Biodiversity and Conservation (2024) 33:1303–1324
https://doi.org/10.1007/s10531-024-02795-z

ORIGINAL RESEARCH

Patterns and predictors of lichen rarity in a biodiversity hotspot

Grant L. Vagle[1] · **James C. Lendemer**[2,3] · **Erin A. Manzitto-Tripp**[1,4] · **Christy M. McCain**[1,4]

Received: 19 July 2023 / Revised: 21 December 2023 / Accepted: 21 January 2024 /

Abstract

Understanding the spatial distributions of rarity and diversity is crucial for both targeted conservation efforts and elucidating the mechanisms that underpin species richness patterns. Existing studies suggest local communities with greater species richness also hold higher numbers of low abundance species. Rarity hotspots at the global scale tend to be spatially divergent from species richness hotspots and differ among many taxonomic groups, but much less work has been done to understand rarity patterns at the regional scale. Here, we used a large-scale dataset of comprehensive lichen diversity from a global biodiversity hotspot in eastern North America to explore the relationships of rarity, species richness, and elevation, while also examining the key plot characteristics that support increased rarity within the system. We found a mid-elevation slump in lichen rarity, with increased rarity at low and high elevations, contrasting with the mid-elevation hump in species richness for lichens in the same system. Additionally, important plot-level predictors of rarity changed with elevation. Rocky, open habitats hosted increased levels of rarity at low elevations, and the highest, coldest plots at the high elevations also hosted increased levels of rarity. Our results illustrate a contrast between elevational patterns and important plot characteristics for lichen rarity and species richness, suggesting a need for separate, complementary conservation efforts to protect both areas with high species richness and areas with high numbers of rare species.

Keywords Elevation · Species richness · Rare species · Habitat quality · Rarity metric · Appalachians

---

Communicated by David Hawksworth.

✉ Grant L. Vagle
vaglegrant@gmail.com

[1] Department of Ecology and Evolutionary Biology, University of Colorado, Boulder, Boulder, CO, USA

[2] Research & Collections, The New York State Museum, Albany, NY, USA

[3] Biology PhD Program, Graduate Center, City University of New York, New York, NY, USA

[4] Museum of Natural History, University of Colorado, Boulder, Boulder, CO, USA

Introduction

As a result of climate change, habitat modification and loss, and other anthropogenic impacts, numerous species are at risk of or are actively experiencing range reductions or shifts (e.g., Engler et al. 2011; Allen and Lendemer 2016a, b; McCain et al. 2021), reductions in abundance (e.g., McCain and King 2014; Allen et al. 2019; Forister et al. 2019), or extinction (e.g., IUCN Red List, Öckinger and Nilsson 2010). This is especially true for rare species with small geographic ranges and/or low abundance, which leads to increased risk of extinction (Davies et al. 2004; Williams et al. 2009; Harnik et al. 2012). Therefore, understanding the spatial distributions of species rarity and the mechanisms that produce those patterns is vitally important to conservation.

Prior studies have found that sites with high species richness tend to contain disproportionately high numbers of low abundance species (Ulrich et al. 2020), suggesting that rarity (defined as low abundance in local studies) and species richness may be positively related. However, evidence from global-scale studies (with rarity usually defined by geographic range size) shows that this is generally not the case, with substantial discordance of rarity and species richness hotspots (Grenyer et al. 2006; Albuquerque et al. 2019; Enquist et al. 2019). Rarity hotspots (and species richness hotspots) have also been shown to be divergent among taxonomic groups, even within vertebrates (Grenyer et al. 2006). Global-scale studies of rarity show that large numbers of range-restricted species occur in areas of rare or localized climates (Ohlemüller et al. 2008), suggesting that rare species may be adapted to globally rare climates. Notably, mountainous regions support disproportionate numbers of rare species given their global land area (Albuquerque et al. 2019; Enquist et al. 2019; Rahbek et al. 2019) and host many diversity hotspots as well (Grenyer et al. 2006). At the regional scale, a study of plants along an elevational gradient on the Korean peninsula found that climatic variables better predicted numbers of rare species than total species richness (Lee et al. 2013). Identifying locations that host large numbers of species and/or rare species to optimize coverage with protected areas is a key focus of conservation reserve planning (Astudillo-Scalia and Albuquerque 2019), but most studies have not focused on the mechanisms that produce the observed spatial patterns.

Despite this current knowledge, there is much to learn regarding the spatial patterns of rarity and how it relates to diversity (with a focus on species richness here). Most studies to date have focused on global patterns (Grenyer et al. 2006; Ohlemüller et al. 2008; Albuquerque et al. 2019; Enquist et al. 2019), but regional-scale patterns may be more relevant to the scale at which many conservation practices are implemented (e.g., land management practices, creation of nature preserves). Additionally, studies at such large scales are often reliant on remotely sensed data due to the difficulty of sampling local habitat variables across large spatial extents. In addition to the climatic factors demonstrated to be important predictors of rarity in multiple studies (e.g., Enquist et al. 2019), local habitat variables may also be relevant yet uncollected at such large scales. Focused attention at the regional scale within montane systems could greatly advance the understanding of rarity, as mountains host large numbers of rare species (Albuquerque et al. 2019) and have distinct climate and species richness gradients (Rahbek et al. 2019).

Broadening understanding of rarity across a range of taxonomic groups is also key as to date, studies have focused largely on vertebrates (e.g., Grenyer et al. 2006; Albuquerque et al. 2019) and land plants (Lee et al. 2013; Enquist et al. 2019). The present study focuses on lichens, evolutionarily diverse, obligately symbiotic fungi that form dynamic partnerships with photosynthesizing partners (algae or cyanobacteria, termed photobionts) and a cohort of other microbes (Grube et al. 2009; Allen and Lendemer 2022; Spribille et al. 2022; Pichler et al. 2023). While lichens are understudied compared to other taxonomic groups of macroscopic organisms, and their biogeographical patterns are correspondingly less understood (Galloway 2008; Tripp et al. 2016, 2019), decades of focused efforts have established extensive baseline data for some areas including in North America (Nash et al. 2002; Nash et al. 2004, 2007; Hodkinson 2010; McCune 2017a, b; Allen et al. 2019). Many studies have found that lichen species richness is highest in undisturbed, high-quality habitats (McCune et al. 1997; Barry et al. 2015; Allen and Lendemer 2016b; Lendemer et al. 2016; Tripp et al. 2019), while others have shown the influence of climatic factors on species richness (McCune et al. 1997; Arsenault and Goward 2016; Bässler et al. 2016; McCain et al. unpub.). Overall, spatial patterns of lichen rarity remain poorly understood, with most lichen rarity studies focused on a narrow taxonomic group or single species (e.g., Lendemer et al. 2014), or narrow geographical areas (e.g., Tripp 2015). Additionally, most (e.g., Rosso et al. 2000) but not all (e.g., Root et al. 2011; Lendemer et al. 2014) lichen rarity studies focus on macrolichens and exclude microlichens. A recent continental scale study, that used presence across biomes as a proxy for rarity, found that lichen rarity was linked to the morphological traits of species and partner selection across North America (Manzitto-Tripp et al. 2022). Meanwhile, two studies of lichens in Italy found abundance of rare lichen species to be dependent on habitat type and climate (Nascimbene et al. 2012; Nimis et al. 2018), while a separate study in the Mediterranean region found rare lichens to be the primary contributors to species turnover among sites (Brunialti et al. 2021). The difficulty of sampling rare species (with many singleton species) has also impeded full spatial analyses in at least two studies (Edwards et al. 2004; Root et al. 2011).

Here, we examine the spatial patterns of lichen rarity in the southern Appalachian biodiversity hotspot of southeastern North America. We define rarity using the number of plot occurrences within the study region to serve as a reliable, directly measurable, regional measure of rarity. First, we assess how lichen rarity is related to latitude, elevation, and species richness. Second, we assess which plot characteristics (e.g., climate, tree density, land cover) are most important for rare lichens. We then explore these patterns to hypothesize mechanisms driving rarity based on existing biodiversity theory. In addition to contributing a novel organismal perspective to general understanding of rarity, this study provides an important regional context that is directly relevant to conservation and management strategies in a threatened global biodiversity hotspot (Noss et al. 1995; Richardson et al. 2003; McManamay et al. 2011; White et al. 2012; Allen and Lendemer 2016a).

Methods

Study system

The southern Appalachian region of the southeastern United States is one of the most biodiverse regions in North America for a variety of taxa including lichens (Hodkinson 2010; Tripp and Lendemer 2019, 2020; Tripp et al. 2019) in addition to vascular plants, salamanders, beetles, and other groups (White 1982; Petranka 1998; Carlton and Bayless 2007). This is primarily due to the large range of elevations (spanning 1800 m) and high primary productivity in the region which lead to highly heterogeneous climatic and habitat distributions across the landscape, harboring a large diversity of species (Carlton and Bayless 2007; Lendemer et al. 2013; Tripp and Lendemer 2020). While the southern Appalachians have experienced considerable human disturbance along with the rest of the eastern United States (Drummond and Loveland 2010; Tripp and Lendemer 2020), the region is also home to relatively large, protected areas of forest and other habitats. Previous work in the southern Appalachian foothills showed lichen species richness to be heavily dependent on habitat quality (Tripp et al. 2019). Within the plots considered here, lichen species richness shows a mid-elevation peak, with tree species richness and canopy cover strongly and positively influencing lichen richness (McCain et al. unpub.).

Data collection

Taxonomically comprehensive, complete lichen biodiversity inventories were conducted at 208 sites (Fig. 1). Experts identified all unique lichen species within a 1-hectare (100 × 100 m) plot, collecting voucher specimens for each species (as in Tripp et al. 2019). These inventories are especially useful in addressing questions related to rarity. Because the lichen inventories were continued until the lichen experts could find no more unique species, even rare species of low abundance were regularly detected. Thus, this set of lichen inventories is uniquely suited for rarity study, as most studies struggle to sample the rarest species.

Plot locations were selected across axes of disturbance (highly disturbed to intact old growth), elevation (165–2015 m), and aspect (N, S, E, W, flat) to ensure there was relatively even distribution across the study region. Each sampling trip had predetermined target plots across those three axes, thus, during the five years of field work the axes were fully sampled. Within those plots, tree and rock substrate density, woody tree diversity, and slope varied widely. Plots were sampled in mountainous regions of Alabama, Georgia,

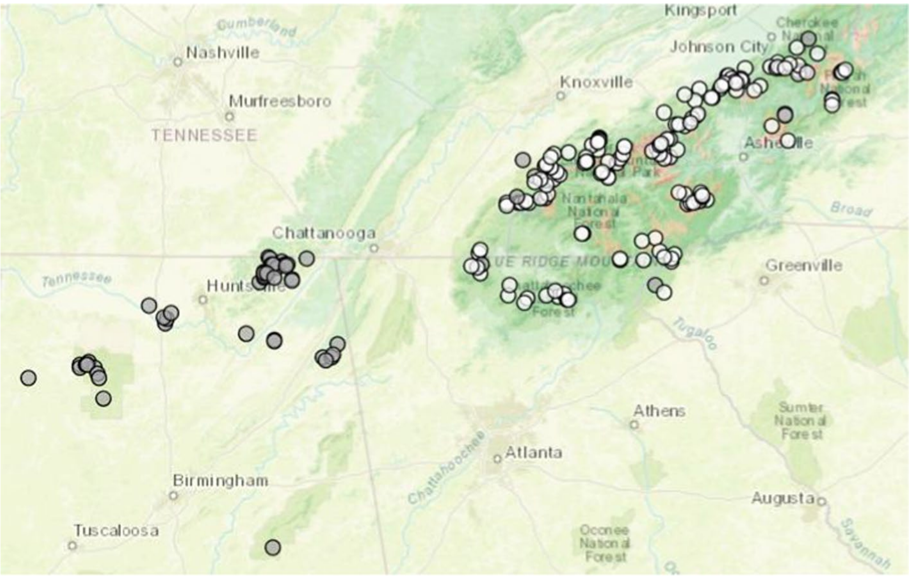

Fig. 1 A map of all plots sampled for lichens. Gray circles were excluded for spatial isolation or low habitat quality, white circles were included in the final analyses

North Carolina, South Carolina, and Tennessee in the southeastern United States. A number of discrete morphological traits were scored for each species using the specimen material collected for this study (as in Manzitto-Tripp et al. 2022), including dominant reproductive mode (sexual, asexual, polymorphic), primary photobiont partner (coccoid green algae, *Trentepohlia* green algae, cyanobacteria, polymorphic, absent), growth form (crustose, foliose, fruticose, squamulose), and primary growth substrate (bark, calcareous rock, non-calcareous rock, humus, leaf).

Plot-specific variables (Table 1) were collected both in the field and via remotely sensed datasets. Variables measured in the field included several local habitat variables described in Parkes et al. (2003) and Tripp et al. (2019) (rock cover, large trees, canopy cover, understory, weediness, recruitment, litter, quantity of logs, patch size, neighborhood, distance to core, habitat quality summary) as well as sum and average diameter at breast height (DBH) measured for a 10 × 10 m subplot, and the number of woody plant species (trees and shrubs, with taxa categorized based on growth form). Additionally, annual climate measurements from WorldClim (1 km resolution; Fick and Hijmans 2017), primary productivity from MODIS estimates (MOD17A3, 1 km resolution; Zhao et al. 2005), and land use and land cover data from the National Land Cover Database (30 m resolution; Dewitz 2019) were collected for each plot location. Air pollution measurements of carbon monoxide (CO), particulate matter ($PM_{2.5}$), ozone, sulfur dioxide (SO_2), and nitrogen dioxide (NO_2) were collected via Pargasite (10 km resolution; Greenblatt and Himes 2019) for each plot location, because previous research has shown lichens to be highly susceptible to poor air quality (Allen et al. 2019).

Plot subsetting

Before calculating rarity metrics, we first selected a subset of 149 plots from the original full set of plots (Fig. 1: white circles = retained plots; gray circles = excluded plots). We excluded plots in Alabama due to their relative spatial isolation and distinct lichen species assemblages so that the plots remaining (Georgia, North Carolina, South Carolina, and Tennessee) represented more even spatial coverage of the region. We also excluded plots with very low habitat quality (< 45 habitat quality summary score, calculated as in Parkes et al. 2003) as we aimed to assess rarity in less anthropogenically disturbed habitats.

Plot-level rarity metric

First, we calculated a rarity weight for each species detected based on the number of occurrences. Number of occurrences is simply the number of plots at which a lichen species was found, within the final set of plots. Number of occurrences was the most reliable metric of rarity in our dataset because abundance data were not captured as part of this study. Other measures of rarity such as habitat specificity and geographic range size were considered but ultimately not used due to the high number of extremely rare species that were found only at a single plot (i.e., for singleton occurrences of species found in one plot, it is not possible to measure the breadth of a habitat characteristic within which that species is present; hence it is not possible to determine whether the species is a habitat specialist or simply found at very low density). Thus, we summarized the rarity weights (based on a species' number of occurrences) among all species present in each plot to give each plot a single measure of rarity, congruent with the plot-level predictor variables.

Table 1 Candidate and included (bold) variables in the final models

Variable group	Potential predictor variables *bold = included*, *non-bold = excluded*	Abbreviation (used in figures)
Geographic/topographic	**Slope angle**	
Collected pre-sampling or in the field	**Aspect**	
	Jurisdiction/land manager	**Jurisdiction**
Local habitat	**Rock cover**	
Collected in the field	**Large trees**	
*(*Parkes et al. 2003*)*	**Canopy cover**	
	Weediness	
	Recruitment	
	Litter	
	Quantity of logs	**Loggy-ness**
	Patch size	
	Neighborhood	
	Distance to core	
	Habitat quality (summary)	**Habitat Quality**
	Sum DBH	
	Average DBH	
	Number of shrub species	**Shrub diversity**
	Number of tree species	**Tree diversity**
	Number of woody species	# woody spp
	Understory	
Climate	**Net primary productivity**	**NPP**
WorldClim;	**Mean annual temperature**	**Mean Ann Temp**
MOD17A3	**Mean annual precipitation**	**Ann Precip**
	Temperature seasonality	**Temp Seas**
	Temperature annual range	Temp Range
	Precipitation seasonality	Precip Seas
	Mean annual diurnal range	Diurnal Range
	Isotherm	
Land use/land cover	**Habitat type from NLCD**	**Land cover**
National Land Cover Database (NLCD)	**% Developed open space (50 m)**	**Dev Open 50 m**
	% Open water (50 m)	**Open Water 50 m**
	% Grasslands/herbaceous (50 m)	**Grasslands 50 m**
	% Shrubland/scrub (50 m)	**ShrubScrub 50 m**
	% Pasture (50 m)	**Pasture 50 m**
	% Evergreen forest (50 m)	**Ev Forest 50 m**
	% Mixed forest (50 m)	**Mix Forest 50 m**
	% Deciduous forest (50 m)	**Decid Forest 50 m**
	% Woody wetlands (50 m)	Woody Wetland
	% Cultivated croplands (50 m)	Cult Crop
	% Medium development (50 m)	Dev Med
	% Low development (50 m)	Dev Low

Table 1 (continued)

Variable group	Potential predictor variables ***bold = included***, *non-bold = excluded*	Abbreviation (used in figures)
	Land cover Shannon diversity (1 km)	**LC Shannon Div**
	Land cover richness (1 km)	**LC Richness**
	% cover agriculture (1 km)	**Ag 1 km**
	% cover developed habitats (1 km)	**Dev LC 1 km**
	% cover natural habitats (1 km)	Nat LC 1 km
Air pollution	**Average annual PM2.5 2005–17**	**PM air poll**
Pargasite	**Average annual Ozone 2005–17**	**Ozone air poll**
	Average annual CO 2005–17	**CO air poll**
	Average annual NO2 2005–17	NO2 air poll
	Average annual SO2 2005–17	SO2 air poll

For each species, we calculated rarity weight as in Leroy et al. (2012): $w_i = e^{-\left(\frac{Q_i}{Q_{\max}}\times n+1\right)^2}$, where w_i is the species' rarity weight, Q_{max} is the maximum number of occurrences for any species in the dataset, Q_i is the number of occurrences for species i, and n is a scaling parameter that determines the threshold for rare vs. common. This goes beyond the dichotomous rare versus common and gives higher rarity weights to extremely rare species compared to species that are 'rare' but not extremely rare. Beyond a specified threshold (defined by n), the species' rarity weight is asymptotically zero, so that all 'common' species are assigned very similar, low rarity weights (Fig. 2).

We used three thresholds when calculating rarity weights: 4%, 10%, and 25% of the maximum number of occurrences for any species (141 occurrences; Fig. 2). This allowed for the comparison of trends between an overall picture of plots that harbor rare species more broadly (with 14 or fewer occurrences at the 10% threshold, and 35 or

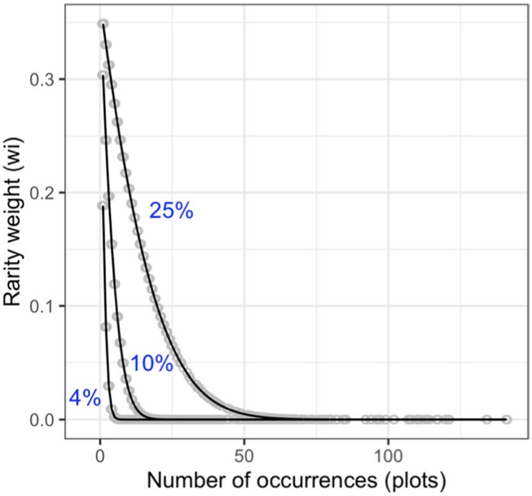

Fig. 2 Examples of species rarity weight (w_i) with rarity thresholds of 4%, 10%, and 25% of the maximum number of occurrences for any species in the dataset

fewer occurrences at the 25% threshold) and a closer look at plots harboring extremely rare species (with 5 or fewer occurrences at the 4% threshold).

Using the species rarity weights for each threshold, we calculated an index of relative rarity (I_{RR}) which quantified the representation of rare species in each plot (Leroy et al. 2012). Plots with more rare species, especially extremely rare species, receive a higher index of relative rarity. This plot-level metric (I_{RR}) was calculated as:

$$I_{RR} = \frac{\sum \frac{w_i}{S - W_{min}}}{w_{max} - w_{min}}$$

where w_i is an individual species rarity weight (calculated as above), S is the species richness of the local assemblage, w_{max} is the maximum species weight across all plots (the weight of the rarest species), w_{min} is the minimum species weight across all plots. The summation occurs across all i species that occur at a plot. This is a measure of relative rarity among plots, since it is scaled by the absolute minimum and maximum species weight as well as plot-level species richness (Leroy et al. 2012). I_{RR} values can range from zero (all species in the plot are the most common in the dataset) to one (all species in the plot are the rarest in the dataset). This plot-level metric was calculated for the 4%, 10%, and 25% thresholds separately.

General patterns of rarity

For general understanding of how lichen rarity varied across commonly examined variables in biogeography and macroecology, we first investigated the relationship of I_{RR} with latitude, elevation, and lichen species richness. We used simple linear regression with linear terms for latitude, elevation, and lichen species richness (separately) on each threshold (4%, 10%, 25% separately) of the index of relative rarity (I_{RR}). Though species richness and rarity are often closely related, the scaling by plot-level species richness in the I_{RR} metric makes species richness and I_{RR} independent (Leroy et al. 2012) and suitable for a linear regression. Additionally, because of non-linear patterns of species richness with elevation and latitude (e.g., McCain and Grytnes 2010), we fit simple quadratic regression models for elevation and latitude and compared these to the linear counterparts using R^2. For elevation, a randomized resampling procedure was used to account for uneven sampling of plot locations across elevation (Supplemental Material).

Random forest modeling

We used random forest models (Breiman 2001) to predict the index of relative rarity (I_{RR}, dependent variable) based on predictor variables related to geography/topography, local habitat characteristics, climate, air pollution, and land use and land cover (Table 1). A random forest is a predictive model that constructs decision trees or regression trees, randomly selecting variables at each node in the tree to optimize the predicted response variable at the bottom of each tree, then summarizing those predictions across multiple trees. Random forests are resilient to numerous variables and correlated variables, excel at detecting non-linear relationships and interactions between variables, and are interpretable via partial dependence plots (Cutler et al. 2007). Thus, random forest models are well-suited to the exploratory nature of this part of our analysis.

Starting with a set of 51 potential predictor variables (Table 1), we excluded four land cover variables that had very sparsely populated values among plots (proportions of woody wetlands, cultivated crops, low and medium development within 50 m of the plot location). Next, we used a hierarchical clustering approach based on Pearson correlations to reduce the number of highly correlated variables (as in Albuquerque et al. 2019; details in Supplemental Material). We used a correlation threshold of 0.7 (since random forests are quite rigorous in the face of correlated predictors), choosing one variable within each cluster of variables that had correlations of 0.7 or greater (Fig. S2). This eliminated nine variables. Though not included in the hierarchical clustering process because they were categorical, jurisdiction, aspect, and land cover type were included in final models. This left a final set of 38 predictor variables (Table 1).

Separate random forest models were built for each of the 4%, 10% and 25% I_{RR} metrics. In each model, 1000 random regression trees were built by sampling 149 plots with replacement (from the final set of 149 plots), trying six predictor variables at each split in the tree, and with a final node size of five plots. These models were evaluated using a pseudo-R^2 value and the mean squared error of the predicted I_{RR} values. Variable importance for all predictors was evaluated using percent increase in mean squared error. After determining which variables held importance in the model, partial dependence plots were constructed to isolate the marginal effects of individual variables on I_{RR} (Cutler et al. 2007).

Because of the importance of elevation in ecological theory and the observed U-shaped pattern with I_{RR} (see below), we also explored trends of rarity within low, middle, and high elevation plots separately. Plots were binned according to elevation, with the lowest 1/3, middle 1/3, and highest 1/3 of sites placed into their respective bins. Separate random forest models were run for each elevation bin using the same predictor variables as the overall model. These models were only run using the 25% threshold I_{RR} values because that threshold had the most accurate predictions. Variable importance and partial dependence plots were used for each of these models as for the overall models.

Lichen trait compositions

We also used lichen trait compositions of each plot to contextualize results from the above analyses. Rarity weight histograms for each trait group (within photobiont type, growth form, primary growth substrate, and dominant reproductive mode) were examined to visually assess whether certain lichen traits were correlated with rarity. Then, trait-specific species richness in each plot was examined across overall species richness, elevation, and other axes of plot characteristics found to be important from the general patterns and random forest models.

All analyses were run in R version 4.0.5 (R Core Team 2018), with heavy reliance on the *tidyverse* for data manipulation and visualization (Wickham et al. 2019). Maps were produced using *leaflet* (Cheng et al. 2021). Random forest models were built using the *randomForest* package (Liaw and Wiener 2002). Partial dependence trends were constructed using the *rfUtilities* package (Evans et al. 2011).

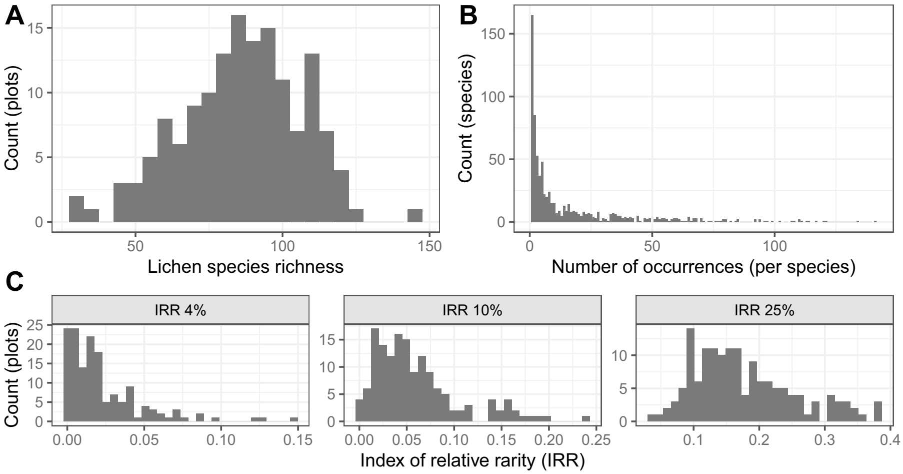

Fig. 3 Histograms of lichen species richness at the plot level (**A**), number of occurrences for each species (**B**), and index of relative rarity at the 4%, 10%, and 25% thresholds (**C**)

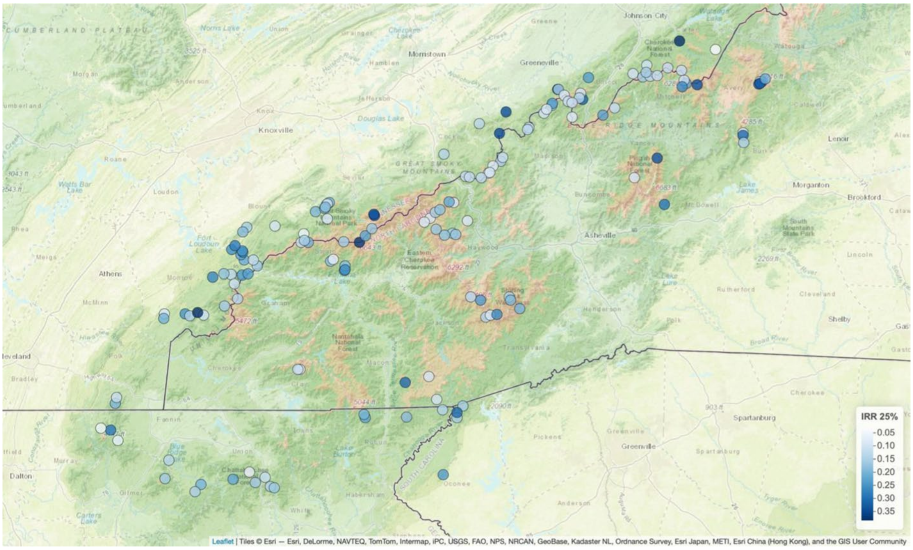

Fig. 4 Map of index of relative rarity values at the 25% threshold (IRR 25%). Higher IRR 25% (darker blue) indicates greater representation of rare lichen species. Black lines represent state boundaries

Results

Across the contiguous and higher habitat quality subset of plots (n = 149), 763 lichen species were detected, with species richness within a plot varying from 31 to 146 (Fig. 3A). Many of these species were very rare, with 165 species (22%) detected at only at a single plot (Fig. 3B). The distributions of the index of relative rarity (I_{RR}) values varied in shape for the 4%, 10% and 25% thresholds, with the 4% and 10% thresholds having strong right skew and the 25% threshold having the most symmetric distribution of the three (Fig. 3C). Upon inspection of I_{RR} values in geographical space, there were no obvious and consistent geographical patterns (see Fig. 4).

General patterns of rarity

To elucidate general patterns of rarity with respect to latitude, elevation, and species richness, we used simple linear regressions. Latitude showed no relationship with I_{RR} at any threshold ($F_{1,147} < 0.90$, $p > 0.05$, $R^2 < 0.01$ for all thresholds), likely because latitude only varied by about 3° in these plots while elevation ranged from 279–2013 m above sea level. Elevation showed a significant U-shaped pattern with all three I_{RR} thresholds (quadratic linear regression: $F_{2,146} = 6.86, 20.40, 37.19$, $p < 0.01$, $R^2 = 0.08, 0.21, 0.33$ for 4%, 10%, 25% thresholds; Fig. 5A). This indicates increased rarity at the lowest and highest elevations, with decreased rarity at middle elevations (Fig. 5A), especially for the broader classifications of rarity (10% and 25% thresholds). This U-shaped relationship was retained when the data were also analyzed using uniform resampling of plots across elevation (Fig. S1), and contrasts with the significant mid-elevation hump in species richness found within these plots (Fig. 5C; more deeply investigated in McCain et al. unpub.). Additionally, these opposite patterns for rarity and species richness do not simply stem from a negative correlation between I_{RR} and species richness. Only two thresholds (4% and 10%) showed significant negative linear relationships ($F_{1,147} = 5.47, 6.91$; $p < 0.05$) between species richness and I_{RR} (Fig. 5B). These relationships were weak, explaining very little of the variation in I_{RR} ($R^2 < 0.04$). Thus, species richness and I_{RR} seem to be weakly related at best, suggesting opposite elevational patterns for lichen rarity and lichen species richness.

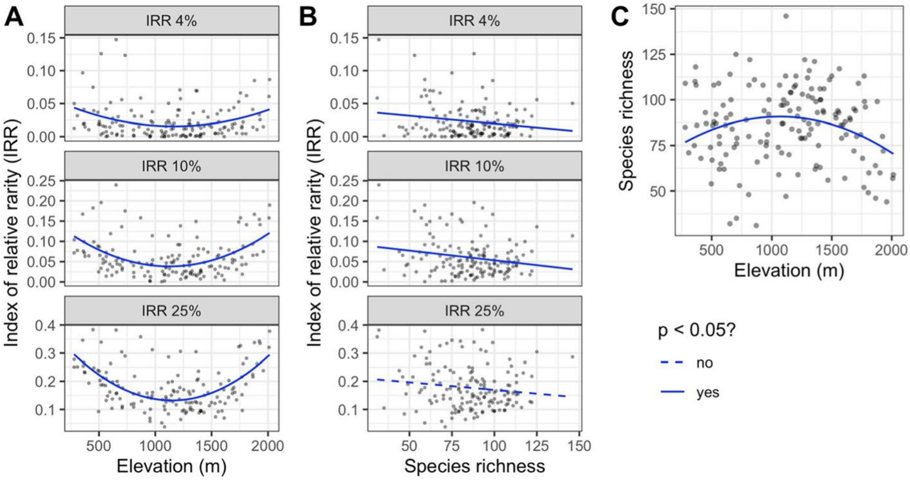

Fig. 5 **A** Index of relative rarity and elevation show a significant quadratic relationship, with increased rarity at high and low elevations and a mid-elevation slump. **B** Species richness and index of relative rarity show weak, negative linear relationships. **C** A mid-elevation hump with lichen species richness and elevation shown here with a significant quadratic relationship. Explored in more depth in McCain et al. (unpub.)

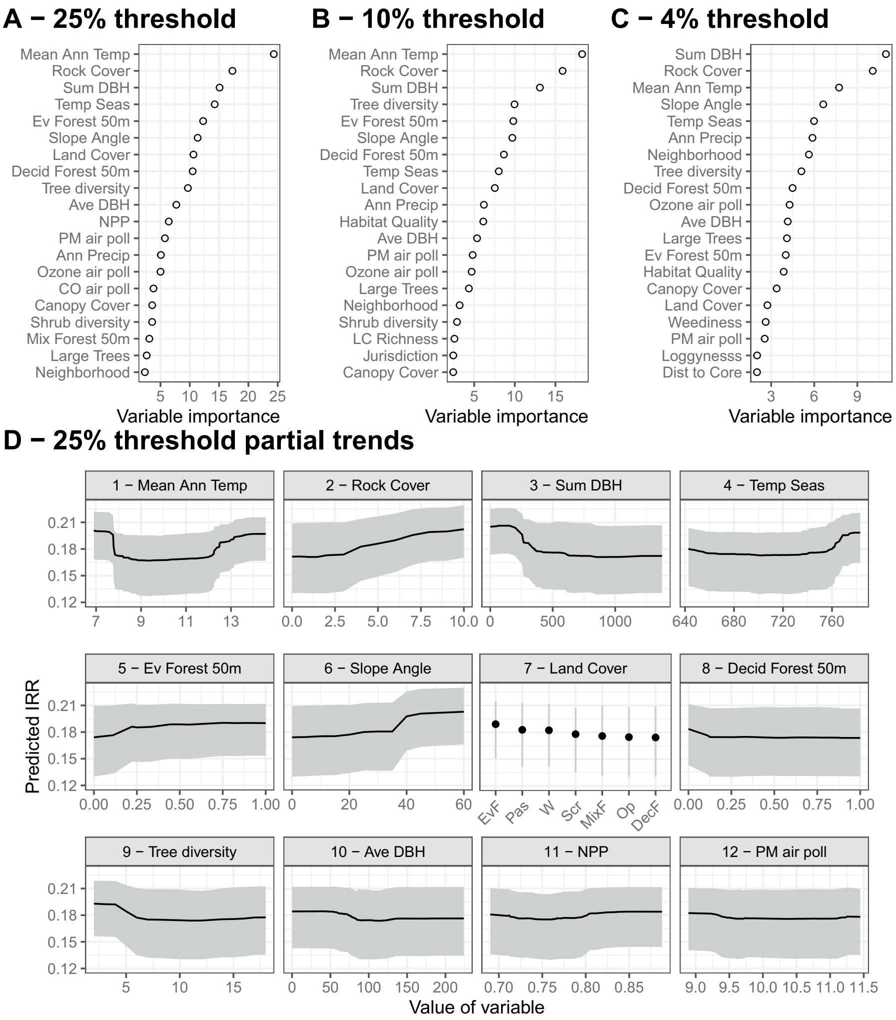

Fig. 6 **A**–**C** Random forest variable importance (calculated as % increase in mean squared error) of the top 20 variables predicting index of relative rarity (I_{RR}) at the 25%, 10%, and 4% thresholds. **D** Partial dependence plots showing predicted I_{RR} trends (black) and 50% confidence intervals (gray) across the range of values for the top 12 variables in the 25% threshold model. Variable abbreviation key in Table 1. Land cover abbreviations: *EvF* evergreen forest, *Pas* pasture/hay, *W* open water, *Scr* shrub/scrub, *MixF* mixed forest, *Op* developed, open space, *DecF* deciduous forest

Random forest results—all plots

To look more closely at plot characteristics, random forest models were built to understand how local habitat, climate, and air pollution variables may be related to lichen rarity. For the broadest classification of rarity (25% threshold), the random forest model explained 42% of the variation in I_{RR} (pseudo-R^2). The 10% threshold model had a slightly lower pseudo-R^2 of 34%. For the strictest classification of rarity (4% threshold), the random forest model performed more poorly (pseudo-$R^2 = 15\%$), likely due to the right skew of I_{RR} values under the 4% threshold (Fig. 3C). Here, we focus on the best model (25% threshold), while comparing the models with stricter classifications of rarity.

Annual mean temperature was the most important variable for the 25% and 10% models, showing a U-shaped pattern (Fig. 6). Along with temperature seasonality (also of considerable importance in the 25% and 10% models), this documents the same previously described pattern with elevation. Rock cover had very high importance in all three models, with increased rock cover predicting increased I_{RR} values. Additionally, sum of tree diameter at breast height (sum DBH) was consistently of high importance in all three models (Fig. 6). Surprisingly, plots with the lowest values of sum DBH (indicating lowest tree density) had the highest rarity while plots with medium–high sum DBH had lower rarity. Evergreen forest habitats (determined from National Land Cover Database) appear to positively predict rarity, while the models showed that plots with very low evergreen forest cover had reduced I_{RR} values (Fig. 6). Plots with steeper slopes also tended to have increased lichen rarity, with slope angle being especially important in the 4% model and of moderate importance in the 10% and 25% models (Fig. 6).

Random forest results—high, mid, low elevations

Because of the observed U-shaped pattern of I_{RR} with elevation and the importance of elevation in ecological theory, we divided plots into high, middle, and low elevation subsets (49–50 plots in each subset) and ran separate random forest models to predict I_{RR} at the 25% threshold. The low elevation model explained 25% of the variation in I_{RR}, the middle elevation model 35%, and the high elevation model 45%. Important variables in these models varied substantially among elevation bins, as detailed below.

For low elevation plots, rock cover was the most important variable in predicting I_{RR} values, and a much stronger predictor than other variables. Like the overall model, increased rock cover predicted increased lichen rarity. Slope angle was quite important at low elevations, with steeper slopes predicting increased I_{RR}. Number of shrub species was another important variable, with more shrub species predicting increased rarity. Mean annual temperature and temperature seasonality were somewhat important, seeming to reflect that the lowest and most seasonal of the low elevation plots had increased rarity. Several other variables had moderate importance in this model, with partial dependence trends in Fig. S3.

Similar to low elevation plots, rock cover was the most important variable for middle elevations, showing a similar increasing trend. Tree density (measured via sum DBH) was the second most important variable, showing a similar pattern as the overall model with the highest rarity at the lowest tree densities. Neighborhood (a measure of habitat contiguity) was important at middle elevations, with less fragmentation predicting increased rarity. Steeper slopes and presence of large trees also positively predicted rarity at middle elevation plots, though with considerably less importance in the model than rock cover, sum DBH, and neighborhood. Several other variables held moderate importance in this model, and their partial dependence trends are included in the Fig. S4.

While climate variables were not among the most important variables for the low and middle elevation plots, at high elevations annual mean temperature was the most important variable, with the coldest (i.e., highest elevation) plots having the highest I_{RR} values (Fig. 7C,F). High elevation plots with low tree species richness predicted increased rarity, and deciduous forest habitats appeared to negatively predict rarity while evergreen forests positively predict rarity, which is likely related to elevation within these high elevation

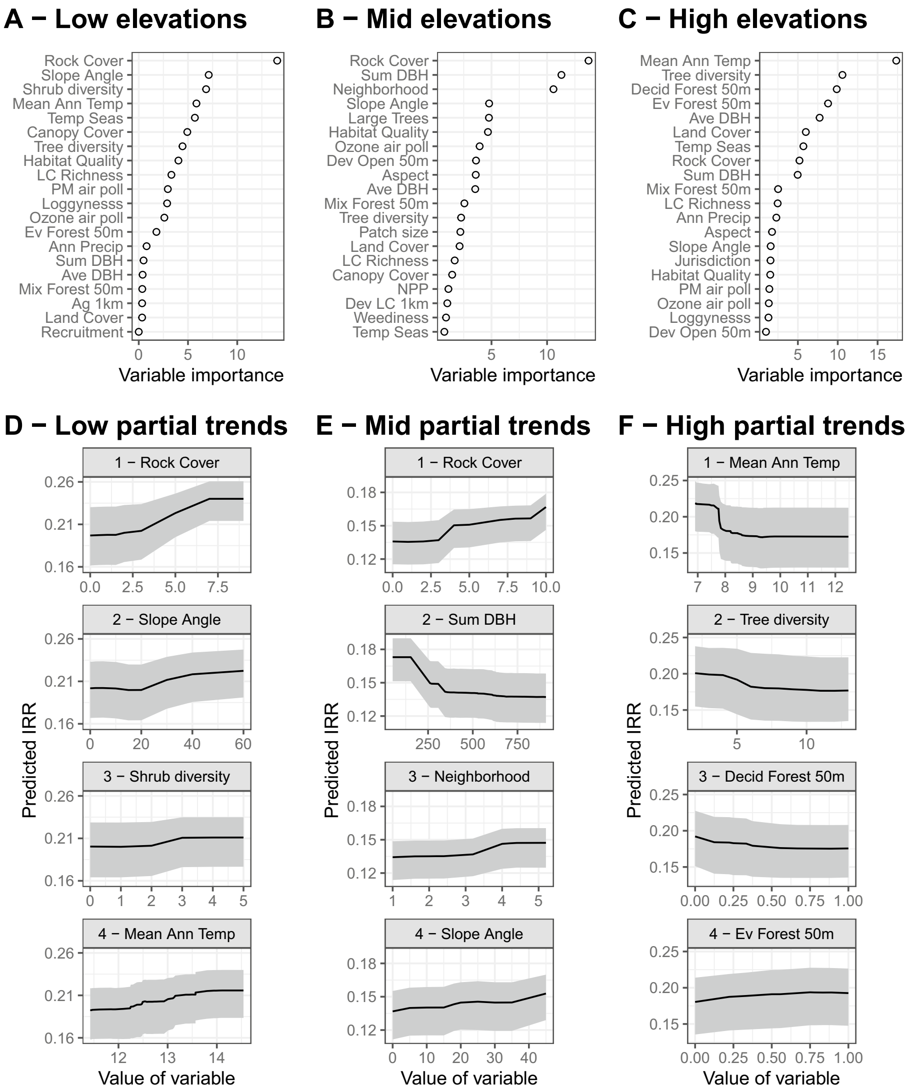

Fig. 7 Random forest variable importance (% increase in mean squared error) for models of index of relative rarity (I_{RR}) at the 25% threshold for low elevation plots (**A**), mid elevation plots (**B**), and high elevation plots (**C**). **D**–**F** show partial dependence plots of predicted I_{RR} values for the top four variables in each elevation model (50% confidence intervals shaded gray). Variable abbreviation key in Table 1

plots. Low average DBH (a measure of tree size within a plot) showed increased rarity at high elevations (Fig. S5). Several other variables held moderate importance in this model, and their partial trends are available in Fig. S5. Notably, rock cover and sum DBH were not among the top variables (ranking 8 and 9, respectively) at high elevation plots despite their consistent importance in the overall models and the low and middle elevation models.

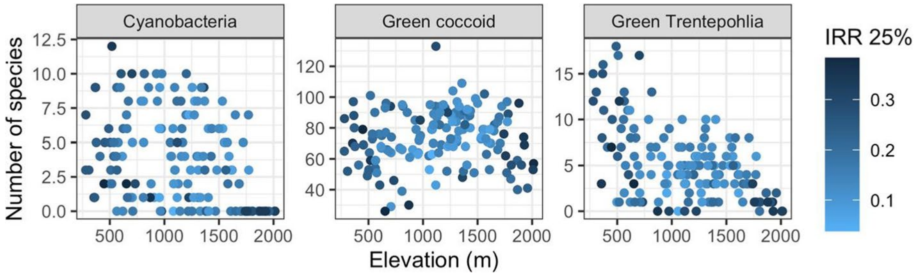

Fig. 8 Number of species by photobiont type across elevation. Point color indicates index of relative rarity (I_{RR}) at the 25% threshold. Most common lichens have coccoid green algae photobionts, but all groups have numerous rare species. Not shown: absent and polymorphic photobionts

Lichen trait compositions

Most common lichens (those with zero rarity weight) had coccoid green algae photobionts, although many rare lichens also share this trait, which reflects the overall dominance of these partners in lichen symbioses across our study system. In contrast, few species with *Trentepohlia* green algae, cyanobacteria, polymorphic, or absent photobionts were common (Fig. S7). Low elevation plots tended to have large numbers of species with *Trentepohlia* photobionts, corresponding with the increased I_{RR} at low elevations (Fig. 8). Interestingly, plots with high rock cover had few species with *Trentepohlia* photobionts, but

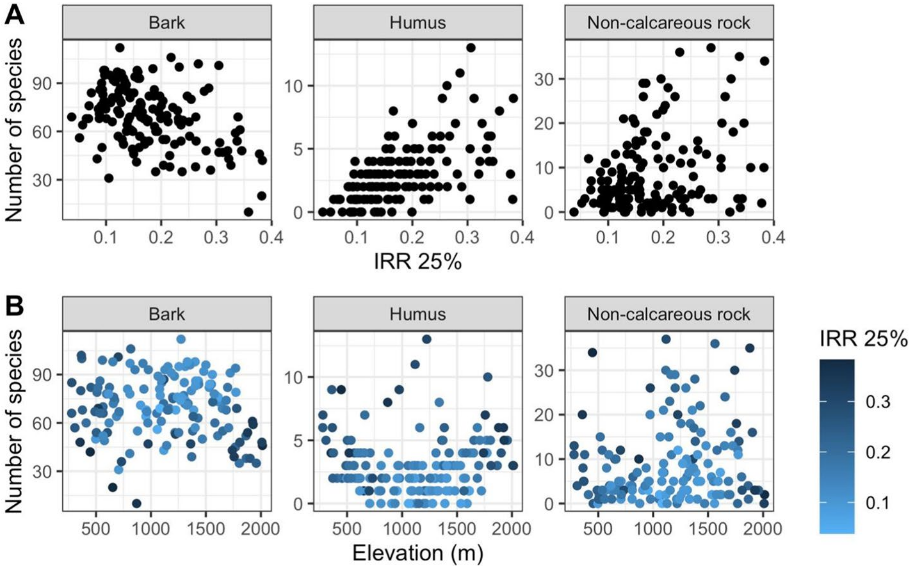

Fig. 9 Number of species per dominant substrate across **A** I_{RR} values and **B** elevation. Most common lichen species are bark-associated, but all substrates have numerous rare species. Note: these are the dominant substrate for each lichen species, but species are not exclusive to certain types of substrate in general. Not shown: substrate groups with maximum plot-level richness of six species or fewer (fungi, lichen, hepatics, leaf, wood, calcareous rock)

low rock cover plots with high I_{RR} values tended to have many species with *Trentepohlia* photobionts (Fig. S7).

The dominant substrate for most common lichens was bark, while rock- and humus-associated species were nearly never common (Fig. S9). Nonetheless, all substrates hosted large numbers of rare lichen species. Middle elevation plots had large numbers of bark-associated lichens, while humus-associated lichens were found in higher species numbers at high and low elevations (Fig. 9). Rock-associated lichen species were found at high richness in plots with high rock cover (as were humus-associated species), where the number of bark-associated species decreased (Fig. S9).

High elevation plots had decreased species richness compared to middle elevations overall (Fig. 5C) and across trait groups (Supplemental Material). There were no clear patterns of trait compositions that might have explained the increased I_{RR} at high elevations, but increased richness of humus-associated species may play a role (Fig. 9).

Discussion

Lichens in the southern Appalachians show increased rarity (summarized at the plot level, based on species' number of occurrences) at low and high elevations, with a mid-elevation slump in rarity. This directly contrasts with the mid-elevation hump in lichen species richness (McCain et al. unpub.). At low elevations in this study area, plots with high rock cover, low tree density, or large numbers of species with *Trentepohlia* green algae photobionts (species which depend on warm, humid climates; Marini et al. 2011; Nascimbene and Marini 2015; Manzitto-Tripp et al. 2022) have the highest rarity. Preference for rock substrates seems to be important for many rare lichens in this region, and rocky plots with reduced tree cover included light gaps that were often dominated by lichens. The coldest and highest plots had increased rarity, but there were no other strong predictors at high elevations. This seems to suggest that high elevations in this region are high elevation 'island' communities with rare lichen species not found at lower elevations, aligning with elevational habitat zones (especially spruce-fir forests) in the region (White 1984; White et al. 2012).

The mid-elevation slump in rarity, directly contradicting the mid-elevation hump in species richness, is not simply the result of a negative relationship between rarity and richness. This suggests that different processes may be at play for rare and common species. While the increased rarity at high and low elevations is a robust pattern here, disentangling the influence of elevation and climate is difficult. The elevational pattern could result from many rare lichen species adapted to the warm climates of low elevations and a separate set of rare lichens adapted to the cold climates of high elevations (untested here). On the other hand, the spatial structure of elevation could produce this pattern (even though this pattern is robust to uniform sampling across elevation), as the highest and lowest elevations are, by definition, at the extremes (and therefore rare) within the study region. Globally, previous work has shown that rare species are found in rare climates (Ohlemüller et al. 2008), and our observed pattern could reflect that at the regional scale. Further theoretical developments regarding the influence of the structure of elevation on rarity patterns (especially when summarized at the plot level), parallel to work on the mid-domain effect which hypothesizes a mid-elevation peak in species richness solely due to geometric constraints and range sizes (Colwell and Lees 2000), are an important next step to disentangling the processes producing this pattern.

Our results may be impacted by use of a single rarity measure, number of occurrences, and by summarizing rarity at each plot. The observed U-shaped pattern with elevation could be derived in part because our rarity metric is based on number of occurrences. Species restricted to certain habitats/characteristics that are rare on the landscape are more likely to have a small number of occurrences. While other frameworks, such as the seven forms of rarity (Rabinowitz 1981), could provide more insight into range size, habitat specialization, and local abundance rarity patterns, we were limited by the presence-absence data in this study. Additionally, because we summarized rarity at the plot level, we are unable to disentangle species-level patterns, and rare lichen species were present across all elevations and a wide range of plot characteristics. However, we are confident that the spatial arrangement of plot locations well-represents the spatial composition of these plot characteristics in the region, so the patterns observed here are unlikely to be artefactual. Using a plot-level summary of rarity measured by number of occurrences provides an overview of lichen rarity patterns in this system for targeting initial conservation efforts, which can be complemented in the future with further study of species-level patterns and additional forms of rarity.

Our models suggest several key conservation targets for rare lichens in the southern Appalachians, which differ from targets to protect sites with the highest species richness. Certain factors that we hypothesized would be important based on the well-established nature of lichens as bioindicators, such as reduced habitat quality (after removing the most disturbed plots), anthropogenic land cover, and air pollution were of little or inconsistent importance in our models (though we did not include the most disturbed plots since they contained very few lichen species and were not indicative of ‘natural’ habitats), with elevation/temperature and rock cover consistently holding greater importance. As a result, rocky sites at low and middle elevations are of particular interest for protecting habitat for rare lichen species. Anthropogenic habitat modification and destruction tends to be a major threat at low elevations (Nogués-Bravo et al. 2008), so efforts to protect low elevation rare lichens should focus on those rocky habitats. At high elevations, climate change is a major risk to rare lichens, since rarity was increased in the highest and coldest locations. These highest and coldest climate zones are projected to shift upwards in elevation, potentially pushing species upward in elevation or even off the mountain tops (Dirnböck et al. 2011; Freeman et al. 2018; McCain et al. 2021). In the southern Appalachians, high elevation lichens are predicted to experience drastic reductions in suitable climate (Allen and Lendemer 2016a), though the levels of climate change experienced by organisms in the region has been shown to depend on topography (Lesser and Fridley 2016). Whether or not individual lichen species will respond to climate change is beyond the scope of this study, but the alignment of rarity and threats from climate change gives reason to be concerned. Identifying mechanisms for lichen adaptation or resiliency to climate change is an important area of future research (Allen 2017). Protecting locations with high lichen diversity (e.g., dense forest, high habitat quality scores) would also be valuable, but here, at least, where rarity and diversity hotspots are not aligned, a decision in conservation priority must be made.

Mountain ranges across the world contain much of global biodiversity and a disproportionate number of rare species (Albuquerque et al. 2019; Enquist et al. 2019). Within the southern Appalachians, the hotspots of lichen diversity and rarity do not align. However, the patterns of diversity and rarity in other mountain ranges and across taxonomic groups are largely yet to be studied. More work is needed to bring what is known from global studies to an actionable scale within the world's mountain ranges where knowledge can be directly applied to conserve the rare and the common, wherever they may be.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s10531-024-02795-z.

Acknowledgements The following are thanked for permission to carry out this project on their managed lands: AL State Parks and Forever Wild, NC State Parks, The Nature Conservancy, TN State Parks and Wildlife, US National Forest Service (Bankhead, Chattahoochee, Cherokee, Nantahala, Pisgah, Sumter, Talladega), US National Park Service (Great Smoky Mountains, Little River Canyon), US Fish and Wildlife Service (Wheeler NWR). Malcolm Hodges, Gary Kauffman, and Paul Super in particular are thanked for their assistance in permitting, logistics, and site selection. The following assisted in field data collection and processing: Jessica Allen, Carly Anderson-Stewart, Laura Boggess, Philip Evich, Robert Helsel, Malcolm Hodges, Jordan Hoffman, Jason Hollinger, Klara Kempter, Kyle Keepers, Will Kuhn, R. Troy McMullin, Zachary Muscavitch, and Kristin White. Ana Maria Ruiz served as project manager at NYBG and was essential to data entry and organization. Melissa Tulig and Joel Ramirez are thanked for implementing database structure and development. Ryan Adams, Laura Briscoe, Dina Clark, and Tim Hogan facilitated herbarium aspects of the study at COLO. This study is a product of National Science Foundation Dimensions of Biodiversity Award to University of Colorado (EAMT, CMM Award #1542629) and New York Botanical Garden (JCL Award #1432629).

Author contributions GLV in collaboration with CMM led development of the study. CMM, JCL, and EAMT designed and implemented the field and associated lab methods. JCL and EAMT led fieldwork, collection of field data, and field identification of vouchers; JCL finalized taxonomic identification and compilation of the species occurrence dataset; CMM led the building of the ecological dataset, GLV led the building of the GIS-derived dataset. GLV conducted the analyses. GLV wrote the initial manuscript and all authors contributed to the final version of the text.

Funding This study is a product of National Science Foundation Dimensions of Biodiversity Award to University of Colorado (EAMT, CMM Award #1542629) and New York Botanical Garden (JCL Award #1432629).

Declarations

Competing interests The authors have no relevant competing interests to disclose.

References

Albuquerque F, Astudillo-Scalia Y, Loyola R, Beier P (2019) Towards an understanding of the drivers of broad-scale patterns of rarity-weighted richness for vertebrates. Biodivers Conserv 28:3733–3747. https://doi.org/10.1007/s10531-019-01847-z

Allen JL (2017) Testing lichen transplant methods for conservation applications in the southern Appalachian Mountains, North Carolina, U.S.A. Bryologist 120:311–319. https://doi.org/10.1639/0007-2745-120.3.311

Allen JL, Lendemer JC (2016a) Climate change impacts on endemic, high-elevation lichens in a biodiversity hotspot. Biodivers Conserv 25:555–568. https://doi.org/10.1007/s10531-016-1071-4

Allen JL, Lendemer JC (2016b) Quantifying the impacts of sea-level rise on coastal biodiversity: a case study on lichens in the mid-Atlantic Coast of eastern North America. Biol Conserv 202:119–126. https://doi.org/10.1016/j.biocon.2016.08.031

Allen JL, Lendemer JC (2022) A call to reconceptualize lichen symbioses. Trends Ecol Evol 37:582–589. https://doi.org/10.1016/j.tree.2022.03.004

Allen JL, McMullin RT, Tripp EA, Lendemer JC (2019) Lichen conservation in North America: a review of current practices and research in Canada and the United States. Biodivers Conserv 28:3103–3138. https://doi.org/10.1007/s10531-019-01827-3

Arsenault A, Goward T (2016) Macrolichen diversity as an indicator of stand age and ecosystem resilience along a precipitation gradient in humid forests of inland British Columbia, Canada. Ecol Indic 69:730–738. https://doi.org/10.1016/j.ecolind.2016.04.015

Astudillo-Scalia Y, Albuquerque FS (2019) Evaluating the performance of rarity as a surrogate in site prioritization for biodiversity conservation. Glob Ecol Conserv. https://doi.org/10.1016/j.gecco.2019.e00639

Barry M, McMullin RT, Horn A (2015) Edge effects on the lichen genus Lobaria in Atlantic Canadian Forests. For Chron 91:534–540. https://doi.org/10.5558/tfc2015-092

Bässler C, Cadotte MW, Beudert B et al (2016) Contrasting patterns of lichen functional diversity and species richness across an elevation gradient. Ecography 39:689–698

Breiman L (2001) Random forests. Mach Learn 45:5–32

Brunialti G, Giordani P, Ravera S, Frati L (2021) The reproductive strategy as an important trait for the distribution of lower-trunk epiphytic lichens in old-growth vs. non-old growth forests. Forests 12:27. https://doi.org/10.3390/f12010027

Carlton C, Bayless V (2007) Documenting beetle (Arthropoda: Insecta: Coleoptera) diversity in Great Smoky Mountains National Park : Beyond the halfway point. Southeast Nat 6:183–192

Cheng J, Karambelkar B, Xie Y (2021) Leaflet: Create Interactive Web Maps with the JavaScript “Leaflet” Library. R package version 2.0.4.1. https://CRAN.R-project.org/package=leaflet

Colwell RK, Lees DC (2000) The mid-domain effect: geometric species richness. Trends Ecol Evol 15:70–76

Cutler DR, Edwards TC, Beard KH et al (2007) Random forests for classification in ecology. Ecology 88:2783–2792. https://doi.org/10.1890/07-0539.1

Davies KF, Margules CR, Lawrence JF (2004) A synergistic effect puts rare, specialized species at greater risk of extinction. Ecology 85:265–271. https://doi.org/10.1890/03-0110

Dewitz J (2019) National Land Cover Database (NLCD) 2016: U.S. Geological Survey data release. https://doi.org/10.5066/P96HHBIE

Dirnböck T, Essl F, Rabitsch W (2011) Disproportional risk for habitat loss of high-altitude endemic species under climate change. Glob Chang Biol 17:990–996. https://doi.org/10.1111/j.1365-2486.2010.02266.x

Drummond MA, Loveland TR (2010) Land-use pressure and a transition to forest-cover loss in the Eastern United States. Bioscience 60:286–298. https://doi.org/10.1525/bio.2010.60.4.7

Edwards TC, Cutler DR, Geiser L et al (2004) Assessing rarity of species with low detectability: Lichens in Pacific Northwest forests. Ecol Appl 14:414–424. https://doi.org/10.1890/02-5236

Engler R, Randin CF, Thuiller W et al (2011) 21st century climate change threatens mountain flora unequally across Europe. Glob Chang Biol 17:2330–2341. https://doi.org/10.1111/j.1365-2486.2010.02393.x

Enquist BJ, Feng X, Boyle B et al (2019) The commonness of rarity: global and future distribution of rarity across land plants. Sci Adv 5:1–14. https://doi.org/10.1126/sciadv.aaz0414

Evans JS, Murphy MA, Holden ZA, Cushman SA (2011) Modeling species distribution and change using Random Forests. In: Drew CA, Wiersma YF, Huettmann F (eds) Predictive species and habitat modeling in landscape ecology: concepts and applications. Springer, New York, pp 139–159

Fick SE, Hijmans RJ (2017) WorldClim 2: new 1km spatial resolution climate surfaces for global land areas. Int J Climatol 37:4302–4315

Forister ML, Pelton EM, Black SH (2019) Declines in insect abundance and diversity: We know enough to act now. Conserv Sci Pract 1:1–8. https://doi.org/10.1111/csp2.80

Freeman BG, Scholer MN, Ruiz-Gutierrez V, Fitzpatrick JW (2018) Climate change causes upslope shifts and mountaintop extirpations in a tropical bird community. Proc Natl Acad Sci U S A 115:11982–11987. https://doi.org/10.1073/pnas.1804224115

Galloway DJ (2008) Lichen biogeography. In: Nash TH (ed) Lichen biology, 2nd edn. Cambridge University Press, Cambridge, pp 315–335

Greenblatt RE, Himes BE (2019) Facilitating inclusion of geocoded pollution data into health studies. AMIA Jt Summits Transl Sci Proc 2019:553–561

Grenyer R, Orme CDL, Jackson SF et al (2006) Global distribution and conservation of rare and threatened vertebrates. Nature 444:93–96. https://doi.org/10.1038/nature05237

Grube M, Cardinale M, De Castro JV et al (2009) Species-specific structural and functional diversity of bacterial communities in lichen symbioses. ISME J 3:1105–1115. https://doi.org/10.1038/ismej.2009.63

Harnik PG, Simpson C, Payne JL (2012) Long-term differences in extinction risk among the seven forms of rarity. Proc R Soc B 279:4969–4976

Hodkinson BP (2010) A first assessment of lichen diversity for one of North America's "biodiversity hotspots" in the southern Appalachians of Virginia. Castanea 75:126–133. https://doi.org/10.2179/09-033.1

Lee CB, Chun JH, Cho HJ, Song HK (2013) Altitudinal patterns of plant species richness on the ridge of the Baekdudaegan Mountains, South Korea: area and mid-domain effect. Forest Sci Technol 8:154–160. https://doi.org/10.1080/21580103.2012.704970

Lendemer JC, Harris RC, Ruiz AM (2016) A review of the lichens of the Dare Regional Biodiversity Hotspot in the Mid-Atlantic Coastal Plain of North Carolina, Eastern North America. Castanea 81:1–77. https://doi.org/10.2179/15-073R2

Lendemer JC, Harris RC, Tripp EA (2013) The lichens and allied fungi of Great Smoky Mountains National Park. The New York Botanical Garden Press, New York

Lendemer JC, Tripp EA, Sheard J (2014) A review of Rinodina (Physciaceae) in Great Smoky Mountains National Park highlights the growing significance of this "island of biodiversity" in eastern North America. Bryologist 117:259–281. https://doi.org/10.1639/0007-2745-117.3.259

Leroy B, Petillon J, Gallon R et al (2012) Improving occurrence-based rarity metrics in conservation studies by including multiple rarity cut-off points. Insect Conserv Divers 5:159–168

Lesser MR, Fridley JD (2016) Global change at the landscape level: relating regional and landscape-scale drivers of historical climate trends in the Southern Appalachians. Int J Climatol 36:1197–1209. https://doi.org/10.1002/joc.4413

Liaw A, Wiener M (2002) Classification and regression by random Forest. R News 2:18–22

Manzitto-Tripp EA, Lendemer JC, McCain CM (2022) Most lichens are rare, and degree of rarity is mediated by lichen traits and biotic partners. Divers Distrib 28:1810–1819. https://doi.org/10.1111/ddi.13581

Marini L, Nascimbene J, Nimis PL (2011) Large-scale patterns of epiphytic lichen species richness: photobiont-dependent response to climate and forest structure. Sci Total Environ 409:4381–4386. https://doi.org/10.1016/j.scitotenv.2011.07.010

McCain CM, Grytnes J (2010) Elevational gradients in species richness. Encyclopedia of Life Sciences. Wiley, Chichester, pp 1–10

McCain CM, King SRB (2014) Body size and activity times mediate mammalian responses to climate change. Glob Chang Biol 20:1760–1769. https://doi.org/10.1111/gcb.12499

McCain CM, King SRB, Szewczyk TM (2021) Unusually large upward shifts in cold-adapted, montane mammals as temperature warms. Ecology 102:e03300. https://doi.org/10.1002/ecy.3300

McCune B (2017a) Microlichens of the Pacific Northwest, vol 1. Wild Blueberry Media, Corvallis, OR, USA

McCune B (2017b) Microlichens of the Pacific Northwest, vol 2. Wild Blueberry Media, Corvallis, OR, USA

McCune B, Dey J, Peck J et al (1997) Regional gradients in lichen communities of the southeast United States. Bryologist 100:145–158

McManamay RH, Resler LM, Campbell JB, McManamay RA (2011) Assessing the impacts of balsam woolly adelgid (*Adelges piceae* Ratz.) and anthropogenic disturbance on the stand structure and mortality of Fraser fir [*Abies fraseri* (pursh) Poir.] in the Black Mountains. North Carolina Castanea 76:1–19. https://doi.org/10.2179/09-059.1

Nascimbene J, Marini L (2015) Epiphytic lichen diversity along elevational gradients: biological traits reveal a complex response to water and energy. J Biogeogr 42:1222–1232. https://doi.org/10.1111/jbi.12493

Nascimbene J, Thor G, Nimis PL (2012) Habitat types and lichen conservation in the Alps: perspectives from a case study in the Stelvio National Park (Italy). Plant Biosyst 146:428–442

Nash TH, Gries C, Bungartz F (eds) (2007) Lichens of the Greater Sonoran Desert Region, vol 3. Lichens Unlimited: Arizona State University, Tempe, AZ, USA

Nash TH, Ryan BD, Diederich P et al (eds) (2004) Lichens of the Greater Sonoran Desert Region, vol 2. Lichens Unlimited: Arizona State University, Tempe, AZ, USA

Nash TH, Ryan BD, Gries C, Bungartz F (eds) (2002) Lichens of the Greater Sonoran Desert Region, vol 1. Lichens Unlimited: Arizona State University, Tempe, AZ, USA

Nimis PL, Martellos S, Spitale D, Nascimbene J (2018) Exploring patterns of commonness and rarity in lichens: a case study from Italy (Southern Europe). Lichenologist 50:385–396. https://doi.org/10.1017/S0024282917000731

Nogués-Bravo D, Araújo MB, Romdal T, Rahbek C (2008) Scale effects and human impact on the elevational species richness gradients. Nature 453:216–219. https://doi.org/10.1038/nature06812

Noss RF, Laroe ET, Scott JM (1995) Endangered ecosystems of the United States: a preliminary assessment of loss and degradation. US Dep Inter Natl Biol Serv - Biol Rep. https://doi.org/10.3368/er.14.1.95

Öckinger E, Nilsson SG (2010) Local population extinction and vitality of an epiphytic lichen in fragmented old-growth forest. Ecology 91:2100–2109. https://doi.org/10.1890/09-1421.1

Ohlemüller R, Anderson BJ, Araújo MB et al (2008) The coincidence of climatic and species rarity: high risk to small-range species from climate change. Biol Lett 4:568–572

Parkes D, Newell G, Cheal D (2003) Assessing the quality of native vegetation: the “habitat hectares” approach. Ecol Manag Restor 4:29–38. https://doi.org/10.1046/j.1442-8903.4.s.4.x

Petranka JW (1998) Salamanders of the United States and Canada. Smithsonian Institution, Washington, D.C., USA

Pichler G, Muggia L, Carniel FC et al (2023) How to build a lichen: from metabolite release to symbiotic interplay. New Phytol. https://doi.org/10.1111/nph.18780.10.1111/nph.18780

R Core Team (2018) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/

Rabinowitz D (1981) Seven forms of rarity. In: Synge H (ed) The biological aspects of rare plant conservation. Wiley, Chichester, pp 205–217

Rahbek C, Borregaard MK, Colwell RK et al (2019) Humboldt’s enigma: what causes global patterns of mountain biodiversity? Science 80(365):1108–1113. https://doi.org/10.1126/science.aax0149

Richardson AD, Denny EG, Siccama TG, Lee X (2003) Evidence for a rising cloud ceiling in eastern North America. J Clim 16:2093–2098. https://doi.org/10.1175/1520-0442(2003)016%3c2093:EFARCC%3e2.0.CO;2

Root HT, Miller JED, McCune B (2011) Biotic soil crust lichen diversity and conservation in shrub-steppe habitats of Oregon and Washington. Bryologist 114:796–812

Rosso AL, McCune B, Rambo TR (2000) Ecology and conservation of a rare, old-growth-associated canopy lichen in a silvicultural landscape. Bryologist 103:117–127. https://doi.org/10.1639/0007-2745(2000)103[0117:EACOAR]2.0.CO;2

Spribille T, Resl P, Stanton DE, Tagirdzhanova G (2022) Evolutionary biology of lichen symbioses. New Phytol 234:1566–1582. https://doi.org/10.1111/nph.18048

Tripp EA (2015) Lichen inventory of white rocks open space (City of Boulder, Colorado). West North Am Nat 75:301–310. https://doi.org/10.3398/064.075.0307

Tripp EA, Lendemer JC (2020) Field Guide to the Lichens of Great Smoky Mountains National Park. University of Tennessee Press, Knoxville, TN, USA

Tripp EA, Lendemer JC (2019) Highlights from 10+ years of lichenological research in great smoky mountains national park: Celebrating the United States national park service centennial. Syst Bot 44:943–980. https://doi.org/10.1600/036364419X15710776741332

Tripp EA, Lendemer JC, Barberán A et al (2016) Biodiversity gradients in obligate symbiotic organisms: exploring the diversity and traits of lichen propagules across the United States. J Biogeogr 43:1667–1678. https://doi.org/10.1111/jbi.12746

Tripp EA, Lendemer JC, McCain CM (2019) Habitat quality and disturbance drive lichen species richness in a temperate biodiversity hotspot. Oecologia 190:445–457. https://doi.org/10.1007/s00442-019-04413-0

Ulrich W, Matthews TJ, Kubota Y (2020) Constraints on the distribution of species abundances indicate universal mechanisms of community assembly. Ecol Res 35:362–371

White P, van de Ge G, Soulé P (2012) Succession and disturbance in an endangered red spruce−Fraser fir forest in the southern Appalachian Mountains, North Carolina, USA. Endanger Species Res 18:17–25. https://doi.org/10.3354/esr00431

White PS (1982) The flora of Great Smoky Mountains National Park: An annotated checklist of the vascular plants and a review of previous floristic work. US Dep Inter Natl Park Serv Res Manag Rep SER-55

White PS (1984) The Southern Appalachian spruce-fir ecosystem: Its biology and threats. US Dep Inter Natl Park Serv Southeast Reg Off Res Manag Rep SER-71

Wickham H, Averick M, Bryan J et al (2019) Welcome to the tidyverse. J Open Softw 4:1686. https://doi.org/10.21105/joss.01686

Williams SE, Williams YM, VanDerWal J et al (2009) Ecological specialization and population size in a biodiversity hotspot: How rare species avoid extinction. Proc Natl Acad Sci USA 106:19737–19741. https://doi.org/10.1073/pnas.0901640106

Zhao M, Heinsch FA, Nemani RR, Running SW (2005) Improvements of the MODIS terrestrial gross and net primary production global data set. Remote Sens Environ 95:164–176