	High	None
8	25m	High	None
9	50m	High	None
10	100m	High	None
11	250m	High	None
12	500m	High	None
13	250m	Low	Scattered trees
14	250m	Low	Blocks of trees
15	250m	Low	Line of trees
16	250m	High	Scattered trees
17	250m	High	Blocks of trees
18	250m	High	Line of trees

Table 2. Scenarios explored for each lichen species and replicated 10 times.

First, the effect of isolation distance on tree colonisation was explored under different woodland management scenarios. Isolation distance between the SW and the RW was increased from 0m to 500m at increments of 0m, 25m, 50m, 100m, 250m and 500m. Each of the distance simulations was run under a low management (LM) scenario where tree composition in the RW transitioned from *Betula pendula* woodland to mixed deciduous woodland, and a high management (HM) scenario where tree composition in the RW transitioned from *B. pendula* woodland to *Fraxinus excelsior* and *Corylus avellana* woodland (known to provide high quality habitat for the target lichen epiphytes (Eaton et al 2017b)). The starting condition for the RW included 250 sapling trees (age < 10) in a block, all of which were *B. pendula* species. Each year 2% of trees were removed from the RW (simulating tree death, as per Figure 5) and the same number replaced (simulating tree establishment). Replacement trees were given random co-ordinates within the RW block, an age of zero and assigned a species (from one of any of the eight tree species in the RW-LM scenario, and one of *F. excelsior* or *C, avellana* in the RW-HM scenario). In this way, through time the RW transitioned from young *B. pendula* scrub to mature deciduous woodland, with trees in the RW subject to maximum tree ages as in the SW (see Figure 5).

Second the effect of tree distribution in the intervening landscape matrix was explored at a single isolation distance (250m) – selected to be out-with the local (within woodland) dispersal effect (as described for the Dispersal Sub-model). Simulated landscape matrices comprised; 1/ scattered trees, whereby 50 trees were scattered randomly in a 230m x 25m belt between the SW and the RW, 2/ a line of trees, whereby 50 trees were set out randomly along a straight line between the SW and the RW, and 3/ blocks of trees, whereby 50 trees were scattered randomly among three 20m x 20m blocks set out equidistantly between the SW and RW. In each of these scenarios, trees in the landscape matrix comprised *Quercus sp., F. excelsior, Alnus glutinosa* or *B. pendula,* in approximately equal proportions.

A sensitivity test was carried out using all possible combinations of the variables distance, management and landscape matrix, explored for the model lichen species *L. pulmonaria* to produce a total of 48 scenarios replicated 10 times using the BehaviourSpace tool in Netlogo. The number of colonised trees in the RW was reported for the years 1, 20, 40, 60, 80, 100, 120, 140, 160, 180 and 200.

Data analysis

Patterns of colonisation in the target species were explored by plotting the mean number of trees colonised per time step for each of the scenarios (averaged over 10 simulations).

In addition, the effect of distance and landscape matrix on patterns of colonisation were explored under HM and LM scenarios by 1/ calculating the difference in the number of trees colonised (per time step) between RW positioned adjacent to the SW (isolation distance = 0m) and those at increasing distances and 2/ calculating the difference in the number of trees colonised (per time step) in the RW when there are no trees in the surrounding landscape matrix, and under each of the connectivity scenarios (scattered trees, line of trees, blocks of trees). Means were taken across all five species and used to produce plots of difference against time along with their 95% confidence intervals.

In order to understand the contribution each of the variables makes to tree colonisation in *L. pulmonaria*, the results from the sensitivity test were subject to regression analysis against the variables distance, management, connectivity and time, with variance partitioned using the hier.part package in R (R Development Core team 2013).

Results

Variability in the magnitude of colonisation (number of trees colonised) and its temporal scale (timing of first colonisation) was found amongst the target species e.g. under a 0m isolation HM scenario, first colonisation events ranged from 5 years (*L. pulmonaria*) to 45 years (*N. parile*), and maximum number of trees colonised ranged from 3 (*N. parile*) to 53 (*P. conoplea*). Although *L. pulmonaria* was the fastest of the target species to begin colonising the RW, after 100 years the number of trees colonised by this species (33) was exceeded by *P. conoplea* (37). *Pannaria rubiginosa* on the other hand was slow to begin the colonisation process, taking 27 years before the first colonisation event occurred, similar to *N. laevigatum* at 28 years. However, *P. rubiginosa* colonised over twice the number of trees compared to *N. laevigatum* (19 trees compared to 9) after 200 years.

Despite this variability, six general patterns in colonisation could be identified, exemplified for brevity by the model species *L. pulmonaria* in Figure 6 (see Appendix 1 for detailed plots relating to *N. laevigatum, N. parile, P. conoplea* and *P. rubiginosa*). Patterns in *N. parile* were somewhat difficult to interpret due to the low number of trees colonised. Nevertheless, species summary patterns (Figure 7) show the mean differences in colonisation among species from a baseline (values for 1/ RW adjacent to the SW (isolation distance = 0m), and 2/ RW with no trees in the landscape matrix), along with 95% confidence intervals. The patterns identified by the scenarios are summarised below:

Pattern 1 - The number of colonised trees was found to increase over time under all scenarios tested. At short distances, in the case of most species the number of colonised trees appeared to reach an equilibrium, suggesting that population size is limited by the amount of suitable habitat within the RW. This equilibrium is higher under HM scenarios than under LM scenarios.

Pattern 2 - Most species showed a distinct isolation signature, with the population size being consistently higher at an isolation distance below a threshold of 100m. Distances below 100m (adjacent, 25m and 50m) produced comparable results and hereafter this group of scenarios will be collectively referred to as short distance (SD). Distances of 100m and over (100m, 250m, 500m), also produced comparable results and will be collectively referred to as long distance (LD). These two grouped patterns were consistent under both HM and LM scenarios. The confidence intervals of the LD group are larger than that of the SD group, particularly under LM scenarios.

Pattern 3 – Under SD scenarios, the RW achieved a ‘colonised’ status in a shorter period of time, with the first colonisation events occurring between 2 and 50 years, compared to between 30 and 120 years for LD scenarios.

Pattern 4 - More trees were colonised under HM scenarios than under LM scenarios. This pattern is consistent across all distances and connectivity comparisons.

Pattern 5 – The presence of scattered trees, a line of trees or blocks of trees in the landscape matrix increased the number of trees colonised relative to the baseline of ‘no trees’. Scattered trees appeared to produce the greatest benefit under both HM and LM scenarios (though confidence intervals were large), whereas blocks of trees appear to be the least effective to colonisation.

Pattern 6 - The difference in the population size under SD scenarios compared to LD scenarios is greater under HM scenarios than LM scenarios. This pattern is supported by non-overlapping confidence intervals for these groups under HM scenarios.

Regression analysis found a total of 64.38% of the variance in colonisation by *L. pulmonaria* could be explained by the variables Time, Distance, Landscape Matrix and Management (F-statistic = 128.6, df = 498, P<0.0001). Hierarchical partitioning showed that Time and Distance as independent effects explained most of the variance in the data (40.20% and 39.01% respectively), followed by Management (15.95%) and Landscape Matrix (4.85%).

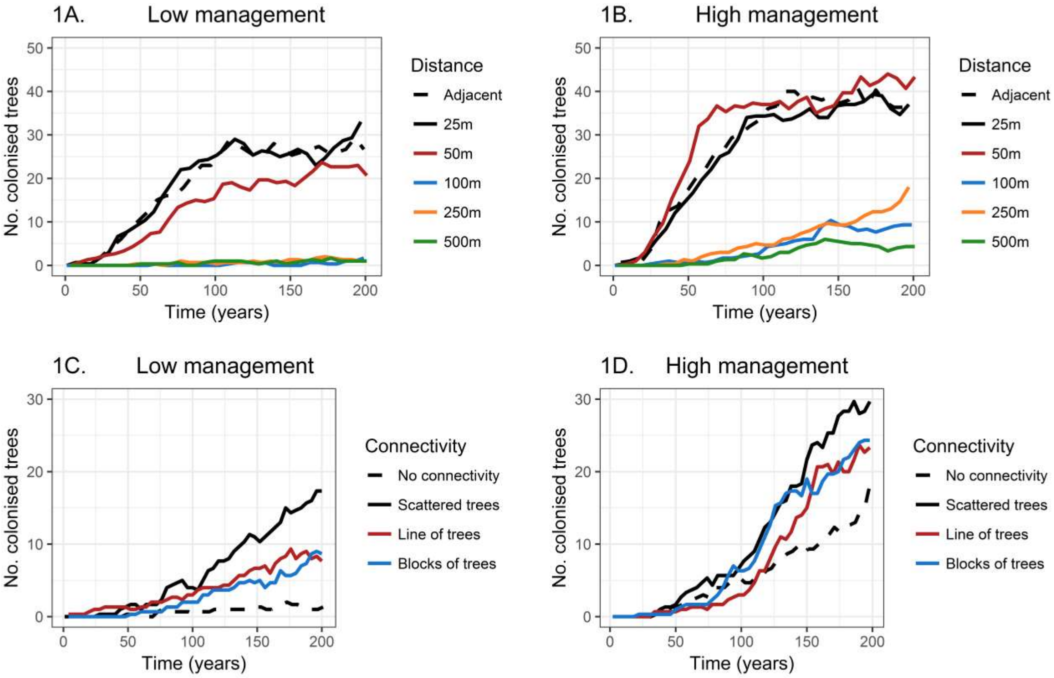


Figure 6. The number of trees colonised by *L. pulmonaria* through time. Figure 2A shows different distances under an LM scenario. Figure 2B shows different distances under a HM scenario. Figure 2C shows the various landscape matrices under an LM scenario. Figure 2D shows the various landscape matrices under a HM scenario.

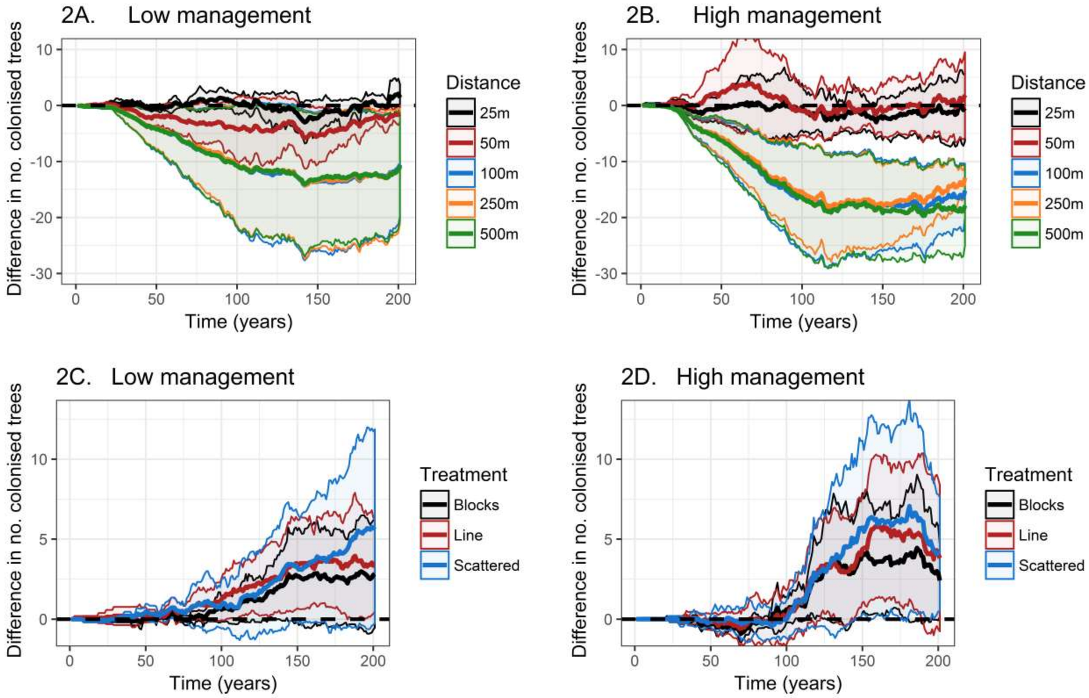


Figure 7. Mean difference in the number of trees colonised through time. Figure 2A shows difference between the number of trees colonised at contrasting distances under an LM scenario, against a baseline scenario of 0m distance (with 95% confidence intervals). Figure 2B shows difference between the number of trees colonised at contrasting distances under a HM scenario, against a baseline scenario of 0m (with 95% confidence intervals). Figure 2C shows difference between the number of trees colonised by varying landscape matrices under an LM scenario, against a baseline scenario of no connectivity (with 95% confidence intervals). Figure 2D shows difference between the number of trees colonised by varying landscape matrices under a LM scenario, against a baseline scenario of no connectivity (with

Discussion

This study used an agent based model to explore the spatial and temporal scale of landscape connectivity for five species of 'old-growth' lichen epiphyte. We found that despite differences in the magnitude and temporal scale of colonisation amongst species, there were many cross-species patterns in colonisation behaviour. These patterns are discussed under the themes of dispersal, habitat quality and their interactions below.

Dispersal

Dispersal limitation, known to be an important factor in explaining epiphyte colonisation patterns (Johansson et al 2012, Snäll et al 2005a), was evidenced as a response to both time (pattern 1) and isolation distance (see pattern 2). Time was found to be the most important factor in explaining variability in colonisation rates for the model species *L. pulmonaria*. Other studies have concluded that time is more important than spatial factors in controlling the dispersal and colonisation of slow growing species (Belinchón et al 2009, Eriksson 1996) consistent with stand age as an important factor explaining epiphytic lichen occurrence (Price & Hochachka 2001). The importance of this temporal effect is widely described for the *Lobarion* (a community of lichen epiphytes within which all the target species are found), identified as indicators of ancient forests (Rose 1988, 1992). Isolation distance was the second most important factor in explaining variability of colonisation rates, again emphasising dispersal limitation, and consistent with previous studies (Belinchón et al 2017, Gu et al 2001, Kiebacher et al 2017, Ruete et al 2014). Thus, colonisation rates were highest when the RW was positioned in the local vicinity of the SW (less than 50m away), with longer isolation distances (100m – 500m) restricting the number of overall colonisation events (pattern 2) as well as increasing the amount of time taken for first colonisation events to occur (pattern 3). Though the presence of trees in the landscape matrix was found to be the least important of the variables affecting colonisation, for all the species it had an effect (particularly *L. pulmonaria* and *P. conoplea*), and was able to compensate to some degree for the negative effect of isolation at a distance of 250m (pattern 5). Uniquely, our results demonstrate the important contribution that isolated trees in the landscape might play in facilitating dispersal and improving connectivity among woodland stands. The large confidence intervals around differences in landscape matrix scenarios (see pattern 5) can however be explained by the species-specific nature of responses e.g. scattered trees have a large positive effect on the number of colonisations by *L. pulmonaria*, but less of an effect for *N. parile* and *N. laevigatum*. This could relate to the composition of trees in the landscape matrix, as in our test case where they were generally less suitable for the *Nephroma* species than for *L. pulmonaria* (Eaton et al

2017a). There are relatively few studies that explore the importance of landscape matrix, particularly the presence and configuration of suitable trees species on epiphyte colonisation patterns (although see Belinchón et al 2009 for studies on the importance of heathland v's pine woodlands in the landscape matrix), and the ability of a model to quantify matrix scenarios highlights its value as a conservation planning tool.

Habitat quality

Habitat quality or suitability, known to be a limiting factor in the establishment and distribution of lichen epiphytes (e.g. Belinchón et al 2017, Öckinger et al 2005) increased as the RW matured. Birch woodland (largely an unsuitable habitat for the target species (Eaton et al 2017a)) underwent succession towards a more diverse range of tree species, providing a broader range of suitable habitat (Eaton et al 2017a), and also explaining the positive relationship between the number of colonised trees and time (pattern 1). The effect of time-restricted dispersal events (see above) is often confounded by change in habitat suitability (Rose 1992, Snäll et al. 2003, Snäll et al. 2005b), particularly when considering colonisation of a regenerating woodland stand (pattern 1).

Variability in colonisation was consistent with the niche preferences of individual lichen species (pattern 3). Under a HM 0m isolation scenario, the suitability of *Fraxinus excelsior* and *Corylus avellana* trees for the target species becomes particularly important, e.g. the first colonisation event for *L. pulmonaria* is predicted to be just 5 years, consistent with the findings of Eaton & Ellis (2014) where hazel stems of around 5 years were shown to be colonised. *Nephroma parile* on the other hand showed the slowest colonisation dynamics of any species, consistent with the dynamics of their preferred habitat; Eaton et al 2017a found that, even when 50 years old, hazel trees in the study system have less than a <0.1 probability of *N. parile* being present, despite hazel being one of the most suitable habitats for this species. The importance of niche specificity in the response of lichen epiphytes to woodland structure has been demonstrated in affecting colonisation rates (e.g. Johansson et al 2012) and lag times associated with an extinction debt (Ellis & Coppins 2007); species with wider ecological niches are found to respond more quickly to landscape/habitat change.

The difference between LM and HM scenarios (both in the number of trees colonised and the rate of colonisation, see pattern 4), further emphasises the important role that habitat limitation plays in lichen epiphyte colonisation processes, while also pointing to the clear 'biodiversity value' of this management technique. The fact that habitat management was found to be an important factor in explaining variability in colonisation rates supports the value of habitat quality in landscape-scale conservation planning.

Interactions

Interactions between dispersal and habitat quality were evidenced through the equilibrium attained in SD scenarios after around 100 years, suggesting that under these conditions, dispersal constraints under shorter time-scales become less of a limiting factor than the availability of suitability habitat over longer time-scales. Evidence of this interaction also explains the variability amongst species to certain scenarios. For example, the large confidence intervals found for the LD simulations (see pattern 2 and 6), particularly under LM scenarios, may be explained by the behaviour of the *Nephroma* species. These species have been described as niche super-specialists in the study system (Eaton et al 2017a) due to their low abundance, and as confirmed by a narrow habitat suitability. As a result, under LM scenarios, even in SD situations when dispersal presents only weak limit to colonisation (particularly for the sexually reproducing *N. laevigatum* whose dispersal rate is high at short distances (Eaton et al 2017b)) colonisation remained limited by the availability of suitable habitat. Thus, there is little difference between the colonisation of LD and 0m isolation distance scenarios in these species under LM scenarios, and it is this particular result that creates the large confidence intervals when pooled with the results for other species that are less limited by habitat availability under LM scenarios (such as *L. pulmonaria, P. conoplea* and *P. rubiginosa*). Such interactions between dispersal (landscape-scale connectivity) and habitat quality (tree-scale factors) have been widely documented in the literature (Belinchón et al 2017, Fedrowitz et al 2012, Johansson et al 2012, Johansson & Ehrlén 2003, Snäll et al 2005a) but we show how this interaction can have contrasting consequences within a simulated landscape, based on the ecology of individual species.

Assumptions

Despite the ecological value of the model, attempts to estimate some of the parameters were based on assumptions that create uncertainty in model predictions. First, the method used for estimating the dispersal weighting/establishment costs to propagules in the SW assumes that lichen populations at the study site had reached an equilibrium at the time of survey. As a consequence of the difficulty of directly measuring establishment in lichen propagules (largely due to their small size and slow dynamics) there is little evidence to evaluate estimates made here, though Belinchón et al 2017 found *L. pulmonaria* propagules to successfully establish with a probability of 3.6E-4 in a propagule seeding experiment, compared to the 1.5E-5 estimated in our simulations.

Second, the stochastic extinction rate was set cautiously high (at around 3% per annum), in line with direct measurements of lichen epiphyte extinction rates (Fedrowitz et al 2012), though this rate has been found to be much lower in other studies e.g. 5% over a 10-year period (Belinchón et al 2017). Third, the distance over which short distance dispersal trajectories operate was set cautiously low (matching a dispersal kernel at 50m described by Walser et al 2001, and consistent with the mean 35m dispersal distance found by Öckinger et al 2005), though local dispersal has been found over greater distances in other studies e.g. a mean dispersal distance of 97m in *L. pulmonaria* (Belinchón et al 2017). Fourth, the density independence assumption of the dispersal sub-model was in keeping with the "single functional individual" theory (Scheidegger & Goward 2002, Scheidegger & Werth 2009). This theory was established to explain mortality of lichen epiphytes and there is uncertainty as to its relevance in colonisation dynamics since it assumes a constant relationship between the species quantity (number, area or reproductive potential on a source tree) and propagule production. There is currently a lack of empirical evidence demonstrating the actual relationship between thallus quantity and propagule production however, which would enable this effect to be incorporated into models of dispersal/colonisation. Such studies might also incorporate rates of self-propagation on a tree bole (same-tree colonisation) and the growth rate of species with a particular emphasis on their reproductive potential/output, for future parametrisation of a within-tree sub-model. Greater resolution in direct measures of dispersal, establishment and extinction of the target species would again strengthen the evidence base for population simulations.

Conclusions

We conclude that agent based models are able to simulate ecologically plausible behaviour in the target species. As a result, some basic principles of landscape-scale management for lichen epiphytes may be drawn; 1. In order to increase probability of sustained colonisation in a regenerating woodland, it should be cited within 100 m of a propagule source. 2. When this is not possible (and there is more than a 100m distance from the nearest propagule source), the greatest improvement will be effected through managed woodland composition in the regenerating stand, and this is essential to the population size over the long-term. 3. Smaller improvements will be evidenced if landscape connectivity is increased alone, and when improving connectivity is the only option scattered trees provide the best strategy. We also caution that monitoring conservation outcomes would ideally occur over many decades, with colonisations by some species not to be expected for over 100 years. Although the principles drawn above are based on emergent behaviours of the model, there is much scope to strengthen predictive capacity prior to application of these principles, particularly by incorporating novel research findings that may allow us to reduce the assumptions made here (e.g. establishment costs and density dependent propagule emission). In addition, the scenarios could be run in less simplistic, spatially realistic woodlands to further test the ecological plausibility of the model.

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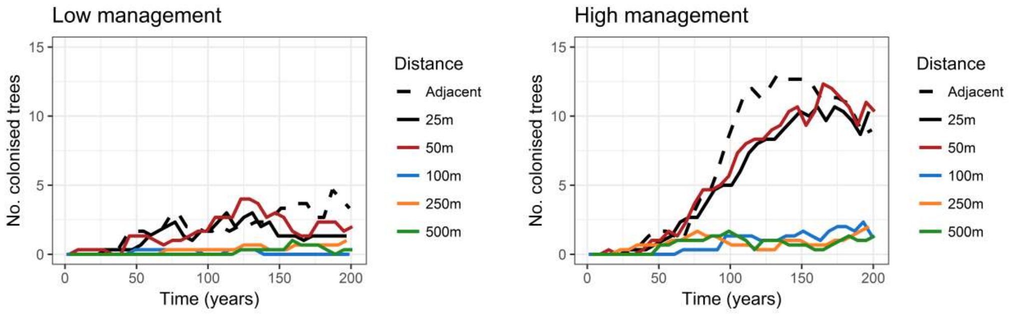
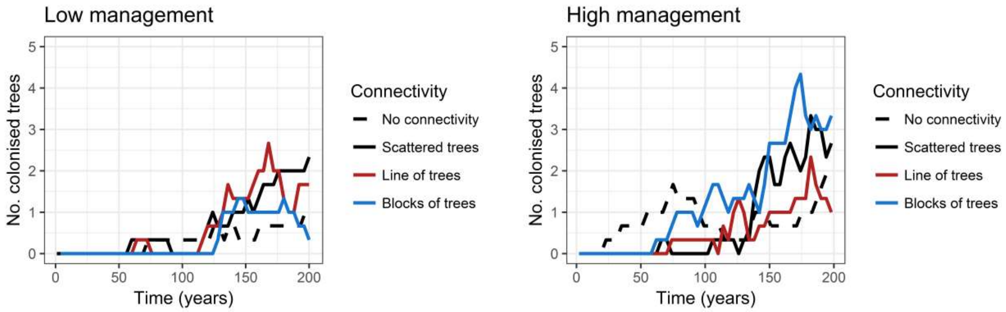
Appendix 1.





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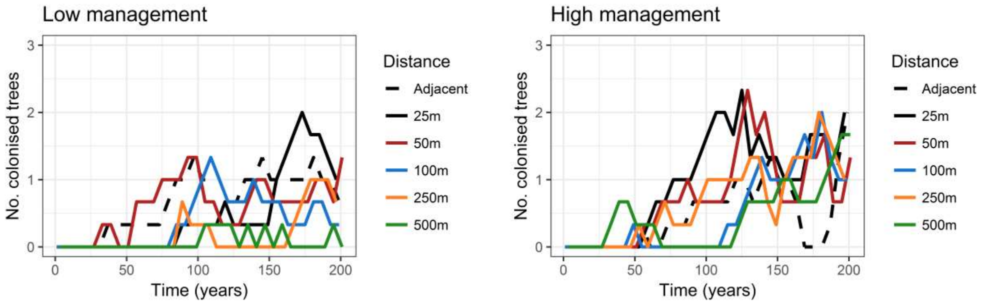

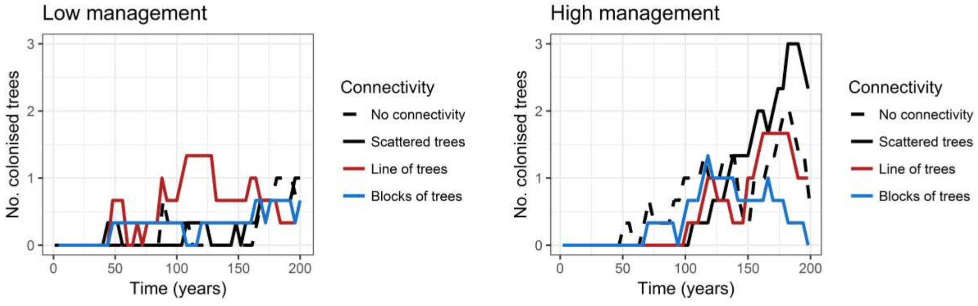

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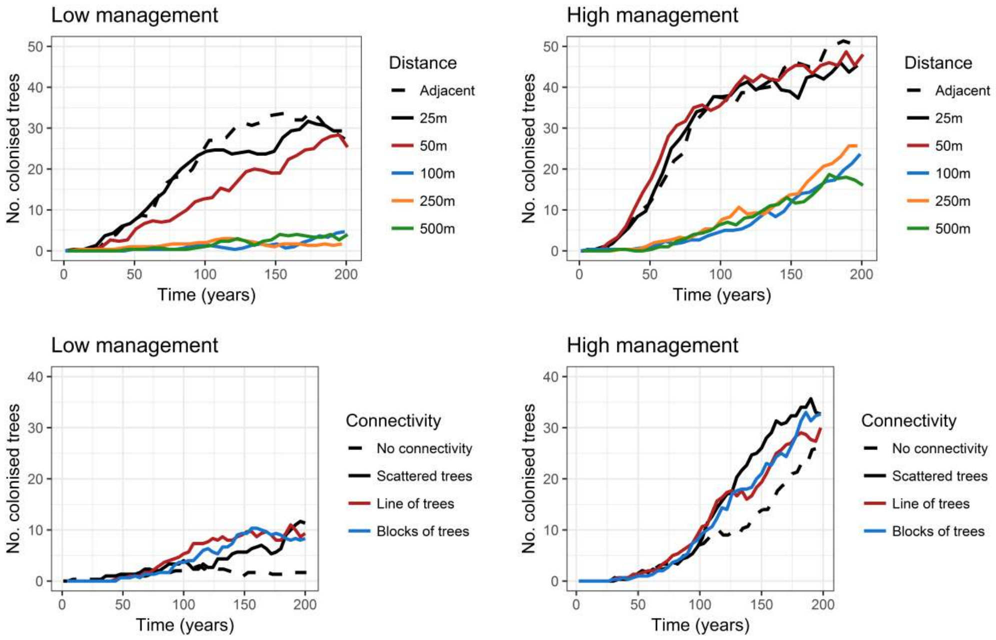
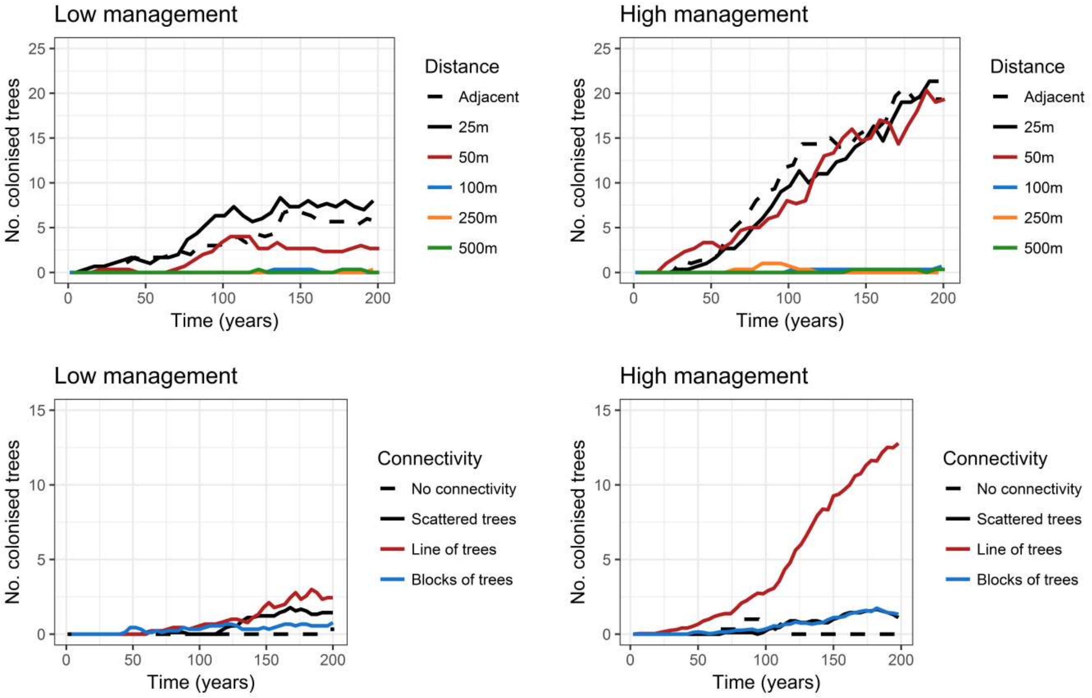


P. conoplea



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