

ORIGINAL
ARTICLE



Biodiversity gradients in obligate symbiotic organisms: exploring the diversity and traits of lichen propagules across the United States

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ABSTRACT

Aim Large-scale distributions of plants and animals have been studied extensively and form the foundation for core concepts and paradigms in biogeography and macroecology. Much less attention has been given to other groups of organisms, particularly obligate symbiotic organisms. We present the first quantitative assessment of how spatial and environmental variables shape the abundance and distribution of obligate symbiotic organisms across nearly an entire subcontinent, using lichen propagules as an example.

Location The contiguous United States (excluding Alaska and Hawaii).

Methods We use DNA sequence-based analyses of lichen reproductive propagules from settled dust samples collected from nearly 1300 home exteriors to reconstruct biogeographical correlates of lichen taxonomic and functional diversity.

Results Contrary to expectations, we found a weak but significant reverse latitudinal gradient in lichen propagule diversity. Diversity was not impacted by urbanization or human population density. We show that propagules of asexually reproducing species have wider geographical ranges than propagules from sexually reproducing species, likely reflecting the lichenized nature of asexual spores that disperse both the mycobiont and photobiont versus non-lichenized sexual spores, which disperse only the mycobiont.

Main Conclusions Our findings of a reverse latitudinal gradient and a relative lack of impact of urbanization on lichen propagules and/or lichen-forming fungal spores suggest that core concepts in biogeography are better informed via consideration of additional patterns from other, less well studied groups of organisms.

Keywords

diversity, fungi, latitudinal diversity gradient, microbial dispersal, symbiotic, trait, urbanization

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INTRODUCTION

Despite conspicuous morphological diversity and well-documented ecological significance, lichens are among the least well understood macroscopic organisms (Lumbsch *et al.*, 2011). For example, despite centuries of lichenology (Acharius, 1803; Tuckerman, 1882), the biogeographical patterns exhibited by lichens remain poorly understood. These patterns have been documented in just a few studies (e.g. Lück-

ing, 1995; Werth, 2011; Leavitt *et al.*, 2012; Lendemer *et al.*, 2014; Holt *et al.*, 2015) and never in the context of the broader literature on the causes and origins of diversity gradients. In contrast, large-scale distributions of many plant and animal taxa have been studied for decades (Pianka, 1966; Tiffney & Niklas, 1990; McCain, 2007), so much so that it is now just the causes of these diversity gradients (e.g. Stomp *et al.*, 2011) rather than their existence and shape that is the subject of debate.

By definition, lichens are composed of two or more unrelated obligate symbionts, with taxonomy based on the fungal partner rather than the algal or cyanobacterial photosynthetic partner. They are unique and important components of diverse terrestrial ecosystems world-wide and contribute to biogeochemical cycling, biomass production, pollutant sequestration, decomposition and soil formation (Cornelissen *et al.*, 2007). They also offer habitat or nutrition sources for many other organisms (Hawksworth, 1991; Szczepaniak & Biziuk, 2003). This functional and ecological diversity contributes prominently to their conspicuous taxonomic diversity and abundance across the globe (Lutzoni & Miadlikowska, 2009).

North America is a global centre of lichen diversity; it is home to nearly a third of all described species (i.e. *c.* 5300 of *c.* 17,000 described species; Esslinger, 2014). Species inventories in North America suggest that lichen biodiversity hotspots are associated with areas of intact native habitat, especially those that contain a diversity of lichen substrates such as hardwoods, conifers and exposed rock (Spribille *et al.*, 2010; Lücking *et al.*, 2011; Tripp & Lendemer, 2012; Lendemer *et al.*, 2013; Lendemer & Allen, 2014). Yet, the more general biogeography and diversity gradients of North American lichens have been the focus of little empirical investigation (but see McCune *et al.*, 1997; Werth, 2011; Holt *et al.*, 2015). On a regional scale, recent study has found no significant link between latitude and lichen diversity, with the latter better explained by other factors linked to longitude such as precipitation and topography (Holt *et al.*, 2015). However, a lack of study on continental or subcontinental scales precludes knowledge of whether lichen biodiversity across larger geographical scales follows the commonly observed latitudinal gradient, with species diversity increasing towards lower latitudes, or which biotic and abiotic factors most strongly impact lichen biogeography at larger scales of enquiry.

Empirical research on biodiversity gradients has focused almost exclusively on individual lineages (Hillebrand, 2004), such as birds, rather than on the varied obligate symbioses that abound in nature (e.g. Fabricius & De'ath, 2008; but see Holt *et al.*, 2015). Because the lichen symbiosis (i.e. the primary mycobiont and photobiont as well as numerous additional symbionts; Rebecchi *et al.*, 2006; Arnold *et al.*, 2009) represents a microcosm of obligate symbionts, these symbioses are well-suited for investigating biogeographical interactions among organisms as well as between organisms and the environment. Moreover, lichens are known to be impacted by local anthropogenic effects (e.g. air quality) such that they are ideal candidates for the simultaneous analysis of large-scale patterns in diversity and the regional effects of human agency (Szczepaniak & Biziuk, 2003). Here, we harness the power of citizen science data from a subcontinental scale sampling (i.e. from the contiguous 48 states that comprise the United States, excluding Alaska and Hawaii) of microbial communities found in the dust on exteriors of homes across the United States to explore abiotic and anthropogenic factors that contribute to lichen biodiversity

gradients. While exterior home surfaces are not typical substrates for mature lichens, they provide an early developmental perspective on lichen spores and spore banks, thus facilitating comparison of where lichen species could potentially occur before local habitat filtering occurs. In other words, these surfaces provide a measure of the pool of lichen reproductive propagules (i.e. sexual and/or asexual spores as well as microscopic reproductive fragments) present at individual locations across the U.S.

Most large-scale biogeographical studies focus on describing gradients in taxonomic diversity (Barberán *et al.*, 2015; but see Beche & Stutzner, 2009). To explore impacts of geography, environment and human development on lichen taxonomic and functional diversity (as in Stuart-Smith *et al.*, 2013), we used this unique sample set to test whether (1) the canonical latitudinal biodiversity gradient is observed in lichens, based on their propagules; (2) whether samples from rural homes have a significantly higher diversity of lichen propagules than samples from urban homes and whether lichen propagule diversity declines as a function of human population density; (3) whether occurrences of specific taxa recovered in dust samples reflect actual extant lichen distributions in the same geographical area; and (4) whether functional traits or sets of traits impact the geographical distributions of lichens.

Given the ubiquity of the canonical latitudinal gradient (e.g. Hillebrand, 2004), we expected to recover a similar gradient in lichens. Likewise, because lichens are particularly sensitive to air pollution, we predicted that urbanization and population density will negatively impact lichen propagule diversity and composition while also influencing what functional groups of lichens inhabit perturbed landscapes. We also expected that asexual lichen species will be overrepresented in urban areas because the establishment of new thalli does not require that the mycobiont encounter a suitable photobiont (and asexual propagules but not sexual propagules already contain both symbiotic partners). We predicted that the geographical distributions of early stages of lichen development, i.e. spores found in dust samples, will closely mirror the geographical ranges of mature organisms given that lichens are sessile organisms. Finally, we expected asexually reproducing species to have smaller geographical ranges than sexually reproducing species because asexual reproductive propagules are physically larger and presumably travel shorter distances (Bailey, 1976; Lendemer *et al.*, 2014) with dispersal ability expected to be positively correlated with range size (Beck & Kitching, 2007).

MATERIALS AND METHODS

Sampling, molecular analyses and sequence processing

The data used in this study derive from a sub-continental scale citizen science project (www.homes.yourwildlife.org). Participants in this project spanned all 48 states in the contiguous United States as well as the District of Columbia

(written informed consent received from all, approved by North Carolina State University's Human Research Committee, Approval #2177). Participants used sterile swabs to sample the upper door trim of the outside surface of an exterior home door, following a standardized protocol available on the Wildlife Homes Project website. Thus, door trim served as a passive collector of dust, which contained reproductive propagules of lichens (i.e. spores or microscopic thalrus fragments) rather than a substrate upon which macroscopic, fully developed lichens were growing.

To genotype fungi, we amplified the first nuclear ribosomal internal transcribed spacer region (ITS1) using fungal-specific polymerase chain reaction primers with amplicons sequenced on an Illumina MiSeq platform. After sequencing and quality-filtering, sequence reads were clustered at the $\geq 97\%$ similarity threshold to assign sequences into phylotypes. Taxonomic classification of the phylotypes was determined using the RDP classifier (Wang *et al.*, 2007) trained on the UNITE database (Abarenkov *et al.*, 2010). After removing samples that contained $< 10,000$ sequences and normalizing sequence counts using a cumulative-sum scaling approach (Paulson *et al.*, 2013), a total of 1289 dust samples were analysed in this study. Full details describing the molecular methods used can be found in Barberán *et al.* (2015). The data associated with this study are accessible at <http://dx.doi.org/10.6084/m9.figshare.1270900>.

Lichen matrices and biogeography

For this project we focused only on those phylotypes representative of lichenized fungi in the phylum Ascomycota (Basidiomycete lichens comprise $< 1\%$ of all lichenized fungi, and none were recovered in our dust samples). The UNITE database classifies sequences to hierarchical levels of taxonomic resolution. Thus, in instances where only higher-level taxonomy was available for a given phylotype (e.g. Lecanoromycetes, without further classification), we conservatively considered only phylotypes in which all members of such groups are known to be lichenized for downstream analyses. We then prepared character matrices describing four lichen traits (and associated character states): (1) mode of reproduction (sexual, asexual, unknown); (2) type of photobiont (coccoid green alga, *Sticococcus*, *Trentepohlia*, cyanobacterium, polymorphic, unknown); (3) growth form (crustose, foliose, fruticose, squamulose, unknown); and (4) substrate [bark (corticolous), soil (terricolous), rock (saxicolous), leaves (foliicolous), decaying wood (lignicolous), multiple substrates (polymorphic), unknown]. The 'unknown' category was used only in instances of unresolved upper level taxonomy such that character states could not be scored. That is, all taxa resolved to species or resolved to genus (the latter when a given trait was fixed among all species in that genus) were scored with some character state other than unknown. Trait scoring was facilitated by a completed trait matrix for all four characters for all 5326 species of lichens

on v.18 of Esslinger's (2014) North American Lichen Checklist (E. Tripp & J. Lendemer, unpublished data). Standard nomenclature for all species cited in this study follows Index Fungorum (www.indexfungorum.org).

To investigate the relationship between known geographical ranges and geographical ranges as predicted by dust samples that contain lichen reproductive propagules, we compared and contrasted distribution maps derived from two types of data. First, we used data from herbarium collections housed at The New York Botanical Garden Herbarium (NYBG) and The University of Colorado Herbarium (COLO) as well as data from the Consortium of North American Lichen Herbaria (CNALH 2015) to construct distribution maps of lichens based on field collections made primarily during the last 100 years, which we here term 'Observed Distribution' (OD). Second, we used the phylotype occurrence data from dust samples, which represent the 'Potential Distribution' (PD) rather than OD, to construct distribution maps of families, genera, and species of lichens. For species PD, we focused on the 19 most abundant named phylotypes, excluding phylotypes that were not identified to species. Our use of the term 'Potential Distribution' (PD) refers to the fact that phylotypes found in dust samples contained reproductive propagules (i.e. sexual and/or asexual spores as well as microscopic reproductive fragments) rather than macroscopic, more fully developed lichens. In other words, PD describes the earliest developmental stages of a lichen, whereas OD describes much later developmental stages that lichen collectors would target during inventory work. Maps from these two types of distributions, i.e. OD and PD, were overlain visually in order to assess the relationship between these two estimates of biodiversity distributions.

Data analyses

Each of the 1289 samples was georeferenced with precise latitude/longitude coordinates to facilitate geographical analyses. Thirteen descriptor variables were compiled for use in predictive analyses: land cover type (forested vs. urbanized landscapes, FOR and URB respectively), mean annual temperature (TEMP), mean annual precipitation (PRECIP), average days of frost per year (FROST), net primary productivity (NPP), vascular plant diversity (VPD), elevation (ELEV), distance to coast (COAST), soil moisture (SM), dust deposition levels (DUST), soil pH (pH), and human population density (POP). Data for these variables were downloaded from the following sources on 5 January 2015: Climatic Research Unit (CRU) at the British Atmospheric Data Centre (<http://badc.nerc.ac.uk/>), NASA Earth Observations (<http://neo.sci.gsfc.nasa.gov/>), NASA Socioeconomic Data and Applications Center (<http://sedac.ciesin.columbia.edu/>), World Soil Information (<http://www.isric.org/>), National Agricultural Statistics Service of the United States Department of Agriculture (<http://www.nass.usda.gov/>), the IUCN Red List (<http://www.iucnredlist.org/>), and Natural Earth (<http://www.naturalearthdata.com/>).

To obtain estimates of community similarity, we only analysed those fungal communities found in samples with at least five different lichenized phylotypes. Community similarity was represented by non-metric multidimensional scaling using the Bray–Curtis dissimilarity distance metric after Hellinger standardization (Legendre & Gallagher, 2001). We tested whether community composition differed between urban versus rural areas using ANOSIM (Clarke, 1993) with samples classified as ‘urban’ coming from areas that are densely developed residential and commercial territories with > 50,000 people, as determined from the 2010 U.S. Census Bureau data (www.census.gov). Multivariate statistical analyses were conducted in using the R 3.1.2 (R Core Team 2014) package ‘vegan’ (Oksanen *et al.*, 2015). Generalized linear models (GLM) with binomial errors (or Poisson errors for richness) were then used to explain the distribution of taxa and traits. Variables were chosen using forward and backward stepwise model selection by the Akaike information criterion (AIC) as implemented in the R function *stepAIC*.

RESULTS

The 1289 dust samples analysed in this study yielded a total of 818 unique lichen-forming fungal phylotypes (402,860 sequences in total). Data demonstrate that species richness of lichens based on propagules in dust samples was highest in portions of the north-western United States and indicated a significant but weak, reverse latitudinal gradient in species richness (Fig. 1; Spearman’s $r = 0.29$, $P < 0.001$; Fig. 1b). The most frequent lichen phylotypes by species, genus and family are shown in Table 1. Asexually reproducing species were particularly overrepresented in the south-eastern United States and, across all samples, have broader geographical ranges than do sexually reproducing species ($P < 0.001$, Mann–Whitney test; Fig. 2b). Asexual taxa were not, however, more abundant than sexual species in urban areas ($P > 0.05$, Mann–Whitney test) or in areas with higher

population density (Spearman’s $r = 0.04$, $P = 0.347$). Lichen photobiont type, growth form and substrate varied substantially across dust samples (Fig. 3). Finally, PD of species were for the most part predicted by their observed distributions (OD), but in several cases PD maps depict only limited portions of a species full range (Table 2).

The 818 phylotypes recovered in this study represent an extremely small proportion (mean = 0.31%) of the total

Table 1 In descending order, most abundant phylotypes (column 1), lichen families with the highest proportional abundance (column 2), and lichen genera with the highest proportional abundances summed across samples (column 3). Phylotypes that were identifiable only to an upper level taxonomy (e.g. ‘unknown Lecanoromycete’) are not shown but comprised four of the 10 most abundant phylotypes in column 1. In columns 2 and 3, heat maps depicting distributions of families and genera across the United States are shown in Figs. S6 & S7 in Appendix S1. Shown in parentheses is the proportion of samples for which a given taxon was detected.

Most abundant phylotypes	Most abundant families	Most abundant genera
<i>Bacidina chlorotricula</i> (0.07)	Parmeliaceae (0.39)	<i>Xanthoria</i> (0.08)
<i>Pertusaria corallina</i> (0.01)	Teloschistaceae (0.24)	<i>Evernia</i> (0.07)
<i>Parmelia</i> sp. (0.14)	Candelariaceae (0.14)	<i>Candelaria</i> (0.05)
<i>Lecanora</i> sp. (0.02)	Physciaceae (0.25)	<i>Usnea</i> (0.07)
<i>Lecanora pruinoso</i> (0.01)	Ramalinaceae (0.15)	<i>Parmelia</i> (0.14)
<i>Hyperphyscia adglutinata</i> (0.03)	Lecanoraceae (0.20)	<i>Caloplaca</i> (0.16)
	Pertusariaceae (0.01)	<i>Candelariella</i> (0.10)
		<i>Lecanora</i> (0.16)
		<i>Physcia</i> (0.15)
		<i>Bacidina</i> (0.11)
		<i>Pertusaria</i> (0.01)

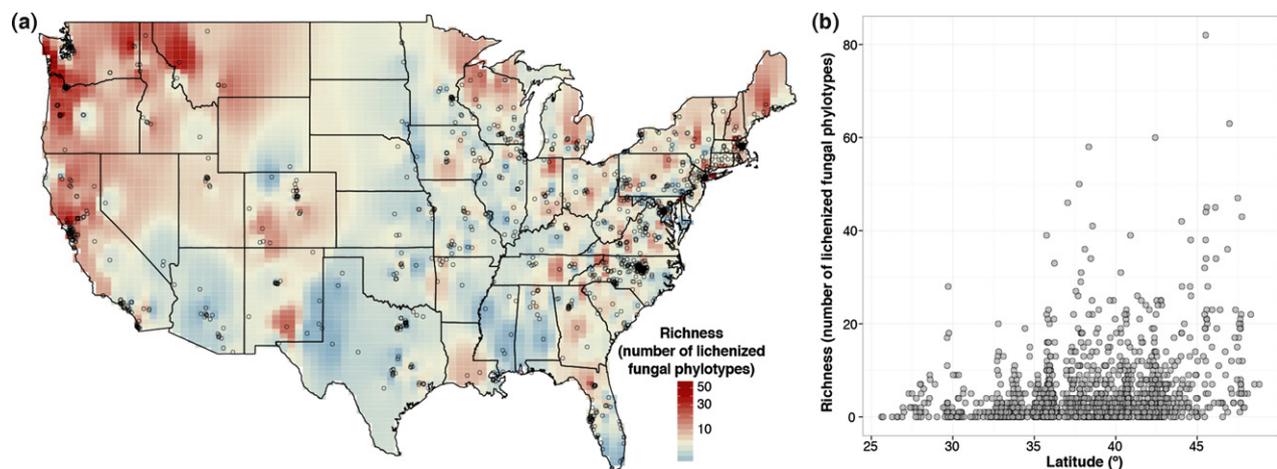


Figure 1 (a) Number of lichenized fungal phylotypes (richness) across subcontinental USA (interpolation using inverse distance weighting on a 100×100 grid cells). (b) Relationship between latitude and number of lichenized fungal phylotypes (richness).

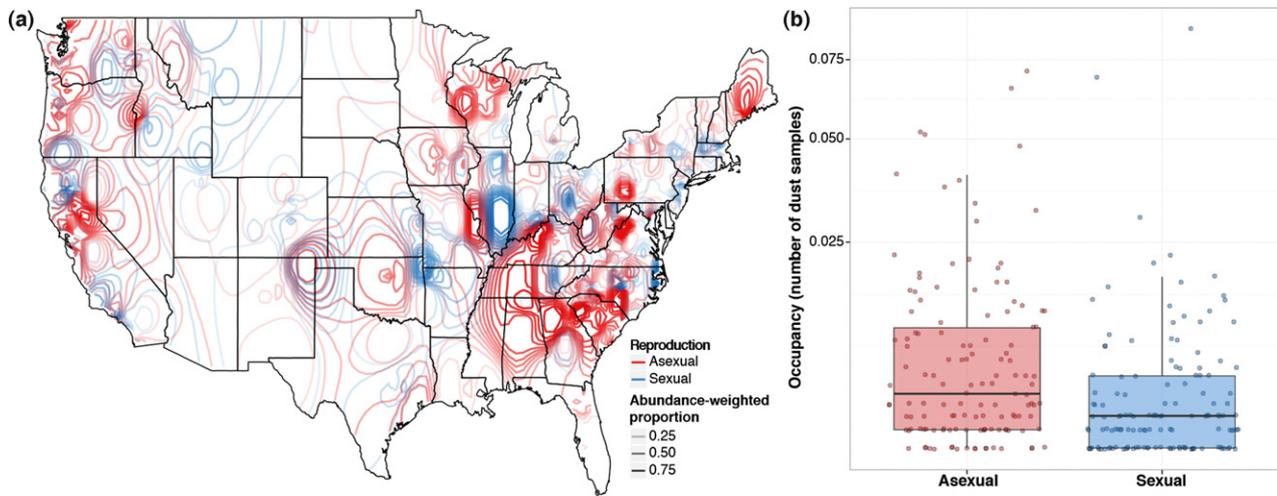


Figure 2 (a) Abundance-weighted proportion of different lichen reproductive traits across subcontinental USA (interpolation using inverse distance weighting on a 100×100 grid cells). (b) Differences in occupancy (number of dust samples where a particular phylotype is present) between lichenized fungi with asexual versus sexual reproduction. Note that the y -axis is squared.

number of fungal phylotypes ($n = 57,224$) recovered in the dust samples, indicating that lichenized fungi are relatively rare in the settled dust that accumulates on home exteriors (see Figs. S1 & S2 in Appendix S1 in Supporting information). Overall, lichen phylotypes were particularly abundant in central Virginia, northern Illinois, north-eastern Ohio, southern Maine, and portions of the Pacific Northwest (see Fig. S3 in Appendix S1). Of the 818 phylotypes, many were identifiable only to higher taxonomic levels (e.g. the class Lecanoromycetes rather than, for example, the species *Lecanora pruinos*). A species accumulation curve suggests that our sampling did not capture total lichen richness achievable via our sampling method (see Fig. S4 in Appendix S1); indeed, the total number of species on the North American checklist is over 5300 (Esslinger, 2014; no checklist is maintained for the United States alone).

Individual samples contained an average of six lichen phylotypes (see Fig. S5 in Appendix S1), but most lichen phylotypes were only found in a small fraction of total sites: only 0.4% of lichen phylotypes were recovered in $> 10\%$ of all samples (see Table 1 for the top phylotypes recovered in all dust samples). Families and genera with the highest proportional abundances are shown in Table 1, and heat maps depicting these distributions can be found in Fig. S6 in Appendix S1 (lichen families) and Fig. S7 in Appendix S1 (lichen genera). Central California, the Pacific Northwest, and western Montana hosted the most diverse lichen communities based on propagules (Fig. 1a). Dust samples collected from locations closer together tended to have more similar lichen propagule communities ($r = 0.45$, $P < 0.001$, Mantel test), with a distance of > 500 km representing the threshold at which propagule communities are no longer more similar to one another than we would expect by chance alone (see Fig. S8 in Appendix S1). These findings indicate a relatively high degree of regional endemism and dispersal

limitation in lichen propagules. Environmental variables that best predicted the geographical variation in lichen character states are shown in Table 3.

We found no significant differences between lichen community diversity ($P > 0.05$, Mann–Whitney test; Fig. S9 in Appendix S1) or community composition (ANOSIM $r = 0.02$, $P = 0.15$; see Fig. S10 in Appendix S1) in airborne dust samples taken from the outsides of urban versus rural homes. Community richness also did not vary as a function of population density (Spearman's $r = 0.04$, $P = 0.347$; see Fig. S11 in Appendix S1). We found a high degree of overlap in where species of lichens have the potential to occur (PD) and where they actually occur (OD) (Table 2 & see Fig. S12; Appendix S1). Finally, lichen functional traits based on dust samples varied substantially geographically (see Fig. S13 in Appendix S1).

DISCUSSION

This study provides a quantitative assessment of how spatial and environmental variables, including human disturbance, shape the abundance and distribution of obligate symbiotic organisms based on reproductive propagules across a large geographical scale: *c.* 4400 km from east–west coast United States and *c.* 2600 km from southernmost Texas to the Canadian border.

Lichens demonstrate a weak reverse latitudinal gradient

One of the most widespread and robust patterns in biogeography is the latitudinal diversity gradient commonly observed for many plant and animal taxa. A comprehensive meta-analysis of the generality of latitudinal gradients assessed nearly 600 taxa (Hillebrand, 2004) and found extensive support for

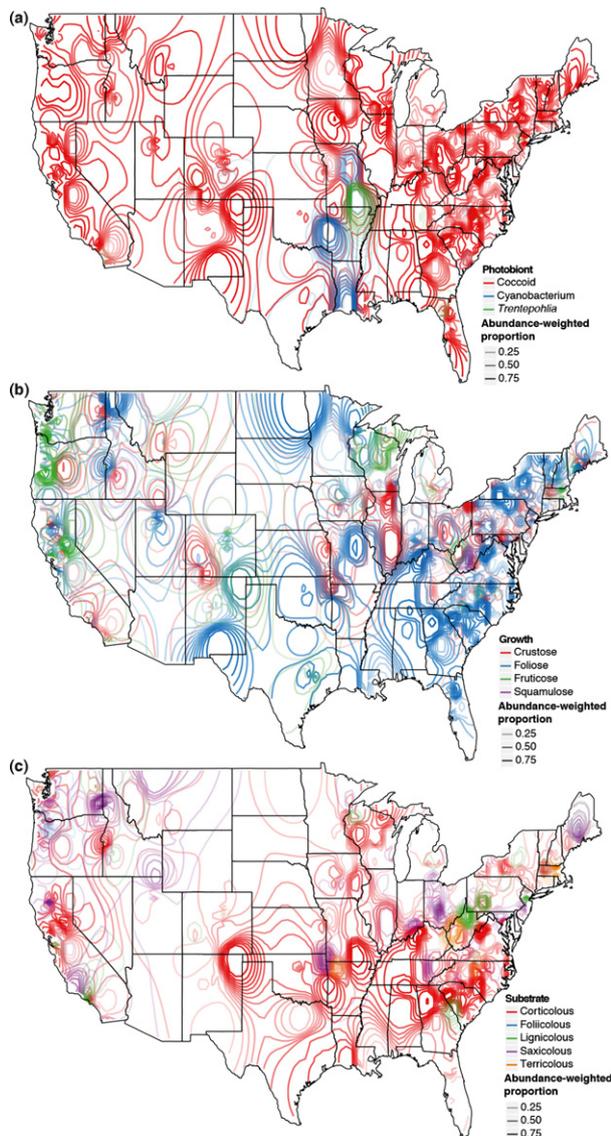


Figure 3 Abundance-weighted proportion of (a) different lichen photobionts, (b) different lichen growth forms, and (c) different lichen substrates across the subcontinental USA (interpolation using inverse distance weighting on a 100×100 grid cells in a through c).

significant increases in taxonomic diversity with decreasing latitudes across different geographical scales, regions, habitat types, groups of organisms, body masses and trophic levels. A much smaller number of taxa including aquatic macrophytes and ichneumonid flies demonstrate exceptions to this pattern, having instead a 'reverse' latitudinal gradient (Hillebrand, 2004). Some microbial and fungal groups similarly do not follow a traditional latitudinal gradient: no correlations were found between soil bacterial diversity and latitude in North and South America (Fierer & Jackson, 2006), a reverse gradient was documented for ectomycorrhizal fungi (Teder-soo *et al.*, 2014), and a recent study in western North America demonstrated no clear relationship between latitude and lichen diversity (Holt *et al.*, 2015). We found evidence

for a reverse gradient in this group of obligate symbiotic organisms as there was a significant, albeit weak, trend towards higher lichen richness based on reproductive propagules at higher latitudes (Fig. 1b).

In our data set, the reverse latitudinal gradient is driven by high community richness recovered in dust samples from northern California, the Pacific Northwest, and northern New England (Fig. 1a). This is not particularly surprising given that species inventory work by previous authors has documented high lichen biodiversity at high latitude sites (e.g. Peterson & McCune, 2003). Perhaps the most striking example of high diversity at northern latitudes is the finding of 766 species in only 53 km² in Klondike National Historical Park, Alaska (Spribille *et al.*, 2010). However, a reverse gradient is at odds with the documentation of rich lichen biotas at southerly latitudes on the subcontinent, such as in Great Smoky Mountains National Park (Tripp & Lendemer, 2012; Lendemer *et al.*, 2013), the southern Appalachians of Virginia (Hodkinson, 2010), the mid-Atlantic coastal plain (Lendemer & Allen, 2014), southern California (Hernandez & Knudsen, 2012), and the greater Sonoran desert (Nash *et al.*, 2004). In our study, the south-western US and south-eastern US both had lower than average community lichen richness recovered in dust samples (Fig. 1a).

It is possible that our finding of a reverse latitudinal gradient derives from a bias in the reference database used (i.e. UNITE) that is missing lichen phylotypes from more southerly latitudes because these taxa have not been sampled and sequenced to the same degree that more northerly species have. Second, amplification bias issues have been documented for fungal communities in prior studies (Lindahl *et al.*, 2013) and may have influenced some of our molecular data. Third, we clustered ITS1 sequences at the 97% similarity threshold, a level of divergence that may not differentiate all lichen species. Alternatively, there may be inherent bias in terms of preservation of lichen propagules in dust samples that covaries with latitude. Finally, this discrepancy might be explained by availability of both partners. Standard taxonomic inventories survey the obligate lichen symbiosis including both the mycobiont and the photobiont, whereas the present investigation of dust samples considered only the mycobiont. Future research that investigates both obligate partners in airborne dust samples may help reveal how the diversity and abundance of one partner potentially limits the distribution of the whole symbiotic organism.

With exception of Holt *et al.* (2015), whose investigation spanned nearly 17° latitude, prior studies of latitudinal gradients in lichens have focused on smaller latitudinal ranges (e.g. the Ross Sea coast of Alaska: no latitudinal gradient found, Colesie *et al.*, 2014; a 2° latitudinal span of southern Europe: reverse gradient driven by climatic variables found, Aragon *et al.*, 2012) or have included only macrolichens (Rapai *et al.*, 2012). In contrast, the present study spans a gradient of 25° latitude, representing the largest north–south span yet considered in a group of obligate symbiotic organ-

Table 2 Congruence or incongruence of taxon distributions based on potential distributions and adult/mature observed distributions (i.e. PD versus OD). Congruence was found for 15 of the 19 most abundant lichen phylotypes. Shown in bold are four incongruences: species for which sexual or asexual spores occur in dust samples (PD) conspicuously outside of the range of the taxon (OD). Only OD occurrences in North America are shown.

Taxon	PD Occurrence	OD Occurrence	PD smaller/ greater than OD
<i>Bacidina chloroticula</i>	North Carolina, Coastal North-western US	Ontario (Great Lakes)	N/A
<i>Bryoria fremontii</i>	North-western US	Western US through boreal Canada to Newfoundland	Smaller
<i>Caloplaca crenulatella</i>	Western US and temperate eastern US	Temperate North America	Smaller
<i>Candelaria pacifica</i>	Maritime western US	Western US	Smaller
<i>Canoparmelia caroliniana</i>	North Carolina	South-eastern US	Smaller
<i>Canoparmelia texana</i>	South-eastern US	South-eastern US	Smaller
<i>Degelia plumbea</i>	Central California	Maritime New England	N/A
<i>Evernia prunastri</i>	Maritime western US	Maritime western North America, maritime north-eastern North America, Great Lakes Region	Smaller
<i>Flavopunctelia flaventior</i>	Central California and Wisconsin	Appalachian-Great Lakes and Greater Sonoran Desert Region	Smaller
<i>Herpothallon rubrocinctum</i>	Florida	South-eastern US	Smaller
<i>Lecanora pruinos</i>	Northern Illinois	Europe	N/A
<i>Melanelixia subaurifera</i>	New England and Coastal North-western US	Boreal North America south in California and Appalachian Mountains	Smaller
<i>Pertusaria corallina</i>	Maine	Europe	N/A
<i>Ramalina farinacea</i>	Maritime western US	Maritime boreal North America and Great Lakes Region	Smaller
<i>Ramalina menziesii</i>	Maritime western US	Maritime western North America	Equal
<i>Ramalina sinensis</i>	New Mexico and Texas	Upper Midwest to south-western US	Smaller
<i>Usnea flavocardia</i>	Maritime western US and Florida	Maritime California, Oregon, and Maine	Smaller
<i>Usnocetraria oakesiana</i>	West Virginia	Eastern North America	Smaller
<i>Xanthoria candelaria</i>	Western US	Boreal and Arctic western North America	Smaller

Table 3 Explanatory power of predictor variables in structuring patterns of lichen richness, type of photobiont, reproductive mode, and substrate. Data are based on generalized linear models (GLMs) with binomial errors (except Poisson errors for richness). Shown in bold are models with moderately high predictive power.

Variable	Predictors	R ²
Richness	FOR+URB+TEMP+PRECIP+FROST+NPP+VPD+ELEV+COAST+SM+pH+POP	0.24
Photobiont coccoid	TEMP+FROST+NPP+DUST+POP	0.16
Photobiont cyano	TEMP+VPD+COAST	0.06
Reproduction asexual	TEMP+FROST+NPP+COAST+DUST	0.19
Growth foliose	FROST+NPP+COAST+POP	0.06
Growth crustose	PRECIP	0.02
Growth fruticose	TEMP+FROST+VPD+ELEV	0.30
Bark substrate	URB+FROST+NPP+ELEV+COAST+DUST	0.23
Rock substrate	FROST+VPD	0.06
Lignum substrate	POP	0.04

isms. Further, it takes into account total lichen richness within dust samples, i.e. including crustose species, which comprise a high proportion of lichen diversity in a given area but are often excluded from analyses owing to challenging identification. In North America, for example, 71% of all lichens (3795 of 5326 species) are crustose [Tripp & Lendemer, unpublished data, based on v.18 of Esslinger's (2014)]. The Holt *et al.* (2015) study emphasized a lichen latitudinal gradient from southern California to northern Washington.

These authors adopted a unique approach that combined vouchered museum specimen data with modelled species distributions, in attempt to overcome biases in collection density regarding the former. In both instances, no linear relationship between lichen diversity and latitude was found. Instead, modelled distributions yielded a 'U-shaped' relationship with variation in richness better explained by longitude, which likely served as a proxy for other environmental factors such as precipitation, topography, suitable habitat and

substrate. Holt *et al.* (2015) concluded that lichen diversity is influenced by local factors such as competition and disturbance – factors that may be less impacting on results from this study owing to our sampling of earlier developmental stages (microscopic propagules). We agree with Holt *et al.* (2015) that factors other than latitude may be driving important patterns of biogeography in lichens and that this subject is ripe for further exploration using data sets across larger spatial scales that incorporate additional dimensions of biogeography and taxon distributions.

Urbanization impacts observed distributions but not potential distributions

The single most important driver of species extinction world-wide is habitat destruction, including fragmentation and other forms of anthropogenic degradation (Pimm & Raven, 2000). The loss of suitable, native habitats is expected to be especially detrimental to obligate symbiotic organisms whose life histories require that all constituent partners are present in sufficient abundance for colonization and subsequent development to occur (Dunn *et al.*, 2009). Indeed, prior studies on observed distributions of lichens have demonstrated negative impacts on diversity and abundance as a function of proximity to urban areas (McCune *et al.*, 1997; Perlmutter, 2010).

Given the well-documented effects of urbanization on lichen distributions, we used data from this study to explore the impacts of human development on lichen PD. Contrary to exceptions, our results demonstrate no significant differences between lichen community richness based on propagules (see Fig. S9 in Appendix S1) or community composition (see Fig. S10 in Appendix S1) in airborne dust samples taken from the outsides of urban versus rural homes. Data also indicate no difference in community richness as a function of population density (see Fig. S11 in Appendix S1), similar to patterns observed for bacteria and non-lichenized fungi (Barberán *et al.*, 2015). Moreover, we failed to find significant associations of particular phylotypes with urban homes or rural homes, suggesting a lack of affinity of specific phylotypes to either urban or rural areas. However, we reiterate that surfaces sampled in this study (sills of exterior doors of homes) are not typical lichen substrates. Second, our study surveyed only lichen mycobionts rather than the full complement of symbiotic partners (namely, the photobiont). It is possible that a study of the impacts of urbanization on both partners would result in different scenarios than that described above. Nonetheless, taken together, these data do not provide evidence that lichen propagule PD is impacted negatively by human development. Thus, at least for the mycobionts, the potential for numerous species of lichens to occur in highly altered landscapes exists based on the presence of reproductive propagules. As such, the observed impacts of urbanization on lichen communities most likely results from filtering during the establishment phase rather than the dispersal process.

As predicted, a comparison of distribution maps based on two different measures of lichen distributions – PD versus OD – demonstrated a high degree of overlap in where species of lichens have the potential to occur (PD) and where they actually occur (OD) (Table 2 & see Fig. S12 in Appendix S1). We surveyed the 19 most abundant lichen phylotypes in our dataset and found that PD/OD congruence was evident for all but four taxa (Table 2 and see below). Despite general congruence, however, PD maps show that numerous lichen species occur in only a small portion of their full range as determined by OD. For example, *Usnoctraria oakesiana* is a common and widespread species in the temperate broadleaf forests across eastern North America, but PD maps generated via our dust sample data indicate that spores from this species were found only in a portion of its total range (West Virginia, primarily; Table 2). This pattern was similarly documented for most other taxa in Table 2 (see Fig. S12 in Appendix S1). We suspect this is driven by the inability of our data to fully capture the total range of mature organisms, in part because of the limited number of samples (*c.* 1300) but additionally because exterior door sills are not normal substrates for mature lichens. Nonetheless, these data do demonstrate the potential utility for using dust samples for lichen distribution surveys, just as dust samples have previously been used to survey airborne bacteria and fungal diversity and distribution (Barberán *et al.*, 2015).

The four taxa for which we found incongruent patterns between PD and OD were *Bacidina chlorotricula*, *Degelia plumbea*, *Lecanora pruinoso* and *Pertusaria corallina* (Table 2). The most likely explanation for these mismatches is that our phylotypes represent taxa not yet included in reference database. Future studies that begin by barcoding an entire lichen biota in which correct taxonomies can be assigned to all species – both mycobiont and photobiont – would facilitate quantitative and comprehensive assessment of congruences or incongruences in diversity estimates based on PD versus OD, including rigorous exploration of potential sources of error (Kress *et al.*, 2009).

Asexual reproduction drives larger range sizes in lichens

Reproduction in lichens is both extraordinarily diverse and complex; even many of the details regarding precise mode of diploidization (i.e. dikaryon formation) and distribution of genetic variability within and among thalli of a given species remains incompletely understood (Nash, 2008). Reproductive propagules in lichens occur in two primary forms: sexual spores (mycobiont only: ascospores) and asexual propagules (mycobiont + photobiont: multicellular, lichenized ‘packages’ such as soredia or isidia). In general, a given species of lichen is considered to be either a ‘sexual species’ or an ‘asexual species’, depending on which mode of reproduction represents the most common mode. Ascospores of sexual species contain only the fungal symbiont and thus require dispersal

to and germination near a suitable photobiont for successful lichen establishment. In contrast, propagules of asexual species contain the full complement of lichen symbionts and thus are fully equipped to germinate and develop immediately into new lichen thalli upon dispersal to new environments.

The dust samples analysed in this study contained an assortment of both types of propagules, with individual samples harbouring on average approximately twice as many asexually reproducing species as sexually reproducing species, indicating a greater overall abundance of asexual phylotypes in our samples. Asexual species were overrepresented in the south-eastern United States, whereas sexual species were overrepresented in the North Carolina coastal plain, southern Illinois and eastern Ozarks (Fig. 2a).

Our *a priori* expectations regarding the relationship of mode of reproduction to lichen biogeography were twofold: first that asexually reproducing species would have smaller geographical ranges in dust owing to the larger physical size of asexual versus sexual propagules (Bailey, 1976; Lendemer *et al.*, 2014), and second that asexually reproducing species would be over-represented in urban landscapes because establishment of new thalli does not require that airborne propagules encounter a suitable symbiotic partner, rather only a suitable habitat (in contrast sexual species require both a suitable partner and a suitable habitat be encountered). Contrary to our first prediction, we found that reproductive propagules from asexually reproducing species have geographical distributions (as assessed by site occupancy) nearly two times larger than sexually reproducing species (Fig. 2b). We suspect that asexual species have larger geographical ranges because of a higher probability of successful dispersal and establishment (even if only temporarily on non-traditional substrates such as door sills) given that the propagules already have both complements of symbiotic partners. It is possible that our finding of larger ranges for asexual species may be skewed by amplification bias (Lindahl *et al.*, 2013) as acknowledged above for latitudinal gradients, and future research that investigates this question from an Observed Distribution (OD) perspective will help to improve understanding of the topic.

Contrary to our second prediction, our data show that asexually reproducing species are not overrepresented in urban landscapes. Although asexuality may be a simpler and more effective approach to reproduction for lichens in highly disturbed or degraded environments (see Howe & Lendemer, 2001), any such advantage is not evident when examining distributional patterns prior to thallus establishment.

Biogeographical patterns in lichen functional traits

In addition to reproductive mode, we focused on three additional traits that reflect primary axes of ecology in these obligate symbionts: photobiont type, growth form and substrate. The distribution of character states per trait varied substantially across dust samples (see Fig. S13 in Appendix S1), as

did the environmental variables that best predicted the geographical variation in those character states (Table 3). However, GLMs had on the whole relatively low explanatory power.

Coccoid green algal photobionts were by far the most common symbiotic partner across lichen communities (see Fig. S13 in Appendix S1), but with no clear geographical hotspots in the United States (Fig. 3a & S13 in Appendix S1). In contrast, lichens with a *Trentepohlia* or cyanobacterial photobiont were concentrated in portions of the Ozark Mountains. Although lichens with cyanobacterial photobionts are known to be sensitive to air pollution and disruption of native habitats (Seaward & Letrouit-Galinou, 1991), reproductive propagules from cyanolichens were no less diverse in urban areas or regions with higher population densities as we predicted ($P > 0.05$, Mann–Whitney test). One explanation for this result might be that our study included only mycobiont phylotypes rather than mycobiont plus photobiont phylotypes such that research that included photobiont phylotypes would demonstrate negative impacts of pollution and habitat disruption on cyanolichens.

The proportion of lichens reproductive propagules from particular growth forms varied geographically (Fig. 3b,c). In our samples, foliose followed by crustose lichens were the most common growth forms (see Fig. S13 in Appendix S1). The most commonly inhabited substrate among North American lichens is tree bark (see Fig. S13 in Appendix S1; Tripp & Lendemer, unpublished data), and species occupying this substrate were especially abundant in the south-eastern US and in maritime regions of the western US, regions with extensive forest cover. Propagules from rock-dwelling species were particularly abundant in western North America where exposed rock is far more abundant than in much of eastern North America. Soil-dwelling lichens were abundant in the Ozarks and portions of the central Appalachians, whereas lignum-dwelling lichens were abundant in scattered areas throughout the country. Finally, leaf-dwelling species were rare in our samples but found primarily in the Pacific Northwest (Fig. 3c).

CONCLUSIONS

We demonstrate the presence of a weak, but significant reverse latitudinal gradient in lichen reproductive propagule richness across a very large spatial scale. We have additionally shown general congruence between extant biodiversity distributions and potential distributions by DNA sequencing-based analyses of lichen propagules in settled dust. This study adds to a large body of literature on how taxonomic diversity is distributed across space, but contributes a less-investigated dimension by exploring trait-based correlates of distributions. We found that propagules of asexually reproducing lichens have larger geographical ranges than propagules of sexual species but the former were no more abundant in urban areas than the latter. Finally, we show that spatial distributions of lichens with different growth forms and

affinities to different substrates largely parallel expectations based on known environmental variation throughout the United States. Future research that focuses on a specific geographical area, expands data collection on distributions of functional traits, and adds biotic axes such as photobiont sampling would permit fuller exploration of the tripartite interactions between organism, abiotic environment, and biotic environment. Additionally, future studies that further explore questions of lichen biogeography may benefit from field sampling strategies that may more effectively capture lichen diversity at a given site, for example sampling more traditional substrates such as bark, rock, and soil. At present, lichen biodiversity in North America is still incompletely documented, yet suitable habitat for these organisms is imperilled by diverse factors such as habitat destruction, sea level rise, increased risk of fire, and air pollution. Thus, immediate action to understand correlates of symbiotic biodiversity in a rigorous, comprehensive manner is imperative.

ACKNOWLEDGEMENTS

We thank the volunteers who participated in the Wild Life of Our Homes project for collecting dust samples and Holly Menninger for coordinating samples and engagement with participants. We also thank Jessica Henley, Jon Leff and other members of the Fierer lab for their help with sample processing and analyses. We are grateful for the time and suggestions of three anonymous referees and Mark Carine who provided helpful feedback on an earlier version of this manuscript. Funding for this work was provided by a grant from the A. P. Sloan Microbiology of the Built Environment Program (to N.F. and R.D.), with additional support from the US National Science Foundation (DEB1432629 & 1542639 to E.T. and J.L., DEB0953331 to N.F., DEB0953331 to N.F., DEB0953390 to R.D., DEB114551 to J.L., DEB1542639 to J.L., DEB1354963 to E.T., and DEB1542629 to E.T.) as well as a James S. McDonnell Postdoctoral Fellowship to A.B.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Online supporting figures.

DATA ACCESSIBILITY

OTU tables with taxonomic information, fasta files with representative sequences for each OTU, a metadata file and

mapping file are available for download at <http://dx.doi.org/10.6084/m9.figshare.1270900>.

BIOSKETCH

This manuscript was co-authored by five individuals with diverse research interests and experiences in the field of biogeography. Two of us (ET and JL) have emphasized the study of biogeographical histories from both vascular plants and lichens, drawing evidence from tropical and temperate latitudes, in our respective careers. The three latter authors (AB, RD and NF) have worked primarily at the microbial level to document and describe patterns and important ecological correlates of fungal and bacterial biodiversity across the planet. Thus, the present investigation represents a unique collaboration made possible by the combined expertise of our research team.

Author contributions: E.T. conceived the study, prepared lichen and trait matrices, and drafted the manuscript; J.L. conceived the study and prepared lichen and trait matrices; A.B. conducted statistical analyses and prepared the graphics; R.D. conceived the study, coordinated the research and coordinated participant engagement and sample collection; N.F. conceived the study, helped draft the manuscript, and coordinated the research.

Editor: Mark Carine