RESEARCH ARTICLE

Most lichens are rare, and degree of rarity is mediated by lichen traits and biotic partners

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Abstract

Aim: Understanding ecological distributions of global biodiversity is stymied by incomplete knowledge of drivers of species rarity. These include trade-offs among life-history traits that impact dispersability, competition, reproductive output and speciation and extinction. In this study, we aim to understand potential drivers of rarity in North American lichens.

Location and methods: With nearly 5500 species and a third of global species richness, North America is a hotspot for lichen biodiversity. Here, we employ a continental-scale dataset on North American lichens to test potential drivers of species rarity. For all species, we determined coarse-scale geographical distribution along with the mode of reproduction, substrate, growth form and photobiont type.

Results: Our analyses found that most lichens are rare and known only from one or two ecoregions. Rare species are not equally distributed across ecoregions: the Eastern temperate hardwood forests and wet tropical forests of southern Florida harbour the vast majority of rare species. Wet to seasonally wet ecoregions of western North America are home to most remaining narrowly distributed lichen species. In contrast, northern ecoregions along with drier ecoregions including the Great Plains and deserts harbour primarily widespread species. Lichen rarity is significantly associated with species that live on bark or leaves, those with a *Trentepohlia* photobiont, those that are small, crustose and live closely appressed to their substrates, and those that reproduce sexually, dispersing only the mycobiont. North American lichens are represented unevenly across trait categories, with 65% of them having a crustose growth form, 73% bearing a *Trebouxia* or other green algal photobiont, 78% living on bark or rock and 77% reproducing sexually.

Main conclusions: Our study, spanning an entire continental-scale biota, helps to establish a generalized relationship among life-history traits and rarity in lichens and highlights the significance of biotic interactions in structuring biogeographical distributions.

KEYWORDS
biotic, correlate, distribution, driver, geographical range size, lichen, rarity, symbiosis

1 | INTRODUCTION

Among the most pressing challenges in global biodiversity research are discerning drivers of species rarity. Rarity, usually defined by local abundance, ecological range size, habitat specificity or some combination thereof (Espland & Emam, 2011; Rabinowitz, 1981), is critically linked to species' conservation and threatened status (e.g. IUCN Red list). Herein we are concerned with the rarity of lichens, a hyperdiverse set of indicator species, which are rarely assessed for geographical patterns, but for which range size estimates are feasible for many species at a coarse scale. Studies examining traits leading to variation in rarity, particularly for plant and animal range sizes, have detected the importance of growth form, habitat type, dispersal capacity and reproductive mode (Birand et al., 2012; Espland & Emam, 2011; Trakimas et al., 2016). These traits also influence patterns of coexistence and persistence, and speciation and extinction. There are, however, numerous trade-offs among traits that impact range size such as those pertaining to competitive ability, resource specialization, reproductive propagule size and dispersal capacity (Birand et al., 2012; Moor, 2017; Sonkoly et al., 2017; Tripp et al., 2016). Trade-offs in plants are particularly well-studied and are both diverse and complex (Angert et al., 2011; Moor, 2017; Sonkoly et al., 2017). Species with high dispersal capacity are, for example, frequently poor competitors (Bin et al., 2019; Jakobbson & Erikkson, 2003). Plants with small seeds are likely to have large geographical ranges (Skarpaas et al., 2011; Sonkoly et al., 2017) but suffer more from herbivory and reduced germination compared with large-seeded species (Turnbull et al., 2004). However, plants with reproductive propagules of extreme sizes can be either broad-ranging or narrow-ranging, and there remains uncertainty regarding emergent properties of range size, rarity and life-history traits (Allred, 1998).

Trade-offs in growth form, habitat, dispersal capacity, reproductive mode and other features (e.g. habitat type) manifest at macroevolutionary scales, such as impacts on lineage diversification (Cardillo et al., 2003). For example, larger range sizes may lead to increased speciation rates as a function of increased opportunities to encounter novel habitats and isolating barriers (Gaston, 2003; Rosenweig, 1995). Indeed, there is evidence for a positive relationship between range size and lineage richness, and a negative relationship between lineage richness and rarity (Linder, 2019). However, a generalized relationship among life-history traits, range size and species richness has yet to be established, and determinants of rarity remain further contested across axes of space, time and evolutionary relatedness (Angert et al., 2011; Brown et al., 1996; Grünig et al., 2017; Kreft & Jetz, 2007; Kunin, 1998; Lester et al., 2007; Linder, 2019; Rahbek, 2005; Sheth et al., 2020). Most prior research has targeted macroscopic plants and animals in understanding rarity (Brown et al., 1995; Harcourt, 2006; Kreft & Jetz, 2007; Moreuta-Holme et al., 2013; Trakimas et al., 2016).

Lichens are unique, obligate symbiotic organisms that are evolutionarily ancient but ecologically diverse and highly successful (Galloway, 1992; Honegger, 2012; Lutzoni et al., 2018; Sipman & Aptroot, 2001). Lichen symbioses are microcosms of unrelated organisms but consist of one primary fungal symbiont that typically associates with one or more photosynthetic partners, in addition to other fungi, algae and bacteria (Honegger, 2012). Among several distinctive attributes of the lichen symbiosis are numerous different types of dispersal propagules, which arise via either sexual or asexual reproduction (Tripp, 2016; Tripp & Lendemer, 2017). Sexual reproduction gives rise to propagules that disperse only the fungus and are typically smaller in size compared with propagules that arise from asexual reproduction, which co-disperse both the fungal and algal (and other) symbiotic partners and are for the most part substantially larger in size (e.g. sexual species: Tripp & Lendemer, 2020; Walser et al., 2001 vs. asexual species: Cernajová & Skaloud, 2020; Kon & Ohmura, 2010; Kristinsson, 1971; Scheidegger, 1995; Walser et al., 2001). Thus, there exists a theoretical trade-off between the benefits of sexual reproduction, for example, recombination and introduction of new genetic variation, versus mobility, establishment and range size: smaller propagules presumably travel further distances but require sex whereas larger propagules should be dispersal-limited but have higher potential for establishment (Tripp et al., 2016). Prior studies have found that asexual species have larger geographical ranges (Allen & Lendemer, 2016; Tripp et al., 2016); however, a comprehensive understanding of the relationship between reproductive mode, rarity and species richness has yet to emerge.

Lichens vary in numerous other life-history features, including substrate for establishment and growth, growth form and photobiont type. Lichens grow on myriad, inert substrates, for example, on the bark of living trees, decaying wood (i.e. lignum, not associated with living trees), rock, soil and leaves. Most species predominantly grow on one type of substrate or subdivisions therein (e.g. calcareous rock, conifer bark, hardwood bark or acidic soils; Brodo et al., 2001; Tripp & Lendemer, 2020). If a substrate is rarer geographically, then those species may be rarer or more narrowly distributed. Similarly, lichens display several growth forms, from macrolichens with leaf-like structures to microlichens with a crust-like, flattened appearance. Growth forms may be linked to range size rarity because lichens do not establish root systems and different growth forms may be variously efficient at accumulating nutrients from the air and water across space and time. Similarly, lichens have symbiotic relationships with photosynthetic partners, varying from cyanobacteria to unicellular green algae (Honegger, 2012). Conceivably, lichens that partner with rarer photosynthetic partners may be, overall, rarer across the landscape. Because of the specificity in substrate use, growth forms and photobionts, we hypothesize that these traits will substantially impact lichen distributions and rarity.

With nearly 5500 species and upwards of a third of global species richness, North America is a hotspot for lichen biodiversity. These species display the full range of variation in reproductive and dispersal strategies, growth forms, substrates, photobiont types and rarity (or commonality) present across global diversity (Brodo et al., 2001; Esslinger, 2012, ongoing). Here, we employ a subcontinental-scale dataset on North American lichens to shed new light on correlates of rarity. We analyse North American lichens in the context of ecoregion-based distributional information as a basis of estimates of rarity, species-levels traits for reproductive mode, substrate, growth form and photobiont type. We use these data to

define the relationships between traits and biogeographical range size, rarity and species richness in an often overlooked group of organisms. This study, spanning a continental-scale biota, reveals emergent correlates of rarity in lichens that are markedly different from patterns in many plant and animal groups. It furthermore highlights the significance of biotic interactions, specifically symbiotic partners, in helping structure biogeographical distribution patterns.

2 | MATERIALS AND METHODS

Rarity has most typically been measured as a function of range size, abundance and/or habitat specificity (Rabinowitz, 1981). We here approach the study of rarity in lichens through quantitative assessments of coarse range size and habitat specificity. Specifically, we first built a matrix of all North American lichens (north of Mexico; hereafter, North America) using version 18 (Esslinger, 2012) of the widely accepted and standardized *North American Lichen Checklist* (current version 23, Esslinger, 2019). This list included 5326 taxa in 663 genera. We culled this list to 4583 taxa (501 genera) that we recognize as valid and which are both lichenized with a photobiont and nonlichenicolous (i.e. parasitic and nonlichenized allied fungi were excluded from the dataset).

We then scored geographical distributions for these 4583 species based on the Environmental Protection Agency's Level I Ecoregions (Figure 1). This classification spans 15 ecological regions including the (1) Arctic Cordillera, (2) Tundra, (3) Taiga, (4) Hudson Plains, (5) Northern Forests, (6) Northwestern Forested Mountains, (7) Marine West Coast Forests, (8) Eastern Temperate Forests, (9) Great Plains, (10) North American Deserts, (11) Mediterranean California, (12) Southern Semi-Arid Highlands, (13) Temperate Sierras, (14) Tropical

Dry Forests and (15) Tropical Wet Forests. All ecoregions were present in our study except region 14 (Tropical Dry Forests, present only in Mexico), which was excluded from subsequent analysis. Using primary species descriptions, monographs, taxonomic revisions, other primary literature and information from herbarium databases (e.g. The New York Botanical Garden's C.V. Starr Virtual Herbarium; The Consortium of North American Lichen Herbaria), we scored all 4583 species as being either absent or present in each ecoregion. For 516 species, we were unable to determine geographical distributions with confidence, and these were excluded from further analyses. For an index of lichen range size, we calculated the number of ecoregions) within which a species has been detected, ranging from a single ecoregion to 14 ecoregions. We recognize this is a coarse resolution for geographical range size, and hence rarity, but such a scale is warranted for a hyperdiverse lineage that has not been as extensively collected (i.e. vouchered for museum purposes) and whose voucher identifications are not as well-verified as have been many other organisms, particularly plants and animals (Allen et al., 2019). Moreover, a coarse geographical scale nonetheless facilitates our objective of understanding rarity across a large spatial extent (e.g. Enquist et al., 2019; Kreft & Jetz, 2007; Trakimas et al., 2016).

To examine whether lichen traits are associated with different range sizes, we assessed each species for growth form, photobiont type, primary substrate type and primary reproductive mode. These represent the most salient and measurable morphological traits of lichens and reflect lichen features aligning with their myriad functions in ecosystems. Growth forms were grouped into crustose (i.e. lichens that grow in tight association with their substrate and cannot be peeled away from it), foliose (i.e. large, leaf-like lichens), fruticose (i.e. large, bushy lichens) and squamulose (i.e. lichens intermediate between crustose and foliose growth
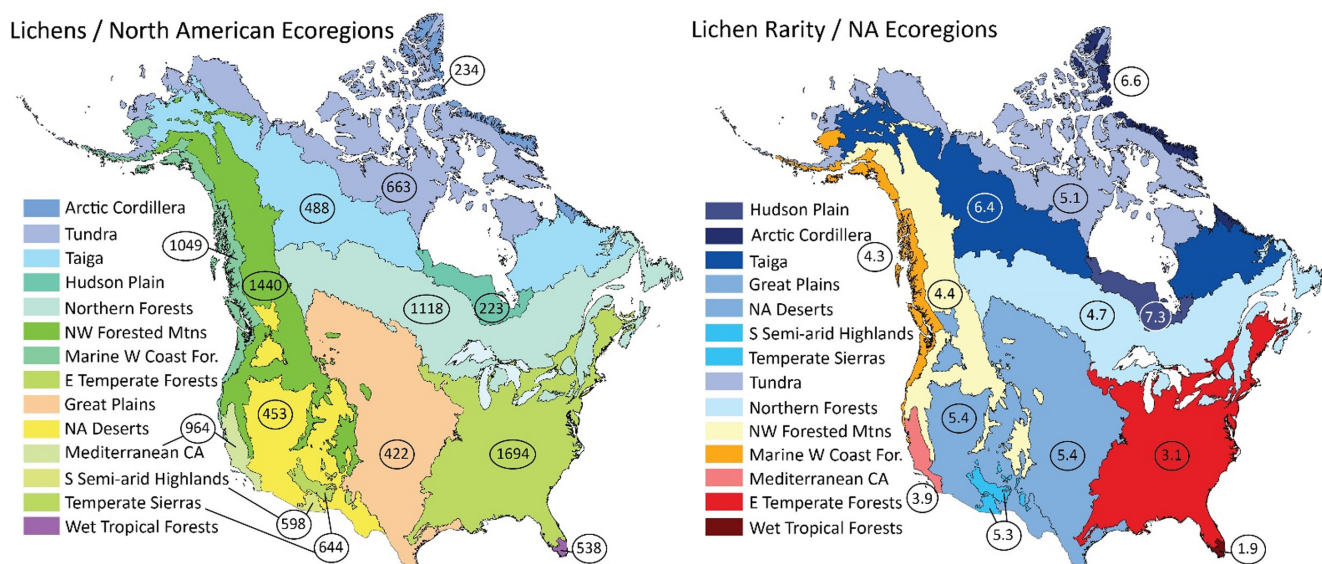
FIGURE 1 Maps of the North American Ecoregions with (a) the total numbers of species of lichens from our analysed dataset known from each ecoregion, and (b) an estimate of species' rarity in each Ecoregion calculated as an average number of ecoregions within which those species were detected. For example, in the wet tropical forests (i.e. southern-most Florida), a rarity value of 1.9 indicates most species from that habitat are found in only 1 or 2 ecoregions

forms). Photobiont types included *Trebouxia*/coccoid green alga, *Stichococcus*, *Trentepohlia*, cyanobacteria, other and polymorphic (i.e. lichens with more than one photobiont or species that can make use of different types of photobionts). Primary substrate types included bark (corticolous), soil (terricolous), rock (saxicolous), moss (muscicolous including species that 'grow over lichens' but are clearly not lichenicolous, i.e. growing on lichens), leaves (foliicolous), wood (lignicolous) and polymorphic (i.e. species that grow on multiple substrates). Primary reproductive mode included predominantly sexual reproduction (i.e. propagation through fungal-only spores derived from meiosis) or asexual reproduction (i.e. propagation through specialized diaspores derived from mitosis). Sexual vs. asexual reproduction is also an indication of dispersal: dispersal of sexual propagules represents only the fungal partner vs. dispersal of asexual propagules (e.g. soredia, isidia, phyllidia, schizidia) contain both fungal and algal cells, and oftentimes other symbionts such as bacteria. An additional 16 species were excluded from further analysis owing to uncertain primary reproductive mode. This yielded a final matrix of 4051 species (486 genera). Rare traits (e.g. <10 species) or unknown traits were left as blanks in the database (Appendices S1 and S2).

We do not examine abiotic factors in these analyses due to the coarse scale of the ecoregions, which most have large latitudinal and longitudinal spans encompassing large variability in temperature, precipitation, productivity and topography, for example. Thus, at this scale, averages are not informative for the entire ecoregion nor in comparisons among ecoregions and only serve to highlight the smallest ecoregions (e.g. wet tropical forests). The effects of climatic and topographical variation are much more robustly examined at smaller spatial scales where the lichen distributional sampling and variation in abiotic factors are more congruent.

2.1 | Statistical analyses

The range size-dependent variable was an ordinal index ranging from 1 to 13 (no species were known from all 14 ecoregions), while the independent variables (growth form, photobiont, substrate and reproduction) were all categorical variables. Thus, Chi-square contingency tables were used to individually assess whether individual traits were more associated with range size than expected by chance. These analyses explore the potential importance and visualize the distribution of each trait. For sufficient sample sizes in Chi-square analyses, we used four levels of range size: rare (1–2 ecoregions); regional (3–5 ecoregions); widespread (6–8 ecoregions); sub-continental (≥9 ecoregions; i.e. including all ecoregions north of the United States-Mexican border). These varied in sample sizes based on the number of species with known values for a particular trait ($n = 3895–4049$). To statistically and robustly detect the best set of trait predictors for lichen range size, given potential collinearity, we used an ordinal logistic regression with all 13 range size categories and the four trait variables. This analysis only included lichen species with complete trait data ($n = 3899$). Lastly, because of the variability in geographic extent among the ecoregions, we assessed whether lichen diversity and lichen rarity

were simply due to variation in ecoregion area (e.g. rare ecoregions are inherently producing rare lichens due to lower overall species richness). To assess the ecoregion area, we clipped the ecoregions shapefiles to the US and Canada (https://www.epa.gov/eco-research/ecoregions-north-america), then calculated the area within each ecoregion using ArcGIS. Then we ran linear regressions of diversity with area (km^2) and by rarity with area (km^2). We additionally repeated these analyses removing the smallest ecoregion (wet tropical forests) from consideration. All analyses were conducted using JMP 14.1.

3 | RESULTS

Most North American lichens are rare: 44% are known from a single ecoregion and 21% known from only two ecoregions, while 23% are detected in 3–5 ecoregions, 9% are widespread (6–8 ecoregions) and only 3% are subcontinental (≥9 ecoregions; Appendices S1 and S2). Rare species are not equally distributed among ecoregions (Figures 1b, 2), as wetter forests of western North America (e.g. Northwestern Forested Mountains, Marine West Coast Forests), Mediterranean California, Eastern Temperate Forests and Tropical Wet Forests contain the vast majority of rare species (76%; green bars in Figure 2). Eastern Temperate Forests harbour most rare species whereas Tropical Wet Forests contain the highest proportion of species. Some ecoregions contain almost entirely widespread and sub-continental species (e.g. Arctic Cordillera, Taiga), while the majority of ecoregions have a variety of rare and widespread species (black line in Figures 1b and 2). The distribution of the total number of lichen species and number of rare species (1–2 species or 1 species/ecoregion) are unrelated to the area of each ecoregion ($r^2 = 0.1029$, $p = .2486$; $r^2 = 0.0243$, $p = .5945$; $r^2 = 0.0059$, $p = .7946$, respectively).

Traits of North American lichens are represented unevenly across categories, with 65% having a crustose growth form, 73% bearing a *Trebouxia* or other coccoid green algal photobiont, 78% living on bark or rock (46% and 32%, respectively) and 77% reproducing sexually. Because so many lichens are rare, there is not a strong tendency for rare species to hold a select set of traits. Nonetheless, certain traits are more commonly linked to rarity than expected by chance. Chi-square contingency tests detected that all four traits were significantly related to range size in North American lichens: growth form ($\chi^2 = 177.7$; $n = 4049$; $p < .0001$); photobiont ($\chi^2 = 328.9$; $n = 3895$; $p < .0001$), substrate ($\chi^2 = 291.7$; $n = 3988$; $p < .0001$) and reproductive mode ($\chi^2 = 34.7$; $n = 3959$; $p < .0001$). The character states strongly and positively associated with rarity (species only present in one or two ecoregions) included a crustose growth form (Figure 3a), a *Trentepohlia* photobiont (Figure 3b), living on leaves or bark (Figure 3c) and sexually reproducing species (Figure 3d; Appendices S1 and S2).

The ordinal logistic regression using all four traits to gauge how strongly each trait was related to range size variation given potential correlations among variables was significant (whole model likelihood ratio chi-square statistic = 430.0, df = 15, $p < .0001$, $n = 3899$). However, only substrate, photobiont and growth form were significant individually in the model based on effect
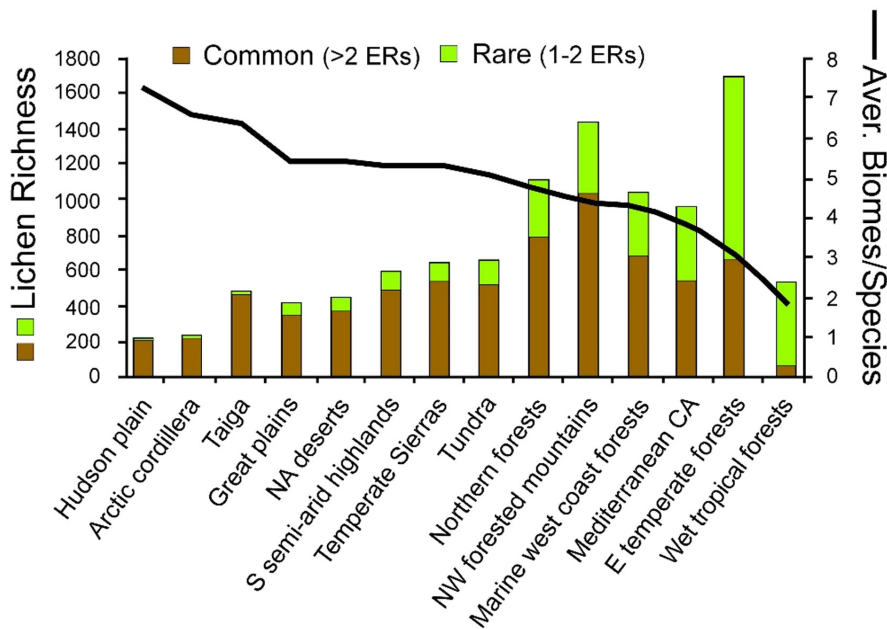
FIGURE 2 The number of lichen species known for each ecoregion (bar height) contrasted against the number of common species (brown: 3–13 ecoregions) and geographically rare species (green: only detected in 1–2 ecoregions). Plot is arranged from ecoregions most dominated by common species (left) to those dominated by rarest species (right). The average number of ecoregions occupied by species per ecoregion is shown with the black line (see Figure 1b for numerical values)
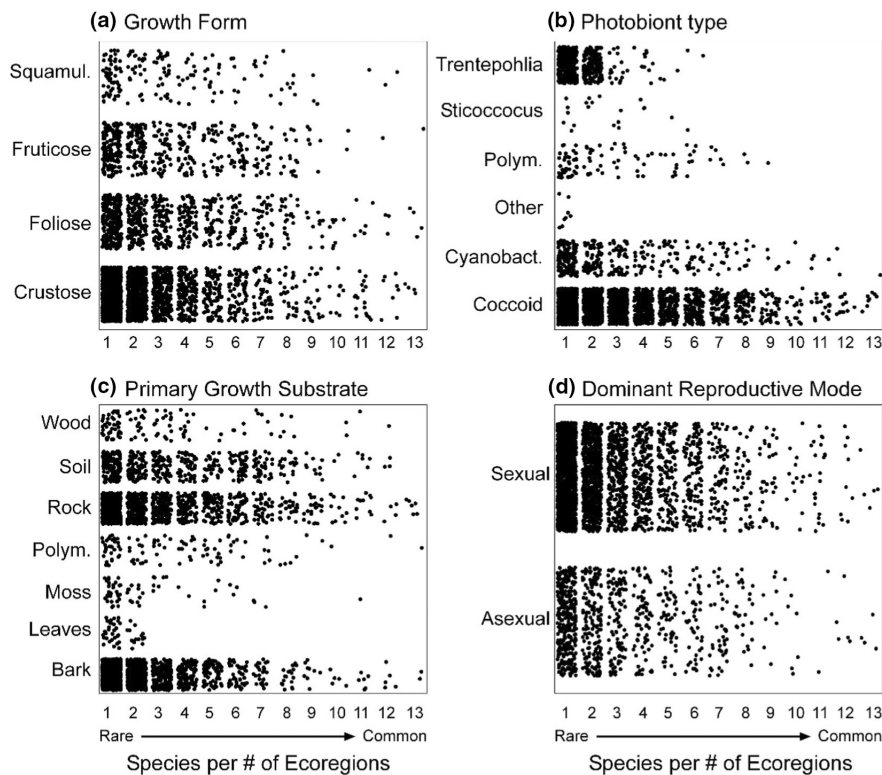
FIGURE 3 The distribution of lichen species' geographical rarity across four trait categories: (a) growth form, (b) photobiont, (c) primary growth substrate and (d) dominant reproductive mode. The rarity axis is the total number of lichen species falling within summed number of ecoregions across North America. This axis ranges from a single ecoregion (rare, on left) to 13 of the 14 ecoregions (common, on right). No species was found in all 14 ecoregions. Each dot per panel is a species, and all panels include 4051 species in our analyses. Abbreviated traits: squamul. = squamulose; polym. = polymorphic; cyanobact. = cyanobacteria; coccid = green coccid alga/*Trebouxia*

likelihood ratio tests (substrate: $X^2 = 107.85$, df = 6, $p < .0001$; photobiont: $X^2 = 99.55$, df = 5, $p < .0001$; and growth form: $X^2 = 43.40$, df = 3, $p < .0001$). Reproductive mode, and hence dispersal capability, was nonsignificant in the multivariate model (effect likelihood ratio test: $X^2 = 0.86$, df = 1, $p = .3545$) most likely due to the strong association of species with *Trentepohlia* photobionts and sexual reproduction (90%) and species with crustose growth forms and sexual reproduction (90%). Results remained consistent after removal of the smallest ecoregion (wet tropical forests) from analyses (Appendix S3).

4 | DISCUSSION

The remarkably varied landscapes that characterize North America are home to approximately one-third of all known lichen species on Earth. Yet, despite this storied biodiversity spanning some 6.6 million square miles, we lack an understanding of ecological and evolutionary correlates of range size and rarity of lichens (Enquist et al., 2019). We have shown that nearly half of North American lichens are rare in that they are restricted to a single ecoregion. Using a subcontinental-scale dataset, we found that Eastern

Temperate Forests and Tropical Wet Forests (i.e. southern Florida) harbour the highest numbers and highest percentages of rare species, respectively. Together these two regions are home to 76% of rare North American lichens. Wet to seasonally wet ecoregions of western North America (i.e. Northwestern Forested Mountains, Northern Forests, Marine West Coast Forest and Mediterranean California) are home to most remaining narrowly distributed species. In contrast, the Great Plains, North American deserts and northern ecoregions (e.g. Hudson Plain, Arctic Cordillera and the Taiga) harbour mostly widespread to sub-continental species. Thus, although not an explicit focus of this manuscript, wetter habitats and coastal areas contain disproportionately more rare species than do drier habitats and habitats at more northern latitudes (cf. Grünig et al., 2017; Kreft & Jetz, 2007). As such, future studies may wish to explore an explicit emphasis on the relationship between annual precipitation and degree of rarity (see Ohlemüller et al., 2008 for the presentation of nuanced relationships between the two). Because some of the areas that harbour high numbers or percentages of rare lichen species reflect regions of high human population density (e.g. Wet Tropical Florida and portions of Mediterranean California), it is possible that biases in collection effort have impacted our results to some degree. However, the prior century of lichen field campaigns across North America has yielded a detailed inventory of numerous portions of the continent, these well-beyond hotspots of human population density. These include in particular: the Sonoran Desert, the Pacific Northwestern mountainous region, portions of the Great Plains, the Ozark Mountains, the southern Appalachian Mountains and Gulf and Atlantic Coastal Plains, the Great Lakes region and central-southern Canada. As such, biases in collection efforts are unlikely to have factored substantively in our analyses and results.

Our study explicitly tested for associations between biogeographical range size and salient morphological and ecological features of lichens. Importantly, these features including substrate, growth form, reproductive mode and photobiont type capture much of the functional diversity of lichens worldwide. Although there is not a strong tendency for rare species to hold a select set of traits given so many lichens are rare, we nonetheless found that rarity was significantly associated with (1) lichens that live on bark or leaves, (2) lichens with a *Trentepohlia* photobiont (i.e. green algae containing carotenoids), (3) small, crustose lichens that live very closely appressed to their substrates and (4) lichens that reproduce sexually, dispersing only the mycobiont. We acknowledge that there are numerous other lenses through which the study of rarity can be explored, including environmental covariates, historical factors such as survival in refugia, evolutionary explanations such as lineage-driven range size variation and intrinsic factors such as degree of specialization (Karron, 1987; Ohlemüller et al., 2008; Raven & Axelrod, 1978; Stebbins & Major, 1965). Nonetheless, to our knowledge, this is the first exploration of trait-based correlates and potential drivers of distributions and rarity in lichens, including biotic features, that span nearly an entire continent.

4.1 | Lichen substrates influence patterns of rarity

Two substrates—the bark and leaves of trees—are highly correlated with small-ranging species of lichens in our dataset. Corticolous or bark-dwelling lichens in particular comprise 42% of the total North American lichen biota. Foliicolous or leaf-dwelling species (1% of NA lichens), which are common in tropical regions, are restricted primarily to the wet tropics of southern Florida and, to a lesser extent, Eastern Temperate Forests. Thus, it is to be expected that lichens restricted to an already rare ecoregion type in North America are themselves rare. In contrast, bark-dwelling species occur instead across the entirety of tree-covered portions of North America. Across this continental scale, however, trees and shrubs oftentimes have limited biogeographical distributions, and the temperate hardwood forests of the East are additionally home to the greatest diversity of trees in North America. Although direct one-to-one associations between lichen species and host trees are rare (but see Tripp & Lendemer, 2020), many studies have documented affinity between lichen species and host tree species or life stages (Adams & Risser, 1971; Hale, 1955; Hamada et al., 1995; Hinteregger, 1994; Wigle et al., 2021) although this is not uniformly the truth (McDonald et al., 2017; Rosabal et al., 2013; Urbanavichus et al., 2020). We therefore hypothesize that rarity of bark-dwelling lichens emerges as a result of tree diversity, tree range size and host affinity of bark-dwelling lichens in North America. Taken together, the distributions of habitable substrates and some degree of specialization of lichens onto these substrates have likely influenced the distributions of North American lichens.

4.2 | Biotic interactions impact lichen rarity

Many authors have lamented a lack of understanding of how biotic factors influence species rarity and range limits (Cunningham et al., 2016; Early & Keith, 2018; Morris et al., 2020). This is exemplified by a lack of biotic variables as predictors of occurrences in species distribution models (Morris et al., 2020). Whereas there is some acceptance that biotic interactions shape spatial distributions at local scales, the influence of such factors at larger spatial scales is oftentimes dismissed (but see Wisz et al., 2013). In this study, we scored photobiont type for all North American lichens at a coarse scale in an attempt to understand how biotic interactions influence the distributions of obligate symbiotic organisms. We found that photobiont type significantly impacts distributions of lichens across the continent. In particular, the presence of a *Trentepohlia* photobiont partner is a significant correlate of rarity. Most lichen species with this photobiont are restricted to Tropical Wet Florida and, to a lesser extent, Eastern Temperate Forests. In contrast, species with cyanobacterial photobionts or green algal photobionts that lack carotenoids tend to have broader geographical distributions. These results demonstrate strongly that biotic partner can and does have a significant impact on distributions across a large spatial scale.

4.3 | The relationship between lichen rarity and growth form

The vast majority of lichen literature has emphasized 'macrolichen' growth forms, primarily leafy (foliose) and bushy (fruticose) growth forms. Yet, our data show that crustose species, which constitute the majority of lichens referred to as 'microlichens', comprise nearly two-thirds (65%) of North American lichens. Additionally, rarity among crustose lichens may be related to their typically smaller thallus sizes (vs. macrolichens), which likely facilitates micro-niche partitioning. Many crustose species, which by definition grow closely appressed to their substrates, have been overlooked based on false perceptions of challenges associated with identification. This study demonstrates the need to explicitly include microlichens into ecological analyses given they comprise the majority of North American lichens, are oftentimes rare and tend to characterize individual ecoregions.

4.4 | The relationship between sex, mobility and rarity in lichens

Reproduction and dispersal capacity are widely appreciated as central to the overall ecological strategy of a given species (Moor, 2017). However, the relationship between rarity and dispersal strategy (or mode of reproduction) has been contested owing to mixed results from prior studies, with no clear picture emerging as to a general relationship (Espland & Emam, 2011; Lester et al., 2007). For example, plants with very large reproductive propagules can be either wide-ranging or narrow-ranging (Allred, 1998; Rabinowitz, 1981). Lichen reproduction and dispersal follow one of two primary themes: (1) sexual reproduction that involves the dispersal of the mycobiont-only, which are fungal spores that are typically small in size (i.e. under 40 μM; Walser et al., 2001; Tripp & Lendemer, 2020) and presumably travel relatively far in air columns (see Ronnås et al., 2017 for experimental confirmation) or (2) asexual reproduction that involves co-dispersal of the mycobiont and photobiont, which yields propagules that are typically larger in size (i.e. over 40 μM; Cernajová & Skaloud, 2020; Kon & Ohmura, 2010; Kristinsson, 1971; Lendemer, 2013; Scheidegger, 1995; Walser et al., 2001) and thus travel shorter distances (Ronnås et al., 2017). Sexual species may thus be establishment-limited by the need to find a suitable partner(s), but their propagules should travel further distances than asexual species because of smaller propagule size. In contrast, asexual species may be dispersal-limited by propagule size, but not establishment-limited because they travel with their biotic partner(s) (Aschenbrenner et al., 2014).

Obligate symbiotic organisms such as lichens thus beg the question: to what degree are distributions impacted by finding a suitable partner vs. co-dispersing with one? Contrary to expectations, we found that species with small, sexual propagules have markedly smaller biogeographical ranges than species with large, asexual propagules. Rarity was significantly associated with sexually reproducing species, although this relationship was not recovered in our multivariate model. As such, sexual reproduction covaries with other, stronger drivers of rarity in this study. Nonetheless, a pattern of smaller range sizes associated with sexually reproducing species similarly emerged in a study based on sequencing of atmospheric propagules, wherein Tripp et al. (2016) found that asexual lichens had larger biogeographical ranges than sexual lichens across North America. We furthermore found that species with typically smaller dispersal propagules arising from sexual reproduction are three times more taxonomically diverse in North America (~75% of NA species) than are species with propagules arising from asexual means (~25% of NA species). Thus, species that are the most widespread reproduce with a partner, but these asexual lichens are less taxonomically diverse, comprising only a quarter of North American lichens. Our data show that in lichens, mode of reproduction and dispersal do impact rarity but may be less important than other traits in driving the extent of biogeographical distributions.

4.5 | Other correlates of richness and rarity across ecoregions

In this study, we sought to test for an explicit relationship between the salient intrinsic traits of lichens and patterns of rarity in a subcontinental framework (e.g. Espland & Emam, 2011; Harcourt, 2006; McCulloch et al., 2017; Sheth et al., 2020; Sonkoly et al., 2017). Although outside the scope of this investigation, we expect that numerous other environmental elements, especially those pertaining to features of a taxon's habitat and occupied ecoregion, also impact patterns of species richness and rarity in North American lichens (e.g. Angert et al., 2011; Goulson et al., 2005; Linder, 2019; Moreuta-Holme et al., 2013; Sheth et al., 2020; Stevens, 1989; Taylor et al., 2019; Whitton et al., 2012). For example, in a landmark review of patterns of richness across taxonomic groups in North America, showed that bird species richness is highest along coastal regions and in the desert sky islands, mammal richness peaks in the southern and central Rockies and Sierras, and freshwater fish and amphibian richness are highest in the southeastern United States. Kartesz (2015) showed somewhat different patterns for vascular plants, where species richness is highest in the California Floristic Province and portions of the Gulf and Atlantic Coastal Plains. Although ecoregions differ markedly in size, in the present study, we show that lichen species richness is notably high in several general areas: the eastern forests, the California Floristic Province, the Pacific northwest, the southwestern deserts and sky islands and the Rocky Mountains (Figure 1a). Lichen rarity similarly tracks patterns of species richness, with the ecoregions encompassed by these general areas hosting the highest numbers and/or percentages of rare species (Figure 1b). Thus, there is overlap in trends among the various taxonomic groups, and the present dataset complements future efforts to summarize general patterns in species richness and rarity across North American Biodiversity.

4.6 | Importance of scale

Numerous authors have articulated the importance of geographical scale when considering species distributions and rarity (Rahbek, 2005; Sheth et al., 2020). Several studies that emphasized similarly coarse spatial scales laid the foundation for understanding global distributional patterns across taxonomic groups. For example, Kreft and Jetz (2007) conducted a global examination of plant species richness and underlying determinants and found that water and energy inputs help predict regions of exceptional richness, including the eastern tropical Andes, the Brazilian Atlantic Forest, northern Borneo and New Guinea. Trakimas et al. (2016) sought to understand the relationship between range size and dispersal traits of European amphibians and found fecundity and life span to be important predictors across this continental-scale dataset. Enquist et al. (2019) assembled a large dataset of global plant diversity and showed that 36.5% of Earth's plant biodiversity is 'exceedingly rare', and further found that climatically stable regions harbour more rare species. However, the issue of scale or grain size is known to influence our perceptions of patterns and processes surrounding determinants of range size (Rahbek, 2005). Similarly, the study of datasets built on finer-scale geographical information may help to more clearly articulate nuances in the data, such as how distributions are impacted by topography, history, elevation, seasonality, specialization, phylogenetic relatedness, niche availability and/or disturbance (e.g. Goulson et al., 2005; Grünig et al., 2017; Harcourt, 2006; Linder, 2019; Sheth et al., 2020; Tripp et al., 2019; Whitton et al., 2012). Additionally, subsequent efforts to understand rarity among North American lichens would benefit from the generation of datasets with finer-scale geographical information and more precise definitions of range sizes and datasets that take abundance into consideration. Future works could then consider whether and how these finer-scale delimitations of species distributions would impact our understanding of rarity in North American lichens.

4.7 | Conservation implications

The need to understand the drivers of species rarity and range size is exacerbated by rapid shifts in geographical distributions as a result of human-induced environmental change (Morris et al., 2020). Moreover, range size is a strong predictor of extinction risk (Sheth et al., 2020). Yet, answers to questions about drivers of range sizes are crucial to understanding species persistence in native habitats (Angert et al., 2011; Taylor et al., 2019). This conservation challenge is especially relevant to the North American lichen biota, where we have shown that nearly half of all lichen species are rare and restricted to a single ecoregion. Species that are generalists are more like to expand biogeographical ranges (Angert et al., 2011). However, among North American lichens, small, specialist crustose species that grow on bark or leaves are among the rarest species,

thus posing further challenges to the conservation of these species: deforestation will strongly and negatively impact the North American lichen biota. Datasets such as that presented in this study thus help to reframe conservation initiatives in light of large-scale distributional patterns, their correlation to functional traits and the need to better incorporate data from other systems beyond plants and animals into nationwide conservation initiatives.

5 | CONCLUDING REMARKS

Lichens are symbiotic organisms that are an evolutionarily ancient assemblage yet highly successful in terms of numbers of species distributed worldwide, including some of the most uninhabited landscapes on Earth such as the Atacama and Namib Deserts. The lichen biota of North America represents an excellent system in which to explore trade-offs among functional traits, biogeographical range size and species richness. Through analysis of the majority of nearly 5500 species of lichens known to North America, we have shown that the rarest lichens are those that live on bark or leaves, have a *Trentepohlia* photobiont partner, are small and crustose, and reproduce sexually. That nearly half of the biota is rare and because most rare species are specialized through biotic interactions or other growth features highlights the magnitude of the conservation challenge of these charismatic and ecologically important elements of North American ecosystems.

DATA AVAILABILITY STATEMENT
All data associated with this contribution are available in Appendices S1 and S2.

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