
2 Ecological Biogeography of Lichen-Forming Fungi

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I. Introduction

“In truth, any statements we make on lichen (bio)geography are bound to be modified, sometimes embarrassingly so, as new collections are made...”
(Hale 1990), p. 34

A long-standing interest in understanding factors that shape distribution patterns of biological communities and evolutionary lineages has resulted in diverse research programs attempting to elucidate meaningful biogeographic patterns and processes shaping those patterns (Lomolino et al. 2006). Biogeographic research generally fits within two major subdisciplines: one focuses on historic events and/or processes (e.g., plate tectonics, dispersal

events, vicariance, etc.) that shape current distributions; and the other investigates the role of ecology in determining distributions. While these two perspectives are not necessarily mutually exclusive, they provide a useful framework for biogeographic research.

Contemporary distributions of species are the result of the dynamic interplay of multiple factors operating across multiple temporal and spatial scales (Hubbell 2001). While important advancements have been made in understanding both historical and ecological factors that determine species contemporary distributions, their respective relative importance and interplay remain largely unknown and difficult to tease apart. For example, Bonada et al. (2005) attempted to quantify the role of historical versus ecological biogeographic factors influencing distribution patterns of caddisflies in Mediterranean rivers. Their study revealed that ecological factors played a more important role in contemporary biogeography than historical factors (21 % vs. 3 %, respectively) and that only 0.3 % was explained by the interaction of history and ecology, with the rest unaccounted for. For most groups of organisms, including lichens, the relative importance and interplay between historical and ecological biogeographic factors in shaping species distributions remains unexplored.

In this chapter, we highlight the current state of knowledge of lichen biogeography, with a focus on ecological biogeography and potential avenues for future research. Lichens are mutualistic associations of a fungus (mycobiont) and a photosynthetic partner (photobiont), either a green alga and/or cyanobacterium, rarely also other groups of algae occur in lichen symbioses. In addition to these two main partners, there are

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also many other fungi present in lichen thalli, including endolichenic and lichenicolous fungi. Also bacteria are commonly found associated with lichens. Lichens are ubiquitous components of most terrestrial ecosystems, playing important ecological roles, for example, as pioneers or as stabilizers of soil.

Specifically, we briefly discuss general perspectives of biogeography of lichen-forming fungi, followed by a synthesis of four major themes directly related to ecological biogeography, including (1) dispersal and establishment of lichens, (2) landscape genetics and gene flow, (3) modeling lichen distributions, and (4) the role photobionts play in determining species distributions. We conclude by discussing the role of ecological biogeography in conservation and climate change research.

Reflection on the broad scope of both past and current views of lichen biogeography can improve our perspective into biogeographic patterns and the underlying processes shaping species distributions, in addition to directing future research. A comprehensive summary of the multifaceted and developing field of lichen biogeography is well beyond the scope of a single chapter. Rather, our emphasis is on summarizing our current understanding of contemporary factors that influence ecological and spatial distributions of species (Monge-Nájera 2008). Our hope is that this review will encourage a more comprehensive perspective of lichen biogeography by promoting the consideration of a wide variety of factors that potentially shape species distributions, in addition to historical processes (traditional phylogeographic perspective). This expanded focus of lichen biogeography should, in turn, promote creative biogeographic research incorporating the fields of ecology, landscape genetics, species distribution modeling, symbiont interactions in lichens, etc.

II. Perspectives of Biogeography of Lichen-Forming Fungi

There has been a tradition of studies attempting to understand distributions of lichen-forming fungi and the factors that shape these distribu-

tions (Galloway 1988, 2008; Galloway and Aptroot 1995; Culberson 1972; Werth 2011; Du Rietz 1940). However, with the increasing availability of molecular data, our understanding of lichen phylogeography has dramatically improved in recent years. This is due, in part, to the increased recognition of the importance of cryptic, or previously unrecognized, lineages in lichen-forming fungi (Lumbsch and Leavitt 2011; Crespo and Pérez-Ortega 2009; Crespo and Lumbsch 2010), large-scale collaborative projects (Lumbsch et al. 2011), and developments in analytical approaches (Yang and Rannala 2006; Rabosky et al. 2014; Ree and Smith 2008). A general perspective of lichen biogeography is presented by Galloway (2008), and Werth (2011) also provides a valuable review.

Lichens exhibit biogeography and/or ecological distribution patterns that in many cases differ from other co-occurring biota (e.g., vascular plants, animals, etc.; Galloway 2008; Culberson 1972). For example, a disproportionately high number of lichen-forming fungal species have bipolar distributions, meaning that they occur in polar regions of the Northern and Southern Hemisphere (Wirtz et al. 2008; Fernández-Mendoza and Printzen 2013; Myllys et al. 2003; Lindblom and Søchting 2008); other species occur in ecologically and geographically restricted regions (Lücking et al. 2014); and many species occur across incredible ecological and geographic distances (Leavitt et al. 2013b; Printzen et al. 2013). Traditionally, it has been thought that species with broad, intercontinental distributions have high dispersal abilities and general ecological preferences. Broad distributions have alternatively been explained as older species of lichen-forming fungi that have had more time to disperse and reach extensive distributions (reviewed in Werth 2011). However, increased interest in species delimitation research and estimating divergence times for groups of lichen-forming fungi have challenged these traditional perspectives (Amo de Paz et al. 2011; Divakar et al. 2012; Leavitt et al. 2015a; Otálora et al. 2010). For example, in the genus *Melanohalea*, many of the species-level lineages with more ancient diversification histories, including *M. multispora* s. lat. and *M. ushuaiensis* s. lat., have geographically restricted

distributions in western North America and southern South America, respectively. In contrast, species with more recent diversification histories, including *M. elegantula* and *M. exasperatula*, generally have much broader geographic distributions (Otte et al. 2005; Leavitt et al. 2013a).

Iconic examples of phylogenetic structure corresponding to major biogeographic regions or major tectonic events are relatively scarce in the groups of lichen-forming fungi that have been investigated to date, although other striking biogeographic patterns have been observed in a number of cases (Miadlikowska et al. 2011; Lücking et al. 2013; Del-Prado et al. 2013). Rather than biogeographic patterns driven by dispersal limitations or vicariance, it appears that major climatic shifts may have played the dominant role in the diversification and distributions of lichen-forming fungi in the family Parmeliaceae (Amo de Paz et al. 2011, 2012; Kraichak et al. 2015).

Ultimately, the interplay of climate-driven diversification, dispersal and establishment, and vicariance results in biogeographic patterns that may be difficult to generalize. The *Rhizoplaca melanophthalma* group (Lecanoraceae) provides an interesting example of the challenges inherent to elucidating biogeographic patterns in lichen-forming fungi. *Rhizoplaca melanophthalma* s. lat. occurs on all continents, except Australia, in a broad range of habitats, from extremely arid continental habitats to upper montane coniferous forests and the lower portions of the alpine tundra (Leavitt et al. 2013b). Although *R. melanophthalma* s. lat. was traditionally assumed to represent a single, cosmopolitan species, molecular sequence data support the conclusions that this nominal taxon is comprised of multiple species-level lineages, three of which occur across broad intercontinental distributions, and the remaining lineages are known exclusively from western North America (Leavitt et al. 2011, 2013b). All of the known species within the *R. melanophthalma* group can be found within a limited geographic region in the southwest USA; species have not been shown to have distinct ecological preferences nor do distributions of species, otherwise cor-

respond to distinct biogeographic regions, with the exception of *R. shushanii* which is known exclusively from subalpine habitat on the Aquarius Plateau in southern Utah, USA (Fig. 2.1; Leavitt et al. 2011, 2013b).

Our limited understanding of morphological adaptations is also exemplified by the presence of cryptic species that are only distantly related but occur under similar ecological conditions. For example, *Parmelina quercina* was believed to occur in areas with Mediterranean-type climate throughout the world, but molecular studies have demonstrated that distinct species occur in each continent, with the Australian taxon now being classified in a separate, unrelated genus, *Austroparmelina* (Argüello et al. 2007; Crespo et al. 2010a, b). Another example is *Physcia aipolia*, which was believed to occur in temperate to subtropical regions of the Northern Hemisphere but also in Australia (Moberg 2001). However, the Australian samples were shown by molecular data to represent a group of three separate species, unrelated to the populations in the Northern Hemisphere (Elix et al. 2009).

Given our limited ability to make generalizable inferences and predictions on species distributions within a historical biogeographic framework, we emphasize that more effective incorporation of an ecological biogeographic perspectives into biogeographic research of lichen-forming fungi will provide an improved understanding of the range of factors shaping the geographical distributions of species.

III. Assessing Dispersal Capacity of Lichen-Forming Fungi

Accounting for differences in reproductive strategies and dispersal capacities of lichen-forming fungal species is central to understanding and interpreting biogeographic patterns. Lichen-forming fungi generally use two major reproductive strategies, sexual reproduction via meiotically produced fungal spores and vegetative reproduction using asexually produced diaspores. Sexual reproduction is restricted to characteristic fungal fruiting bodies (ascomata)

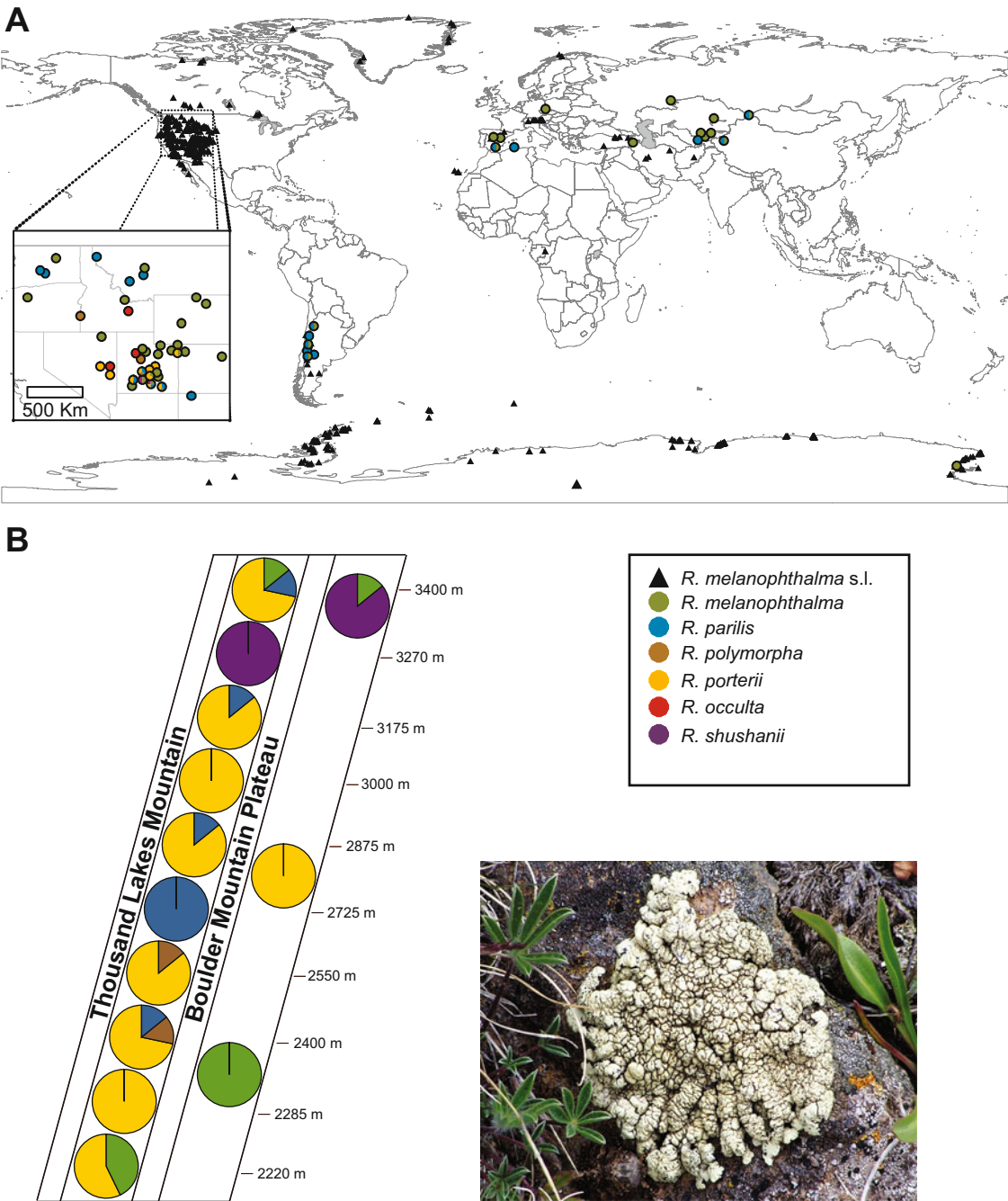


Fig. 2.1 (a) Worldwide distribution of the *Rhizoplaca melanophthalma* group; (b) Distribution of species along an altitudinal gradient on the Aquarius Plateau in southern Utah, USA; and habitat of *R. shushanii*,

endemic to subalpine habitats in the southern Utah, USA. Modified from Leavitt et al. (2011) and Leavitt et al. (2013b)

that produce meiospores (ascospores). Ascospores are dispersed independently of the photosynthesizing partner (photobiont) and

usually require acquisition of the appropriate photobiont partner in order to reestablish the lichenized condition. Ascospore ejection

appears to be temporally gauged toward maximum efficiency of dispersion and germination (Pyatt 1973; Favero-Longo et al. 2014; Trail and Seminara 2014). In contrast, other lichens commonly propagate asexually by means of vegetative diaspores produced in characteristic structures termed isidia or soredia. These specialized vegetative reproductive propagules contain both fungal and algal or cyanobacterial symbionts and potentially a core fraction of the lichen microbiome (Aschenbrenner et al. 2014), eliminating the need for independent acquisition of the appropriate symbiotic partners. Isidia and soredia are usually not actively dispersed but require physical separation from the parent lichen by wind, animals, or other physical disturbances. In some cases, it appears that hygroscopic movement also facilitates soredia dispersal (Jahns et al. 1976). Fertile lichens—those bearing ascomata which produce ascospores—only rarely produce vegetative diaspores (exceptions include *M. elegantula*, *Letharia vulpina* s. lat., *Lobaria pulmonaria*, and others); likewise, lichens that typically reproduce vegetatively rarely form apothecia (exceptions include *Hypogymnia physodes*, *Physcia tenella*, and others).

The general efficacy of dispersal for major reproductive strategies is now beginning to be better understood. Traditionally, lichen fungi reproducing via ascospores were considered to be more effective at long-distance dispersal due to the relatively smaller size of the meiospores when compared to vegetative diaspores, although Bailey (1966) suggested that soredia are more effective dispersal agents than ascospores. However, effective dispersal does not equate to successful establishment, and successful fungal meiospores establishment may be abysmally low due to the small likelihood of encountering the appropriate symbiotic partners after dispersal. This has led to the widespread acceptance that sexually reproducing lichens commonly occur as juvenile parasites on other lichens from which they presumably obtain the photosynthetic partner (Poelt 1956, 1987, 1990; Poelt and Steiner 1971; Hawksworth 1982; Friedl 1987). In addition, the temporal viability of lichen-forming fungal spores remains largely unexplored.

While species-specific differences in morphological and physiological traits of the diaspores play a major role in successful establishment (Hilmo et al. 2011), Werth et al. (2014) demonstrated that size is not necessarily a good predictor of local or regional structure in three species of *Lobaria* that generally reproduce clonally. In fact, it has long been recognized that species using a vegetative reproductive strategy often have a larger distributional range than their fertile counterparts, at least in foliose and fruticose groups (Bowler and Rundel 1975). This conclusion is generally supported by molecular phylogenetic studies that commonly reveal broad intercontinental distributions and no phylogeographic substructure in many lichens reproducing via vegetative diaspores (Leavitt et al. 2012; Wirtz et al. 2008, 2012). In maritime Antarctic lichens, soredia were found to be the most abundant airborne propagules, more so than ascospores, further highlighting the importance of asexual reproduction in some lichen communities (Marshall 1996).

Although studies suggest that vegetative diaspores are able to effectively disperse and successfully establish across broad distributions, empirical studies generally reveal much shorter dispersal capacities. For example, the vegetative dispersal distance between host trees and *Lobaria pulmonaria* (Fig. 2.2) was found to be only 15–30 m (Jüriado et al. 2011). However, Schei et al. (2012) highlight the fact that the observed spatial distribution patterns in *Lobaria* species are the result of dynamic interactions of environmental factors with dispersal capacity and that single site patterns are not readily generalizable. It appears that lichen fungi that reproduce via passively dispersed small propagules tend to exhibit patchy populations with extensive distributions at the landscape scale (Gjerde et al. 2014). In the sorediate lichen *Hypogymnia physodes*, wind dispersal has been shown to deposit most soredia within 5 cm of the parent thallus, with a maximum measured dispersal distance of 80 cm in wind speeds of 9 m/s, empirically demonstrating that air currents directed over the surfaces of lichen thalli would be able to effectively disperse soredia vertically and horizontally within a tree canopy (Armstrong 1994).



Fig. 2.2 Habit of the lung lichen (mycobiont = *Lobaria pulmonaria*) in the Great Smokey Mountains, USA. This lichen has become a model species for ecological biogeographic research, including investigations into dispersal capability, landscape genetics, symbiont interactions, and conservation. Photo credit: Jason Hollinger, <http://www.waysofenlichenment.net>



Fig. 2.3 *Flavocetraria* sp. (Parmeliaceae) and *Thamnolia* sp. (Icmadophilaceae) used as nesting material in an American golden-plover (*Pluvialis dominica*) scrape near Coffee Dome, Seward Peninsula, Alaska, USA. Photo credit: Wikipedia CC BY-SA 3.0

Although wind is generally considered an important dispersal agent for lichen propagules, water-mediated dispersal is also a potential mechanism for propagule dispersal (Bailey 1966). Laboratory experiments have assessed dispersal by water droplets and suggest that falling water can effectively disperse lichen propagules on the scale of centimeters to meters (Armstrong 1987). Some lichen propagules may also be abundant in runoff water, although successful establishment may be limited by a shortage of suitable sites for the attachment of propagules (Armstrong 1981).

Animal-mediated dispersal may be another important mechanism for dispersal, although reports of lichen propagule dissemination by animals are rather scarce. For lichens that disperse via thallus fragmentation, the thallus fragments may disperse effectively across short distances in open vegetation habitats but generally ineffective for long-distance dispersal; and wind and animals likely play a major role in the dispersal of thallus fragments across longer distances (Heinken 1999; Rosentreter 1993).

Birds are commonly implicated as agents of long-distance dispersal of lichens, particularly in cases where lichen distribution and not readily accounted for by atmospheric air current patterns (Bailey and James 1979). Birds frequently use lichens as nesting material (Fig. 2.3), and this presumably plays a role in

lichen dispersal. In addition to lichen dispersal by birds for nesting, Bailey and James (1979) demonstrated a small-scale transport of lichen fragments in New Zealand by large seabirds, and this study indicates that, at least theoretically, these birds could be effective agents of long-distance dispersal of lichen propagules. Although bryophyte diaspores have recently been documented in the plumage of transequatorial migrant birds (Lewis et al. 2014), there is, however, little direct evidence at this time supporting long-distance dispersal of lichen propagules by birds.

Vertebrates, arthropods, and gastropods may also mediate dispersal of reproductive propagules. For example, in Central Maine, USA, a quarter of oribatid mites (*Humerobates arborea*) were found to have soredia externally adhered to their bodies (Stubbs 1995), although the estimated average distance for transferal via mite was estimated to be relatively short (<5 cm; also see Seyd and Seaward 1984). Insect-mediated soredia dispersal has also been reported for ants (Lorentsson and Mattsson 1999; Bailey 1970) and potentially lacewings larvae, which construct and carry lichen “packets” (Skorepa and Sharp 1971). Intuitively, one could assume that a wide range of insects groups that occur alongside lichens could serve as a potential means of propagule dispersal, including tardigrades, nematodes,

springtails, etc. (Pickup 1988; Stubbs 1989; Apt-root and Berg 2004).

Endozoochory, diaspores carried within an animal, plays an important role in seed plant dispersal, and it appears that gastropods grazing on lichen communities likely serve as important vectors for lichen dispersal (Boch et al. 2011; McCarthy and Healy 1978). Boch et al. (2011) found that two lichens, *Lobaria pulmonaria* (Fig. 2.2) and *Physcia adscendens*, were able to regenerate from fecal pellets after passing through their digestive tracts of common snail species occurring in temperate Europe. This gastropod–fungus–alga association represents another level of complexity in lichen symbioses, and endozoochory provides a previously overlooked mechanism for lichen dispersal. Viable lichen fungal spores and photobionts have also been in fecal pellets from slugs (McCarthy and Healy 1978), and lichenivorous mites have also been shown to distribute lichens with their feces including viable cells of both fungal and algal partners (Meier et al. 2002). Rotifers have also been shown to ingest ascospores of *Xanthoria parietina* and deposit viable spores in their feces (Pyatt 1968).

Given the range of distribution patterns in lichen-forming fungal taxa, increased interest in understanding mechanisms for fungal dispersal and variation in dispersal capacity will likely provide novel insight into biogeographic patterns in lichens. Recent advancements in sampling environmental DNA (eDNA) and “next-generation” sequencing technologies provide promising avenues for more accurately characterizing dispersal capacities of lichen-forming fungi (Shokralla et al. 2012). Rather than relying exclusively on visual observations of lichen propagules, eDNA collected from migratory birds and other animals can be used to determine if animals consistently carry evidence supporting animal-mediated lichen dispersal. Similarly, eDNA can be used to assess the presence of lichen-forming fungal DNA from air and water samples. In the foreseeable future it is reasonable to assume that source populations of eDNA samples could be accurately identified by using highly variable DNA markers, affording an exciting avenue for future research.

IV. Ecological Biogeography

In contrast to historical biogeography, the study of ecological biogeography attempts to elucidate contemporary factors that influence ecological and spatial distributions of species (Monge-Nájera 2008). The study of contemporary biogeographic relationships focuses on biotic interactions among organisms, environmental changes that potentially impact a species distribution, and how landscape and environmental features influence gene flow and population structure. While evolutionary patterns may not be explicitly of interest in ecological biogeography, there is no distinct boundary between historical and ecological biogeography; and ecological biogeography can extend back in time to reconstruct demographic histories, ecological interactions, environmental controls, and evolutionary relationships (e.g., Richardson and Meyer 2012; Chan et al. 2011; Lira-Noriega et al. 2015).

A. Ecological Biogeography and Lichens

The overall importance of ecology in determining the distributions of lichens is well known (Renhorn et al. 1996; Kantvilas and Minchin 1989; Culberson and Culberson 1967). The distributions of some lichen-forming fungal species and overall diversity are commonly determined by microclimatic differences (Palmqvist and Sundberg 2000; Renhorn et al. 1996; Hauck et al. 2007; Ranius et al. 2008), and a wide variety of contemporary factors potentially influence lichen distributions. For example, Nelson et al. (2015) recently demonstrated that different combinations of lichen functional traits, including choice of photobiont, dispersal capacity, microsite specificity, and water relations, peak along environmental and disturbance gradients.

The distribution and abundance of species can be explained by the combination of dispersal and environmental filtering. The occurrence of a particular species is the product of the probability of establishment (environmental filtering), and the number of propagules arriving at the site (dispersal) (Schei et al.

2012). Schei et al. (2012) underscore that the relative importance of local dispersal and environmental filtering varied widely among sites in deciduous forests in southwest Norway, particularly in terms of abundance patterns. However, environmental filtering by tree species was more important than local dispersal overall (Schei et al. 2012). Of course inferences from any study investigating the relative roles of dispersal and environmental filtering are scale dependent (Jackson and Fahrig 2014). Other studies of fine-scale epiphyte distribution patterns have revealed somewhat conflicting views of the overall importance of dispersal versus environmental filtering.

It has been found that traditional biogeographical variables explain little of the variance in lichen richness in the Antarctic Peninsula at local and regional scales (Casanova et al. 2013). Interestingly, while the majority of variability in moss richness at a region scale in the Antarctic Peninsula was explained by summer mean sea surface temperature, lichen richness in the same region was not correlated with any of the variables investigated (Casanova et al. 2013). These data suggest that site-specific habitat characteristics that were not investigated (substrate, water availability, etc.) likely play an important role in explaining variance in lichen richness.

In biological soil crusts in western North America, lichen community composition is strongly related to vascular plant species, soil texture and pH, and climate variables (Root and McCune 2012). While species-rich biotic crust lichen sites were scattered throughout the region, areas impacted by physical disturbances, including grazing, fire, etc., had the lowest overall lichen richness (Root and McCune 2012). Strikingly, a third of the nearly 100 lichen-forming fungal species encountered in this study were only observed a single time, highlighting the fact that a substantial proportion of lichen diversity may not be found ubiquitously even across relatively similar habitats. Interspecific competition among lichens and other biotic interactions have also been shown to be the major drivers of lichen community structure in soil crust communities in central Spain (Maestre et al. 2008).

In a saxicolous lichen community in coastal Norway, vegetation cover, rather than radiation, maritime influence, and microhabitat variables, was the predominant factor explaining variation in community composition (Bjelland 2003). However, in this study over 90 % of the total variation in lichen community composition remained unexplained. A combination of a variety of factors potentially contribute to our ability to more fully account for community composition and species' occurrences, including ignoring local historical factors affecting contemporary distributions, failing to account for influential environmental variables, stochasticity in species establishment, and/or lack of fit of data to response models.

Cladonia species occurring in the Wisconsin Pine Barren ground-layer lichen-moss community tend to occupy slightly different habitats (Lechowicz et al. 1974). Although there is some overlap in microdistributional patterns, differences in net photosynthesis temperature responses appear to underlie the distributions of *C. arbuscula* subsp. *mitis*, *C. carolinensis*, *C. rangiferina*, and *C. uncialis*, highlighting the putative role of temperature in structuring species distributions. While the eco-physiological responses observed for these *Cladonia* species provide some intuitive insight into their biogeography and microhabitat selection in the Wisconsin Pine Barrens, the nuanced interactions remain largely unaccounted for.

Assessing the combined biological effects of light, temperature, and humidity on photosynthetic activity of *Usnea sphacelata* in Antarctica, Bölter et al. (1989) demonstrated that although individual microhabitat conditions (e.g., light, humidity, and temperature) show long periods of favorable conditions for metabolic activity in *U. sphacelata*, the combined analysis of these variables considering threshold values for metabolism drastically shortens favorable periods for growth. Experimental manipulations revealed that the combination of light with desiccation has caused photoinhibitory damage in pendulous lichens that commonly occur in boreal forests and that the species-specific production of suncreening fungal pigments plays a major role in the verti-

cal canopy gradient of epiphytes (Färber et al. 2014). Specifically, high-light-tolerant *Bryoria* species producing melanin are more commonly found in the upper canopy than light-susceptible species in the genera *Alectoria* and *Usnea* (sunscreening pigment = usnic acid) (Färber et al. 2014).

The interplay between the source of hydration and light availability plays a major role in structuring epiphytic lichen distributions (Gauslaa 2014). Lichens utilize a variety of sources for water, including rain, dew, and humid air, facilitating active photosynthesis. Sources of hydration vary on temporal and spatial scales (e.g., regional, landscape, stand, tree); and distinct atmospheric hydration sources influence and shape lichen diversity and distributions (Gauslaa 2014).

In short, the studies highlighted above demonstrate that a variety of environmental, ecological, and historical factors have the potential to significantly influence lichen distributions. However, identifying the specific factors and teasing apart their relative contributions remains challenging. Similarly, determining the most appropriate scales for sampling poses a significant challenge. The contribution of these factors in structuring lichen distributions may vary dramatically across different temporal and spatial scales, and extrapolations between studies can potentially be misleading.

1. Landscape Genetics and Gene Flow

From a landscape genetic perspective, researchers attempt to understand how geographic and environmental factors impact gene flow and genetic structure in populations and individuals. Two of the major objectives of modern landscape genetics are (1) to improve our understanding of how recent global change (e.g., climate change, land use, etc.) affects neutral and adaptive genetic variation and (2) understand if species are likely to adapt to ongoing global change on an ecological time scale (Manel and Holderegger 2013). While assessing gene flow is a central component in understanding landscape dynamics, it is worth

noting that dispersal does not equal to gene flow. Some lichen-forming fungi may be able to effectively disperse, but without successful reestablishment and reproduction, the dispersal event has no impact. Only those dispersal events that occur in suitable habitats, with compatible symbiotic partners, and at the appropriate spatial and temporal scales will have the potential to contribute to gene flow and impact genetic structure.

Colonization rates of epiphytic lichens appear to be tied to a number of crucial factors, including connectivity to occupied patches and species traits (e.g., niche breadth and propagule size, local and long-distance dispersal, and patch dynamics) (Johansson et al. 2012). The majority of studies of landscape genetics in lichen-forming fungi have focused on the model epiphyte genus *Lobaria pulmonaria* (Fig. 2.2; Werth et al. 2006, 2007; Walser et al. 2005; Walser 2004; Widmer et al. 2012). Among the first studies of landscape dynamics in *L. pulmonaria*, Walser et al. (2005) used microsatellite loci to elucidate regional population differentiation and isolation by distance in populations in western North America (British Columbia, Canada) and central Europe (Switzerland). The use of highly variable microsatellite markers revealed striking genetic differentiation among populations of *L. pulmonaria*, with Swiss populations being distinct from those occurring in British Columbia, with additional differentiation between coastal and mainland populations in western North America (Walser et al. 2005). Subsequent studies of *L. pulmonaria* suggest that its occurrence may not be limited by dispersal capacities, but that ecological constraints at level of the sampled tree stands result in establishment limitations (Werth et al. 2006). However, dispersal characteristic of *L. pulmonaria* appears to be at least as important as landscape configuration in determining the spatial scale of population connectivity (Wagner et al. 2006). In fragmented relict stands in the boreal rainforest in central Norway, nearly all genetic variation found in *L. pulmonaria* could be attributed to variation within sites and spatial genetic structure was absent or appeared on very small scales (5–10 m; Hilmo et al. 2012). While this study high-

lights that relict stands may contain high levels of genetic diversity, disturbances (e.g., fire and intensive logging) may have long-lasting negative consequences on adaptive potential and reproduction in epiphytic lichens (Singh et al. 2014). Overall, studies of landscape genetics in *L. pulmonaria* support the conclusion underscored by Werth et al. (2007) that dispersal in *L. pulmonaria* is quite effective, but not spatially unrestricted.

Arctic and alpine ecosystems are facing significant impacts from global climate change, including ongoing increases in temperature and altered precipitation patterns (Ernakovich et al. 2014). Two species in *Flavocetraria* (Parmeliaceae), *F. cucullata* and *F. nivalis*, have widespread arctic-alpine distributions in the Northern Hemisphere but also occur in a few disjunct populations in the Southern Hemisphere. Geml et al. (2010) found high genetic diversity and effective long-distance dispersal capacity among populations of both *F. cucullata* and *F. nivalis* occurring in the Northern Hemisphere. Long-distance gene flow appears to have prevented pronounced genetic differentiation among disjunct populations and suggests that these taxa are able to effectively track their potential niche during climatic shifts (Geml et al. 2010).

Long-distance, intercontinental dispersal and subsequent gene flow appear to be common in a number of other lichen-forming fungal species. For example, in the rock-dwelling lichen *Porpidia flavicunda* (Lecideaceae), a lack of fixed nucleotide polymorphisms and wide sharing of identical haplotypes between disjunct geographical regions indicates recurrent long-distance gene flow of propagules (Buschbom 2007). Similarly, lichens of the genus *Thamnolia* (Icmadophilaceae) occur at high altitudes/latitudes across incredibly broad geographic distances without any evidence of phylogeographic structure (Nelsen and Gargas 2009), although gene flow among disjunct populations has not been explicitly tested. The broad distribution and lack of phylogeographic structure is particularly striking given that this taxon is thought to reproduce almost exclusively via vegetative fragmentation and ascospores are unknown in this genus. While the

charismatic epiphyte *Letharia vulpina* (Parmeliaceae) is known to occur in western North America, Europe, the Caucasus, and Morocco, European populations are genetically depauperate, resulting from an apparent genetic bottleneck caused by limited long-distance dispersal (Högberg et al. 2002; Arnerup et al. 2004).

Similar patterns of effective gene flow have also been observed at regional scales. In western North America, the epiphytic lace lichen (mycobiont = *Ramalina menziesii*) occurs in inland foothills along the Pacific Coast, ranging from Baja California northward to Alaska. Sork and Werth (2014) demonstrated that broad range of this epiphytic lichen has been shaped not only by long-distance dispersal across suitable habitats but also by lineage formation and persistence. While the majority of genetically distinct *R. menziesii* lineages tended to occur in distinct ecoregions, high migration out of populations in coastal and the Pacific Northwest into inland California populations was observed. In contrast, populations of *R. menziesii* in Baja California appear to be relatively isolated. Previously, a complete lack of local genetic structure was observed in *R. menziesii* populations growing on distinct oak species in an oak-savanna ecosystem in southern California (Werth and Sork 2010). The low level of local genetic structure in some lineages within *R. menziesii* is consistent with high effective gene flow in other epiphytic lichen species. While population structure corresponding to different host trees was not observed in *R. menziesii*, population differentiation was observed in *Xanthoria parietina* populations occurring in different habitats (rock vs. bark) but not in populations occurring in the same habitat (Lindblom and Ekman 2006). Therefore, in some cases habitat isolation, rather than dispersal limitations, may play an important role affecting gene flow.

Population structure corresponding to geographic regions has been observed in some species of lichen-forming fungi with broad, intercontinental distributions. Fernández-Mendoza et al. (2011) demonstrated striking genetic structure in *Cetraria aculeata* (Parmeliaceae) corresponding to distinct geographic regions.

However, robust hypotheses of species boundaries in the *C. aculeata* group are lacking, and additional data will be required to accurately circumscribe species and adequately characterize gene flow among disjunct populations (Printzen et al. 2013).

Ongoing research into landscape genetics of model systems, such as *Lobaria pulmonaria*, will likely continue to provide novel insight into how geographic and environmental factors impact gene flow and genetic structure in lichens. Fortunately, many of the molecular techniques that have previously only been available for model systems can now be incorporated into studies of non-model groups using genomic data generated from high-throughput sequences (Ekblom and Galindo 2011). Incorporating non-model groups into landscape genetic studies of lichen-forming fungi will ultimately provide a much more nuanced perspective into how lichens respond to changing environments.

2. Modeling Distributions of Lichens

Modeling species distributions has the potential to play a pivotal role in biogeographic research. While species distribution models have become commonplace in biogeographic research, only a limited number of studies of lichen-forming fungi have incorporated modeling approaches to elucidate biogeographic patterns. Modeling distributions of species is most commonly based on pattern-recognition approaches, where associations between records of a species geographic occurrence and a suite of predictor variables are explored to allow an estimation of the species' ecological requirements. Accurate modeling depends, in part, on how the appropriate use of occurrence data and the adequacy of the predictors used for model building (Anderson et al. 2003).

Many lichens show significant relationships with macroclimatic variables (Giordani and Incerti 2008; Glavich et al. 2005), and overall it appears that there is general support for bioclimatic modeling in lichens (Braidwood and Ellis 2012). Species distribution models have been used in a number of ecological-, biogeographical-, and conservation-related studies. McCune et al. (2003)

used habitat models to forecast the frequency of occurrence of epiphytic lichens under different forest management strategies in northwestern USA. These habitat models were able to successfully estimate the occurrence of lichens modeled, and forecast that forest management strategies reducing even-aged stands will increase the frequency of epiphytes associated with old-growth forests. Logistic regression models have been shown to accurately predict the occurrence of six lichen epiphytes in Switzerland, including two threatened or vulnerable lichens, by using the statistical relationships between response and explanatory variables to predict the distribution of lichens in previously unsampled geographic areas (Bollinger et al. 2007). Shrestha et al. (2012) used nonparametric multiplicative regression analysis to model the potential distribution of the sensitive indicator species *Usnea hirta* (Parmeliaceae) in western North America. Their predictive model suggested that average monthly minimum and maximum temperatures, precipitation, and solar radiation were the major macroclimatic factors influencing the distribution of *Usnea hirta*, providing a useful ecological niche-based approach to forecast the distribution of air pollution-sensitive lichens based on macroclimatic variables (Fig. 2.4). Similarly, ecological niche modeling has also played an important role in improving survey design of rare epiphytic macrolichens in the Pacific Northwest, USA (Edwards et al. 2005).

Recently, Martellos et al. (2014) utilized ecological niche modeling to characterize differences in the distribution of two varieties of the soil crust lichen *Squammarina cartilaginea* in Italy. Their study highlights not only the role the modeling plays in forecasting distributions but also the potential for using ecological niche modeling for species delimitation research. In fact, within an integrative species delimitation framework, distribution modeling serves as an important independent line of evidence to corroborate lineage separation (Leavitt et al. 2015a; Pelletier et al. 2014). The study by Martellos et al. (2014) provides the first implementation of ecological niche modeling for resolving taxonomic issues in lichen-forming fungi.

While distribution modeling can provide important insight into species distributions

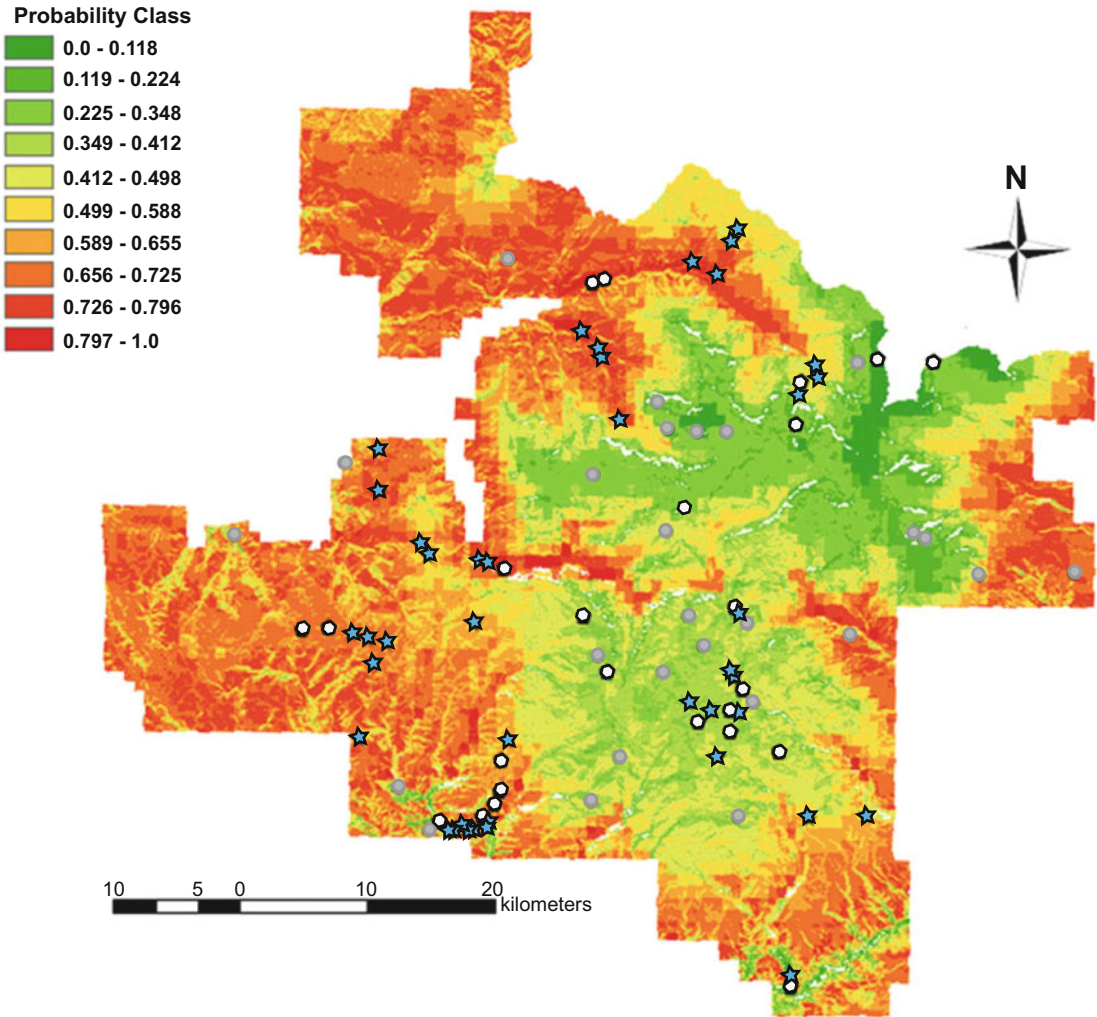


Fig. 2.4 Modeled distribution map for *Usnea hirta* in the White River National Forest in central Colorado using nonparametric multiplicative regression analysis. Blue stars represent sites where *U. hirta* was recorded,

white hexagons represent sites with no *U. hirta*, and grey circles represent inaccessible sites. White areas represent no data value due to lower average neighborhood size. Modified from Shrestha et al. (2012)

and biogeographic patterns, effective distribution modeling faces a number of general challenges, including: (1) clarification of the niche concept; (2) weaknesses in sampling ability and design; (3) variation in parameterization within each technique, potentially providing different modeled distributions; (4) a need for improved model selection and predictor contribution; and (5) a need for more robust model evaluation strategies (Araújo and Guisan 2006).

Among the most practical issues of distribution modeling is effective sample survey

design, the results of which will impact all downstream analyses (Edwards et al. 2006). Even when occurrence data is relatively well characterized, bioclimatic modeling may not provide results congruent with known species occurrences. Distribution models for the rare lichen species *Staurolemma omphalarioides*, known for its disjunct distribution in the Mediterranean region and central Norway, well outside of the main range of the species, indicate that either the species has not reached its potential distribution or the models fail to

accurately characterize the actual species distribution (Bendiksby et al. 2014). Furthermore, while models can incorporate macroclimatic variables, as indicated above, lichens are inherently sensitive to microhabitat variation, and measuring and incorporating this variation remains challenging. As an example, microhabitat conditions, including proximity to water-courses and bark pH, play important roles in determining the occurrence *Platismatia norvegica* (Parmeliaceae) in suboceanic habitats at the fringe of the species' distribution (Lidén and Hilmo 2005). Similarly, the distribution of some epiphytic lichens in different forest types is strongly influenced by vertical position within the forest canopy (Coxson and Coyle 2003; Antoine and McCune 2004). Land use intensity has been shown to influence the local variation of lichen diversity in Mediterranean ecosystems (Giordani et al. 2010). However, other lichen communities appear to be unaffected by human activity and are predominantly determined by macroclimatic factors (Werth et al. 2005).

Going forward, species distribution modeling holds important promise in ecological biogeographical research of lichens. Due to the fact that species distributions reflect the dynamic interplay of geographic and environmental processes with biotic factors, including species dispersal capabilities and interactions with other species, developing a stronger link between ecological factors and modeling will be beneficial for developing more approaches for distribution modeling. Advances in spatial data technologies, geographic information system (GIS) data, and modeling approaches will continue to facilitate ecological and evolutionary insight and predict distributions of lichen-forming fungi.

3. Role of Photobionts in Ecological Biogeography

Lichens represent iconic examples of symbioses, and therefore taking their symbiotic partners into account in biogeographic research is likely to provide valuable insight into elucidating biogeographic patterns. Gener-

ally, lichen photobionts are considered the subsidiary member of lichen associations; however, it now is clear that at least some photobionts exhibit differential preference for environmental factors (Peksa and Škaloud 2011). Algal preferences potentially limit the ecological niches available to lichens, further supported the idea of habitat-specific lichen guilds, where lichen communities growing in similar habitats share the same photobionts (Rikkinen et al. 2002). Factors such as photobiont availability (Werth et al. 2006; Rikkinen et al. 2002), fungal specificity in photobiont choice (Yahr et al. 2004), ecological constraints (Peksa and Škaloud 2011), and symbiont interactions (del Campo et al. 2013; Werth et al. 2013) have all been shown to have a major impact on the occurrence of lichens.

The spiny heath lichen (mycobiont = *Cetraria aculeata*; Fernández-Mendoza and Printzen 2013; Pérez-Ortega et al. 2012; Fernández-Mendoza et al. 2011; Printzen et al. 2013), lace lichen (mycobiont = *Ramalina menziesii*; Werth and Sork 2010, 2014), and lung lichen (mycobiont = *Lobaria pulmonaria*; Werth et al. 2006; Dal Grande et al. 2012; Singh et al. 2014) have become model groups for understanding the dynamic roles that photobionts play in determining lichen distributions. Based on broad geographic sampling of the spiny heath lichen (mycobiont = *Cetraria aculeata*), Fernández-Mendoza et al. (2011) provide evidence that photobiont switches played an important role in increasing the geographical range and ecological niche of lichen mycobionts by associating them with locally adapted photobionts in climatically distinct regions. In this specific case, the photobiont switch allows *C. aculeata* that is common in temperate and alpine habitats to extend into semiarid regions in the Mediterranean. In the lace lichen (mycobiont = *Ramalina menziesii*), ecological specialization of the photobiont (*Trebouxia decolorans*), geography, and climate shape the distribution of this lichen (Werth and Sork 2014). Algal specialization on local environmental conditions, including macroclimatic factors and substrate ecology, allows *R. menziesii* to associate with locally adapted photobiont strains. As discussed previously, dispersal limitations of the mycobiont

Lobaria pulmonaria is not the most important mechanism underlying differentiation among populations. Availability of the appropriate photobionts has been proposed as a potential mechanism generating population structure in *L. pulmonaria* (Werth et al. 2006, 2007).

While species richness of lichen-forming fungi is associated with both climate and forest structure variables, specific responses to these different variables were dependent on the type of photobiont. A study of patterns in lichen richness across Italy highlights the photobiont-dependent response of species richness to various environmental factors (Marini et al. 2011). Mycobiont species paired with chlorococcoid green algae was correlated with increasing forest cover. While species richness of cyanolichens—lichen-forming fungi associating with photosynthetic cyanobacteria—was related to area and precipitation, lichens with *Trentepohlia* algae were enhanced by rainy and warm climates (Marini et al. 2011). In some cases, the mycobiont's habitat preferences may be determined by factors that are independent of those of the photobiont at the landscape level (Nadyeina et al. 2014). The differential responses of lichens associating with different types of photobionts to ecological, climatic, and other environmental factors demonstrate the challenges in predicting lichens distributions.

These studies clearly indicate the potential importance of carefully taking the role of the photobiont into consideration when considering ecological biogeography. Currently, studies of species interactions in lichen symbioses are limited by uncertainty in the circumscription photobiont species (Kroken and Taylor 2000; Sadowska-Deś et al. 2014; Blaha et al. 2006; Dahlkild et al. 2001; Tibell 2001). For example, in spite of the fact that traditional morphology-based species circumscriptions have consistently been shown to be inadequate to characterize species-level diversity in *Trebouxia* (Kroken and Taylor 2000; Sadowska-Deś et al. 2014; Blaha et al. 2006; Dahlkild et al. 2001), only a limited number of studies have implemented objective methods for delimiting species-level lineages (Sadowska-Deś et al. 2014; Kroken and Taylor 2000). We argue that there is a pressing need to develop and adhere to a practical,

species-level classification system for major groups of lichen photobionts in order to enhance communication about diversity, distributions, ecological patterns, and interactions in lichen symbioses (Leavitt et al. 2015b).

IV. The Role of Biogeography in Conservation and Climate Change Research

Lichens are not easy targets for conservation measures due to the fact that lichens represent the symbiotic phenotype of multiple interacting species (Scheidegger and Werth 2009). This challenge is further confounded by the fact that many lichens have specific habitat requirements that are not generally shared with other organisms. An ecological biogeographic perspective of lichen-forming fungi highlights the importance of seeing distributions of species as the result of dynamic interactions among symbionts and ecological and environmental factors. Scheidegger and Werth (2009) provide an invaluable perspective into lichen conservation biology, including potential strategies to effectively protect lichens and develop priorities for conservation approaches. Here we only highlight in brief a number of examples from lichen conservation biology literature, emphasizing the role of maintaining habitat quality, connectivity, and size.

Relative to more charismatic species, conservation of lichens generally receives very limited attention from governmental organizations and other institutions. Conservation status of most lichens is unknown, and therefore, conservation approaches may fail to protect vulnerable lichen and lichen communities. For example, the Natura 2000 Program was established in the European Union as the main instrument for nature conservation, focusing on protecting the most threatened habitats, ensuring the long-term survival of species, and reducing the loss of biodiversity caused by anthropogenic impact (<http://www.natura.org/>). While Martínez et al. (2006) demonstrate that the Natura 2000 network may include key habitat in conserved forests and mountain

ranges for a number of lichens in Spain, the effectiveness of the Natura 2000 network in protecting Mediterranean lichens is quite low (Rubio-Salcedo et al. 2013). Natura 2000's reserve network, based mainly on vascular plant data, may be ineffective for neglected taxonomic groups, like lichens, and highlights the need to include "noncharismatic" species to improve reserve design and other conservation strategies (Rubio-Salcedo et al. 2013). However, even when explicitly taking lichens into consideration when developing models to predict species richness, it appears lichen surveys are critical for assessing species abundance, dynamics, and viability (Waser et al. 2007).

Ultimately, successful lichen conservation is contingent on a wide variety of factors, including effective approaches for prioritizing the protection of vulnerable habitat and species (Bowker et al. 2008), promoting interdisciplinary collaborations (Campbell 2005), incorporating population/landscape genetics into policy decisions (Scheidegger and Werth 2009), and increasing the number of bio-inventory surveys which include lichens. Lättman et al. (2009) suggested that dispersal capability is likely to be commonly underestimated for lichens defined to habitat with long ecological continuity, and this perspective was corroborated for epiphytic lichens occurring in the boreal rainforest in central Norway (Hilmo et al. 2012). Therefore, successful conservation of some lichens may be possible even when a suitable habitat is highly fragmented.

Lichens are included among a suite of indicators of ecosystem health, which also includes bryophytes (Frego 2007; Pesch and Schroeder 2006), vascular plants (Coulston et al. 2003), some terrestrial and aquatic invertebrates (Hodkinson and Jackson 2005), and other sensitive species and/or communities (Leavitt and St. Clair 2015). Rather than abiotic metrics, bio-indicators are likened to canaries in a coalmine, serving as a direct surrogate for assessing disturbances on biological communities. Lichens are particularly useful as bio-indicators due to the fact that many live and grow continuously for decades, or even hundreds of years, showing cumulative responses to ecological changes, including climate change, land management

practices, changes in atmospheric pollution levels, etc. Measurable responses of individual lichen thalli (e.g., differential accumulation of atmospheric pollutants) and lichen communities (e.g., changes in community composition and population density) can provide a means to quantitatively assess ecosystem health (McCune 2000).

Climate change is forecast to promote major ecological shifts worldwide (Parmesan and Yohe 2003; Araújo and Rahbek 2006). Species that are unable to tolerate or adapt in situ to altered environmental conditions or migrate to suitable habitats face potential extinctions. Alternatively, climate change may lead to major shifts in species distributions. Some components of cryptogamic communities, including lichens, have been shown to be particularly sensitive to climatic shifts (Cornelissen et al. 2001; Bjerke 2011). Although lichens are well-known indicators of air quality (Leavitt and St. Clair 2015), recent studies indicate that they may also be useful in assessing ecological shifts related to climate change (Bjerke 2011; Ellis et al. 2007a, b; Cornelissen et al. 2001). Some lichens, due to their sensitivity, may play an important role in monitoring the potential impacts of climate change.

In general, specific responses of most species, including lichen-forming fungi, to rapid climate changes in vulnerable habitats remain uncertain, and detailed, long-term monitoring will be essential to accurately assessing biologically meaningful shifts in community composition and species distributions (Eaton and Ellis 2012). On a global scale, macrolichens in climatically milder arctic ecosystems may decline if and where global changes cause vascular plants to increase in abundance (Cornelissen et al. 2001). In the UK, the southern elements of Britain's lichen flora, and other lichen species adapted to warmer climates, are projected to expand northward, while the montane species appear to be disproportionately threatened by climate change (Ellis et al. 2007b). Other data suggest that a warmer, humid climate in Norway will likely be beneficial for the generalist species *H. physodes*, but detrimental to the subalpine birch specialist *Melanohalea olivacea* (Evju and Bruteig 2013).

These studies highlight the importance of continued research on specific responses of lichen species and communities to changing climate. Only by consistently coupling efficient quantitative methods with accurately characterized species- and/or community-specific responses to changing climatic conditions will we be able to effectively document climate change related impact on vulnerable lichen communities. However, biological communities are threatened not only by changing climate but a wide range of other environmental disturbances, including habitat degradation, invasive species, air pollution, etc. Dynamic interactions among multiple types of disturbances make characterizing risks to biological communities and their potential responses quite difficult (Ellis et al. 2014). Principles from ecological biogeography should play a central role in climate change research, facilitating more effective study design and appropriate interpretation of results.

V. Conclusions

Current research has dramatically increased our understanding of the geographical distribution of lichens and allowed new insights in the importance of the photosynthetic partners for shaping the spatial distribution of these symbiotic organisms. Novel methods, including the increased availability of data from environmental sampling, will further enhance and refine our hypotheses to explain distribution patterns. These are truly exciting times—with the help of next-generation sequencing techniques, increased number of species for which micro-satellite markers have been identified, and improved analytical tools, biogeographical questions can be addressed that were beyond our reach only a decade ago. Improved understanding of species delimitations of the fungal partners has allowed us to better understand distribution patterns, and in tandem with enhanced knowledge of species diversity of photosynthetic partners, this provides an avenue to better understand patterns that explain distribution patterns at an ecological level.

Currently, ecological biogeographical studies focus on a few species that provide great insights, but we look forward to seeing these exemplary studies extended to other lichens, including phylogenetically distant groups and also tropical species, which are currently severely understudied. The extension of research to include a wider amplitude of species will also strengthen predictions of the impact of global climatic change to lichen distribution.

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