



# Habitat quality and disturbance drive lichen species richness in a temperate biodiversity hotspot

Erin A. Tripp<sup>1,2</sup> · James C. Lendemer<sup>3</sup> · Christy M. McCain<sup>1,2</sup>

Received: 23 April 2018 / Accepted: 30 April 2019 / Published online: 15 May 2019  
© Springer-Verlag GmbH Germany, part of Springer Nature 2019

## Abstract

The impacts of disturbance on biodiversity and distributions have been studied in many systems. Yet, comparatively less is known about how lichens—obligate symbiotic organisms—respond to disturbance. Successful establishment and development of lichens require a minimum of two compatible yet usually unrelated species to be present in an environment, suggesting disturbance might be particularly detrimental. To address this gap, we focused on lichens, which are obligate symbiotic organisms that function as hubs of trophic interactions. Our investigation was conducted in the southern Appalachian Mountains, USA. We conducted complete biodiversity inventories of lichens (all growth forms, reproductive modes, substrates) across 47, 1-ha plots to test classic models of responses to disturbance (e.g., linear, unimodal). Disturbance was quantified in each plot using a standardized suite of habitat quality variables. We additionally quantified woody plant diversity, forest density, rock density, as well as environmental factors (elevation, temperature, precipitation, net primary productivity, slope, aspect) and analyzed their impacts on lichen biodiversity. Our analyses recovered a strong, positive, linear relationship between lichen biodiversity and habitat quality: lower levels of disturbance correlate to higher species diversity. With few exceptions, additional variables failed to significantly explain variation in diversity among plots for the 509 total lichen species, but we caution that total variation in some of these variables was limited in our study area. Strong, detrimental impacts of disturbance on lichen biodiversity raises concerns about conservation and land management practices that fail to incorporate complete estimates of biodiversity, especially from ecologically important organisms such as lichens.

**Keywords** Biodiversity · Disturbance · Hotspot · Linear · Symbiotic

## Introduction

It is widely recognized that disturbance plays a major role in determining species diversity, distributions, and functions (Hutchinson 1953; Connell 1978; Johst and Huth

2005). Approaches to understanding the impacts of disturbance have included examining effects of variables across trophic levels (Wootton 1998), spatial scales (Witman et al. 2008; Limberger and Wickham 2012), and temporal scales (Svensson et al. 2007; Zemanová et al. 2017). Others have explored how disturbance affects functional diversity and ecosystem services (Biswas and Mallik 2010; Thom and Seidl 2016), whether choice of diversity measure matters (Mackey and Currie 2001; Johst and Huth 2005; Svensson et al. 2007), and how species traits such as dispersal respond to disturbance (Johansson et al. 2013). This has yielded a nuanced understanding of how, and in what contexts, disturbance explains spatial variation in diversity and function across organisms and ecosystems.

Despite the above advances, few large-scale studies have examined how disturbance—natural or anthropogenic—impacts the lichen symbiosis. Specifically, the establishment and development of a lichen requires that a minimum of two compatible, yet often unrelated symbionts, be

---

Communicated by Anne Pringle.

---

**Electronic supplementary material** The online version of this article (<https://doi.org/10.1007/s00442-019-04413-0>) contains supplementary material, which is available to authorized users.

---

✉ Erin A. Tripp  
erin.tripp@colorado.edu

<sup>1</sup> Department of Ecology and Evolutionary Biology, University of Colorado, Boulder, CO 80309, USA

<sup>2</sup> University of Colorado, Museum of Natural History, Boulder, CO 80309, USA

<sup>3</sup> The New York Botanical Garden, Institute of Systematic Botany, Bronx, NY 10458-5126, USA

present in any given environment. This suggests that, in contrast to some organisms, lichens and other obligate symbionts may be especially sensitive to disturbance because their life strategies are initially constrained by biotic interactions. Further, such organisms may respond differently to disturbance in comparison to non-obligate organisms. For example, classical disturbance models predict responses based on tradeoffs between disturbance tolerance and competitive ability (Hutchinson 1953; Connell 1978; Huston 1994, 1979; Wilson 1994; Violle et al. 2010). However, obligate symbiotic diversity and distribution, such as that of lichens and many other organisms, may be governed more strongly by intrinsic biotic factors such as whether or not all symbionts are present in the environment at the earliest stages of development (Honegger 2012; Tripp et al. 2016).

If the above is true, theoretical underpinnings of classical models, which serve as umbrellas under which the interplay among disturbance, diversity, and abundance is interpreted (Shea et al. 2004; Sheil and Burslem 2013) may not fully explain patterns in lichens and other obligate symbiotic organisms in nature. Understanding whether and how lichens respond to disturbance has widespread implications considering the proliferation of studies documenting the prevalence of microbiomes and symbiomes, or co-evolving sets of unrelated symbionts (Röthig et al. 2016; Tripp et al. 2017; Brodie et al. 2017).

Lichens are obligate symbiotic organisms composed of a minimum of one fungus and one alga or cyanobacterium (Brodo et al. 2001). A given lichen also often harbors numerous other symbionts including bacteria, additional algal genotypes, and additional fungi (Arnold et al. 2009; Bates et al. 2012; U'Ren et al. 2012; Fleischhacker et al. 2015; Muggia et al. 2016; Chagnon et al. 2016; Fernandez-Mendoza et al. 2017). Thus, lichens function as hubs of trophic interactions, represent a remarkable symbiotic life form and, serve as a source for evolutionary innovation not achieved elsewhere in the fungal tree of life (Honegger 1991; Lutzoni et al. 2001). From a functional perspective, lichens exist via diverse growth forms, display complex morphologies and reproductive modes, and contribute a broad array of ecological services including biogeochemical cycling, biomass production, pollutant sequestration, decomposition, soil formation, and habitat or nutrition sources for an untold diversity of organisms (Szczeplaniak and Biziuk 2003; Cornelissen et al. 2007; Asplund and Wardle 2017). From a biological diversity perspective, lichens are often among the most diverse eukaryotic organisms in a given area, following insects, vascular plants, and non-lichenized fungi (e.g., DLIA 2017).

For nearly two centuries, disturbance has been recognized as having a major role in shaping patterns of lichen diversity and abundance. However, knowledge of lichen disturbance ecology has developed in three focal areas. First,

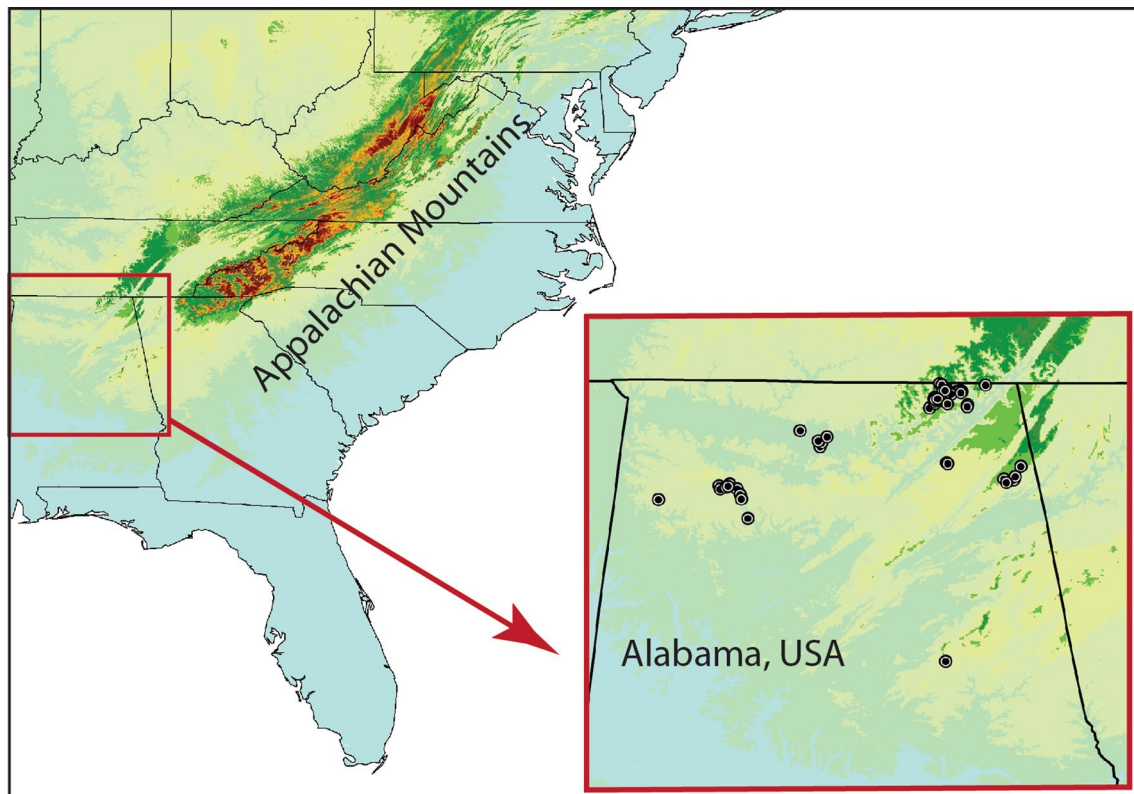
the majority of studies have focused on subsets of lichen diversity, such as macrolichens, foliicolous lichens, or specific species of lichens (Mistry 1998; Dynesius and Zinko 2006; Benítez et al. 2012; Barry et al. 2015; Arsenault and Goward 2016; Tarasova et al. 2017). In contrast, few studies have incorporated data derived from total lichen diversity, with most studies completely excluding microlichens that can comprise more than half the total diversity in an area (e.g., Tripp 2015; Lendemer et al. 2016). Second, research to date has emphasized responses to catastrophic disturbances (Mistry 1998; McMullin et al. 2008; O'Bryan et al. 2009; Ellis and Coppins 2010; Lundström et al. 2013; Bartels and Chen 2015), land management practices (Zemanová et al. 2017; Ray et al. 2015), and pollution (McCune et al. 1997; Ellis and Coppins 2010; Shrestha and St. Clair 2011). In contrast, much less is known about the impacts of milder to moderate forms of disturbance such as patchiness, extent and quality of native habitat, and forest maturity (but see Johansson et al. 2012; Pastore et al. 2014). Third, prior studies have not dissected individual components of disturbance in natural systems via analyses of a suite habitat quality variables in addition to standard ecological metrics and environmental variables. This is particularly important given that extensive work has shown that habitat diversity and complexity, together with climate, are important factors that drive the distributions of biodiversity (MacArthur 1972; Currie 1991; McCain 2009; Kessler et al. 2011).

Understanding of the interplay between lichen diversity and disturbance has developed in the absence of taxonomically comprehensive studies spanning the dimensions of disturbance and environment across full gradients typically found in natural systems. Here, we use a new regional-scale dataset to test whether and how anthropogenic disturbance explains variation in lichen species diversity in a temperate biodiversity hotspot. The dataset spans 47 1-ha plots in the southern Appalachian Mountains of eastern North America and includes more 4000 occurrences representing 509 phenotypically delimited lichen species (see “[Materials and methods](#)”), in addition to data for woody plant diversity, forest density, rock density, climate and geographical factors, ten components of habitat quality.

## Materials and methods

### Study plots

To assess impacts of disturbance and additional biotic and abiotic factors on lichen diversity, we inventoried total lichen biodiversity across 47 one-hectare (ha) sites in the southern Appalachian foothills of northern Alabama (Fig. 1). Site selection spanned several axes of disturbance plus a range of additional variables (tree and rock substrate density, woody



**Fig. 1** Map of the Appalachian Mountain chain of eastern North America (cool to warm color scale depicts increasing 100 m elevational bands from 0 to 100 m of light blue to 2000–2100 m of dark

red). Inset shows the southern portions of the southern Appalachian Mountains and 47 1-ha study sites located in northern Alabama. Color version of this figure is available online

tree diversity, elevation, aspect, slope). These plots were replicated across the above axes as best as possible, following Fierer et al. (2011), McCain (2004, 2009), and McCain and Grytnes (2010). During the site selection process, attempts were made to hold uniform several explanatory variables to minimize potentially confounding effects of extreme within-site variation. For example, in a given plot, we sampled only one aspect (e.g., east-facing), attempted to minimize variation in slope (e.g., 10° throughout the 1 ha), and did not traverse major shifts in habitat type (e.g., dry ridgetop forest vs. wet riparian forest).

### Biodiversity inventory

In each 1 ha plot, a taxonomically comprehensive lichen inventory (all growth forms, all substrates, all reproductive modes) was implemented via expert-based surveys in which each species encountered by a collector was vouchered. These methods have been shown more effective at capturing total diversity than plot- or transect-based methods as well as inventories by non-experts (Coddington et al. 1991; Sørensen et al. 2012). All 47 plots were sampled until total species diversity was vouchered, as determined by the primary collectors (collection times varied between 10 min in

highly degraded sites to 110 min in less disturbed sites). Using species counts per plot, we calculated an accumulation curve via the *specaccum* function in the *vegan* package (<http://vegan.r-forge.r-project.org>) in R. For each voucher specimen, precise geographic locality, habitat, substrate, and other ecological information were recorded. Two individuals (Lendemer, Tripp) completed all taxonomic inventories. Collection of ecological data (see below) was spearheaded by McCain assisted by Tripp, Lendemer, Anderson Stewart, and Hoffman.

Voucher specimens were returned to a temporary, traveling laboratory for preliminary identifications. Unique identifiers were assigned to each collection and its subcollections (e.g., DNA vouchers, photographs). Specimens were curated (e.g., soil stabilized), thin-sectioned to study anatomical features (e.g., ascospore shape, size), and phenotyped for taxonomically important secondary metabolites using a traveling Thin Layer Chromatography lab [TLC methods following Lendemer (2011)]. All specimens were identified using regional keys (Lendemer et al. 2013, 2016; Tripp and Lendemer 2019a, in press) that follow current concepts of phenotypically characterized lichen species (Esslinger 2016, for the most part), many of which have been included in molecular phylogenetic studies and found

to be monophyletic. Identifications were further refined at home institutions of J. Lendemer (New York Botanical Garden, NY Herbarium) and E. Tripp (University of Colorado, COLO Herbarium). Vouchers were collected in duplicate, are permanently deposited at NY and COLO, and resulting data are available at: NYBG's Starr Virtual Herbarium (<http://sweetgum.nybg.org/science/vh/>), COLO's internal database (<https://botanydb.colorado.edu/index.php>), SEI-Net (<http://swbiodiversity.org/seinet/>), and iDigBio (<https://www.idigbio.org/>).

### Phenotypic (morphological) species delimitation

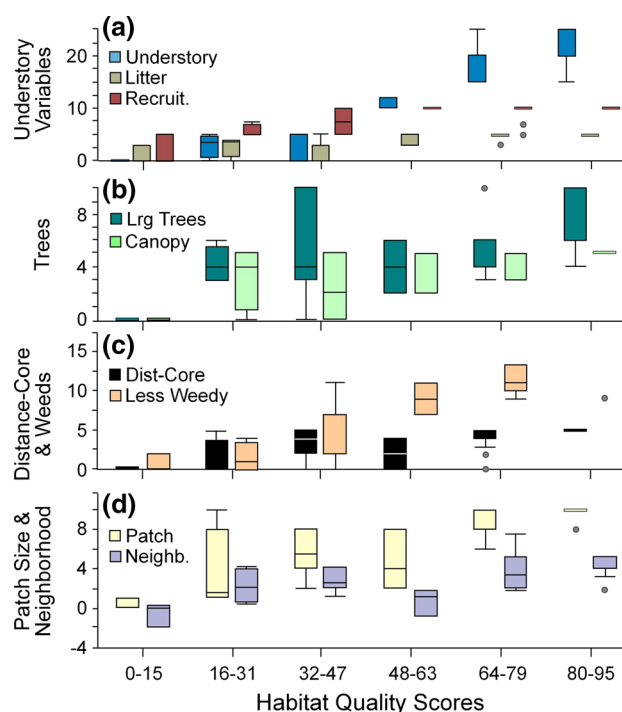
Recognition of species on the basis of phenotypes vs. genotypes varies widely in mycology and is oftentimes group-specific (Balasundaram et al. 2015; Yahr et al. 2016). Species delimitation methods, moreover, vary as a function of density of cryptic diversity (Miadlikowska et al. 2018). In lichen-forming fungi, examples of species that cannot be delimited and recognized using phenotypic (including chemical) characters appear to be rare (for example, the 800 square miles comprising Great Smoky Mountains National Park—the most lichenologically diverse national park in the United States—contains nearly 1000 species, all of which can be identified using standard phenotypic-based methods of delimitation; Tripp and Lendemer 2019a, in press). In fact, in lichens, the vast majority of molecular studies have led to taxonomic redelimitation of species using previously overlooked or inconspicuous phenotypic characters (Yahr et al. 2016; Lücking et al. 2017); this applies even to instances where species were originally purported to be cryptic (e.g., Ossowska et al. 2018). Thus, we assert that the phenotypically delimited species are a reasonable approximation of the actual taxonomic diversity of lichens in a given biogeographic region (Leavitt et al. 2016; Yahr et al. 2016; Magain et al. 2018; Tripp and Lendemer 2019a, in press), as is the case for many other well-studied group of organisms that can be readily examined with a microscope.

### Disturbance assessments

Northern Alabama hosts a spatially mosaicked, broad spectrum of habitat qualities ranging from exceptionally disturbed to moderately intact to near-*virgin* forests that have seen little impact in recorded history. Examples of exceptionally disturbed habitats include cultivated cornfields, immature forest regrowth following clearcutting, and paved parking lots. Examples of moderately intact habitats include the majority of extant, primarily native ecosystems in this portion of the state (e.g., lands managed by the U.S. Forest Service, and Alabama state lands under jurisdiction of Forever Wild, including Wildlife Management Areas). Examples of near-*virgin* forests include old-growth box canyons

in the Sipsey Wilderness (Bankhead National Forest) and small subsets of Little River Canyon National Preserve and Skyline Wildlife Management Area.

We quantified disturbance on a scale of  $-2$  (lowest habitat quality [HQ], or most disturbed) to 95.2 (highest HQ, or least disturbed) using the native vegetation assessment methods of Parkes et al. (2003; note this scale allows for a minimum value that is negative). The HQ of each plot was based on the sum of 10 metrics (value range for each in parentheses; see Fig. 2) and incorporated both site-specific as well as landscape context metrics including: percentage of mature trees (0–10), percentage of native tree canopy cover (0–5), percentage of native understory and degree of anthropogenic modification (0–25), percentage of weed cover (0–15), percentage of recruiting native trees (0–10), percentage of native, expected litter quantity (0–5), percentage of native, expected coarse woody debris (0–5), habitat fragment size (0–10), degree of fragmentation of surrounding hectares ( $-2$  to 5.2), and distance to nearest core area



**Fig. 2** Illustration of the components of our habitat quality metric based on the scores from the 47 plots using quartile box-plots for groupings of habitat quality (value intervals of 15). These scores are inversely related to disturbance: lower values are more highly disturbed. The overall habitat quality metric is a sum of 10 habitat assessments, including: **a** percent native understory, litter, and tree recruitment; **b** percent mature, large trees and native tree canopy cover; **c** distance to nearest core area and percent weediness (most to least); and **d** habitat patch size and degree of fragmentation of surrounding hectares (neighborhood). Course woody increased with habitat quality (not shown); see text for details. Color version of this figure is available online

(0–5) based on Parkes et al. (2003). All disturbance scores were quantified in the field at the time of plot sampling.

### Forest diversity, density, and rockiness assessments

Because total tree diversity and density of woody vegetation present can impact diversity of other organisms, especially sessile taxa such as lichens that utilize trees as primary substrates, we also quantified these factors in each plot. First, a total checklist of all woody, vascular plant diversity (trees and shrubs) was compiled for each plot using existing knowledge and supplemented by standard identification tools, as needed (Weakley 2015). These data were analyzed (see below) with and without inclusion of the shrub component. Second, we established a 10-square meter ( $m^2$ ) representative subplot within which we quantified the total number of trees > 10 cm diameter at breast height (DBH) as well as the diameter and species identification of each tree. Finally, because rocks represent an important substrate that can host highly unique communities of lichens (Flock 1978; Brodo et al. 2001; Henson et al. 2013; Tripp 2015), we assessed the density of exposed rock at each site on a qualitative scale ranging from 1 to 10.

### Environmental variables

Numerous climatic and geographic variables are associated with taxonomic diversity, often with high correlation (e.g., Hawkins et al. 2003; Currie et al. 2004; Dynesius and Zinko 2006; Ellis and Coppins 2010; McCain and Grytnes 2010). For the southern Appalachians, important potential variables related to overall lichen diversity include temperature, precipitation, net primary productivity (NPP), elevation, slope, and aspect. Using geographic coordinates of each plot, we extracted elevation from a digital elevation model (Shuttle Radar Topography Mission (SRTM), NASA, resolution: 90 m) in ArcGIS, whereas we estimated the slope and aspect while sampling the plot. We used mean annual temperature and precipitation from the PRISM 30-year normals (resolution: 800  $m^2$ , 1981–2010), and mean NPP using MODIS estimates (MOD17A3, resolution:  $\sim 1 \text{ km}^2$ , 2000–2013), extracted for each plot using ArcGIS.

### Statistical analyses

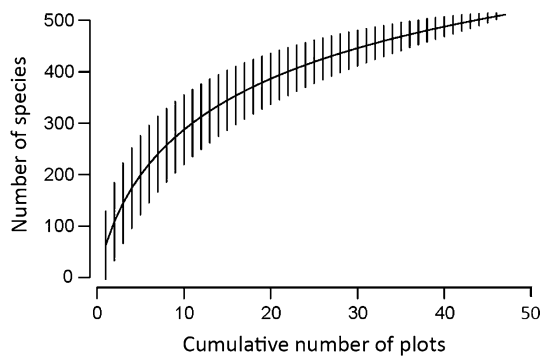
To assess the fit of disturbance models to our data, we compared linear, quadratic, and cubic relationships using AICc weights to extract relationships between lichen diversity and disturbance. To determine which variables were most associated with lichen diversity across these 47 sites, we ran forward, stepwise, multivariate linear regressions for all quantitative variables: elevation (m), disturbance, NPP ( $\text{gC}/\text{m}^2/\text{yr}$ ), precipitation (mm), rock cover, slope, temperature

( $^{\circ}\text{C}$ ), tree diameter (sum DBH), tree quantity (count), and tree richness. For stepwise variable inclusion, we used the minimum BIC cutoff value (models were consistent for BIC, AICc, and  $p$  value cutoff values except that the latter two included more variables, but additional variables were consistently non-significant individually when included). Model fit was assessed with  $r^2$  values and variable strength with  $p$  values. Several of our abiotic and biotic variables are correlated (e.g., temperature and elevation, disturbance and number of trees; see Appendix 2 for a correlation matrix and additional analyses), thus stepwise multivariate regression was chosen to simultaneously assess variable fit and collinearity. But, we also compared best stepwise multivariate regression models with and without disturbance to assess relative importance of the collinear variables, and we conducted a multivariate partial least squares test to detect the key variables that should be included in the model despite collinearity (see Appendix 2 for further details).

For plot orientation, assessed qualitatively (flat vs. facing east, west, south, north), we used ANOVAs to test for differences in lichen diversity as well as disturbance. Additionally, we ran the same multiple regression methods employing additional variables for functionally contrasting groups of lichens [sexually (via fungal-only ascospores, which must later encounter at minimum a new photobiont partner to complete the reproductive process) vs. asexually (via lichenized propagules that co-disperse both the fungal and algal partners, and likely other symbionts) reproducing lichens, microlichens vs. macrolichens, and four dominant growth forms consisting each of a minimum of 20 taxa (crustose, foliose, fruticose, squamulose)] to detect potential biological differences among these groups. Mode of reproduction was determined as the primary mode representative for each species (e.g., some lichens reproduce asexually via lichenized propagules for most phases of their life history but are known to pass through brief, sexual phases; these species were scored as asexual; in contrast, sexually reproducing species are not known to manufacture asexual, lichenized propagules, Tripp and Lendemer 2018). Statistical analyses were conducted using JMP Pro 13.0 (2016 SAS Institute Inc.).

### Results

Across the 47 sites, we documented a total of 509 lichen species. Overall the biota was dominated by microlichens [316 taxa (62%) vs. 193 macrolichens (38%)] while there were slightly more sexually reproducing species than asexually reproducing species [206 asexual (40%) vs. 294 sexual (58%); 9 species unknown]. Crustose lichens were also the most diverse, with 302 species, compared to 129 foliose, 25 fruticose, and 42 squamulose lichens (10 lichenicolous taxa

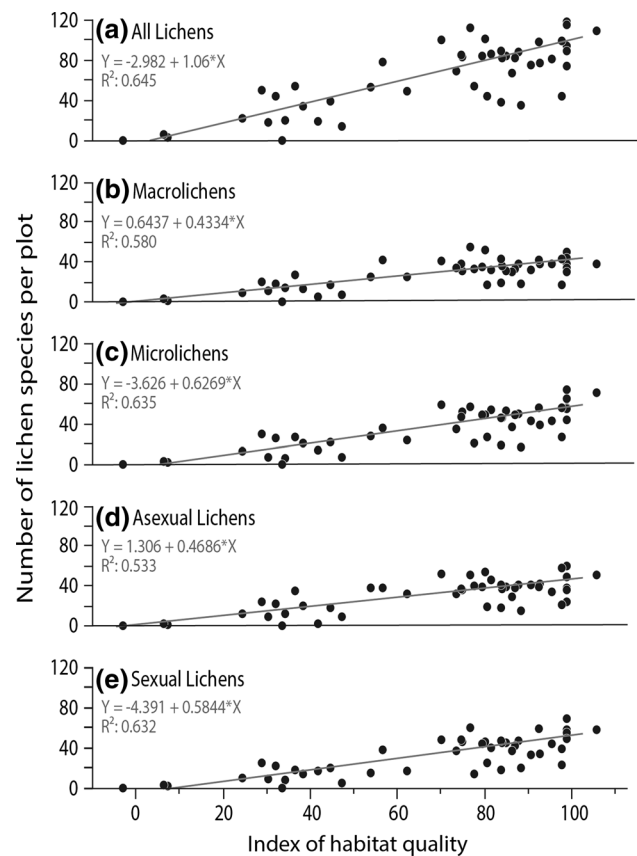


**Fig. 3** Rarefaction curve showing accumulation of lichen species across 47 one-hectare plots sampled for total lichen biodiversity in the present study

plus 1 unknown not included in analyses; Electronic Supplemental Material Appendix 1). The accumulation curve showed that over half of all sampled species were documented after inventory of the first 12 plots but that even after the total number of plots were sampled, accumulation had yet to fully taper off (Fig. 3). The sites spanned a broad distribution of habitat qualities, ranging from 0.00 to 95.2, and specific species responded differently to disturbances (Table 1; Electronic Supplemental Material Appendix 1). Most of the 10 habitat quality metrics increased with habitat quality, but with varying degrees of overlap and strength of importance (Fig. 2). For all lichens, we recovered a strong, unequivocally linearly increasing relationship between the number of lichen species and decreasing disturbance (Fig. 4: All,  $r^2=0.645$ , AICc weights: linear = 0.708, quadratic = 0.222, cubic = 0.070).

The best stepwise, multivariate regression model for the distribution of lichen diversity across all sites included only disturbance ( $r^2=0.645$ ,  $p < 0.0001$ ; Appendix 2). Several of the explanatory variables were correlated, although most were not strong ( $r < 0.30$ ; see correlation matrix in Appendix 2). Thus, the total model, including all 10 biotic and abiotic variables only slightly improved the model ( $r^2=0.696$ ) and the complete model without disturbance was a poorer fit ( $r^2=0.539$ ,  $p < 0.001$ ). To further assess collinearity, partial regression statistics detected that disturbance residuals were minor, whereas the residuals of the collinear variables were large and still had considerable variation unexplained. Disturbance and rock cover are negatively correlated ( $r = -0.4220$ ), and disturbance and several of the tree variables were correlated (Appendix 2), which are likely causal as humans do not have many uses for areas of large rocky outcrops and disturbance negatively influences trees as well as lichens.

The best models for microlichen, macrolichen, and asexual lichen diversity, when analyzed separately (Fig. 4,  $r^2=0.635$ ,  $p < 0.0001$ ;  $r^2=0.580$ ,  $p < 0.0001$ ,  $r^2=0.533$ ,

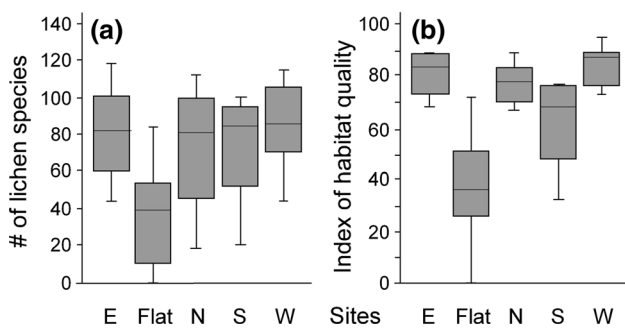
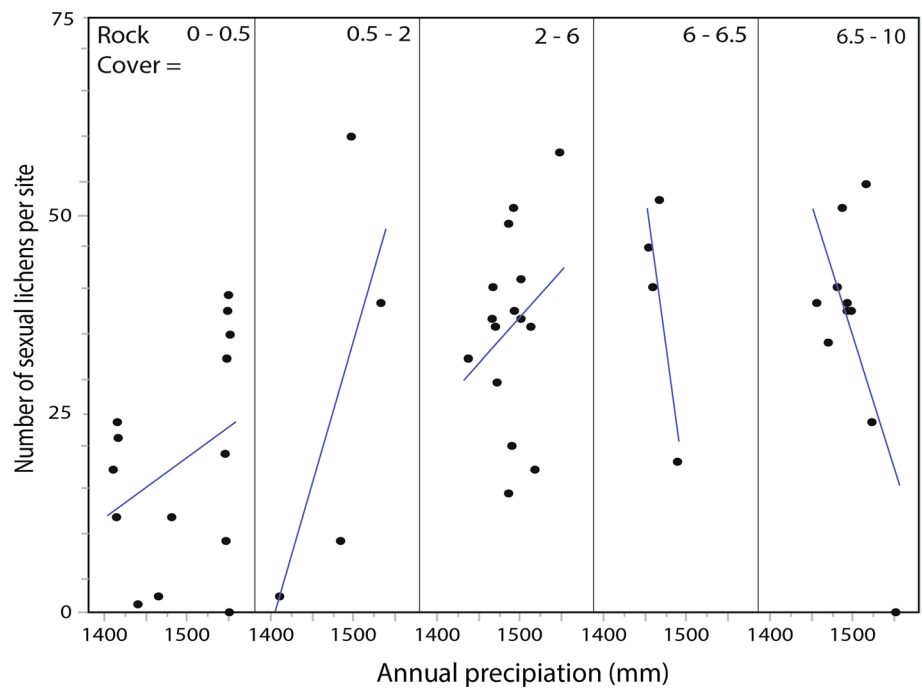


**Fig. 4** Relationship between lichen diversity and habitat quality across **a** all lichens, and four different partitionings of lichen groups: **b** macrolichens, **c** microlichens, **d** sexually reproducing lichens, **e** asexually reproducing lichens. Degree of disturbance (inverse of Index of habitat quality) is consistently supported as the sole multivariate regression model component for all lichen groups

$p < 0.0001$ , respectively), were strongly related only to disturbance. However, sexual lichen diversity was best predicted by decreasing disturbance (Fig. 4,  $p < 0.0001$ ) as well as a trade-off between precipitation ( $p = 0.0181$ ) and rock cover (Fig. 5,  $p = 0.037$ , overall model  $r^2 = 0.707$ ,  $p < 0.0001$ ). With lower rock coverage, sexual lichen diversity was found to increase with increasing precipitation whereas with greater rock coverage, diversity decreased with increasing precipitation. Nonetheless, this precipitation–rock cover interaction explained only a small amount of variation (0.075) beyond disturbance alone ( $r^2 = 0.632$ ).

Among the four dominant lichen growth forms, disturbance was again the best predictor of diversity. It was the only variable in the best models for crustose and foliose lichens individually ( $r^2 = 0.637$ ,  $p < 0.0001$ ,  $r^2 = 0.529$ ,  $p < 0.0001$ , respectively) whereas the best models for less diverse growth forms (i.e., fruticose and squamulose lichens) also included a second variable beyond disturbance as the strongest variable. However, these models were weaker ( $r^2 = 0.391$ ,  $p < 0.0001$ ,  $r^2 = 0.359$ ,  $p < 0.0001$ , respectively). Fruticose lichens

**Fig. 5** Sexual lichen diversity increases linearly with decreasing disturbance as in previous analyses, although two additional variables, precipitation (x-axis), and rock cover (columns) modulate this relationship



**Fig. 6** Number of lichen species (a) and index of habitat quality (b) across 5 different site types: flat, north-, south-, east-, and west-facing slopes

increased with decreasing disturbance ( $p=0.005$ ) and rock cover ( $p=0.019$ ) whereas squamulose lichens increased with decreasing disturbance ( $p<0.0001$ ) and decreased with overall quantity of tree bark (summed DBH,  $p=0.003$ ).

Finally, we found that flat sites had fewer lichen species than sites with slopes facing any direction (Fig. 6a, ANOVA  $r^2=0.403$ ,  $p=0.002$ ). However, when disturbance among sites was compared across aspects, the most disturbed sites were flat sites (Fig. 6b, ANOVA  $r^2=0.620$ ,  $p=0.002$ ).

**Discussion**

Our data strongly support a linear relationship between lichen diversity and habitat quality and disturbance. This result was recovered both from analysis of our full dataset

as well as subsets of the data parsed by important lichen traits such as growth form, reproductive mode, and substrate (all  $r^2$  values  $>0.5$ ). Beyond disturbance, our study recovered minor support for additional factors in explaining lichen biodiversity including effects of precipitation (sexual species), rock cover (sexual species, fruticose species), and tree density (squamulose species). Additionally, several of our explanatory variables were correlated (Appendix 2). In particular, the relationships between disturbance and several forest characteristics (e.g., number of trees, canopy coverage) are likely causal and, therefore, also implicated in the potential mechanisms of lichen decline with human disturbance. Similarly, but in reverse, human disturbance declines in areas of high rock coverage, thus humans have less impact on such regions.

**The disturbance–diversity relationship in lichens**

There is extensive evidence documenting that lichen diversity declines with increasing disturbance (Lücking 1995; Ellis and Coppins 2010; Benítez et al. 2012; Nylén and Luoto 2015; Ardelean et al. 2015; Tarasova et al. 2017; Zemanová et al. 2017). However, while this connection is well-established, prior studies have almost exclusively focused on subsets of total lichen diversity (e.g., macrolichens or epiphytes) and treated disturbance either qualitatively by assigning broadly defined classes (Lücking 1995; Rivas Plata et al. 2008; Benítez et al. 2012) or utilized time since disturbance as a proxy for degree of disturbance (Hestmark et al. 2007; O’Bryan et al. 2009; Ellis and Coppins 2010; Bartels and Chen 2014, 2015; Nelson et al. 2015; Arsenault

and Goward 2016; Tarasova et al. 2017; Zemanová et al. 2017).

The present study provides a new lens with which to view lichen disturbance ecology, as it appears to be the first to directly examine total lichen species richness along a disturbance gradient wherein disturbance was quantified using a standardized suite of habitat quality metrics (Fig. 2). Further, the present study emphasized patterns across a large regional scale in the context of a temperate biodiversity hotspot for both lichens and vascular plants. Our results support the broad conclusion of earlier studies that lichens are negatively impacted by disturbance and decreased habitat quality. We also found that beyond the primary effect of disturbance, there are secondary effects of variation in microhabitat features including annual precipitation and rock cover. Nonetheless, this study highlights that the relationships between lichen diversity, disturbance, and habitat quality are exceptionally strong across the full complement of lichen diversity in this study region. That is, regardless of size, reproductive mode, growth form and ecology, the diversity of lichens is strongly driven by disturbance and habitat quality.

What factors may have contributed to the linear relationship between disturbance and lichen diversity? Huston (2014) hypothesized that exceptionally high or exceptionally low levels of productivity could drive such patterns (e.g., through low colonization/developmental rates or high mortality/competitive exclusion). However, net primary productivity (NPP) did not explain the variation in diversity observed in this study, although we caution that Alabama is not particularly variable in NPP (average = 7152, range = 6102–10,419 g C m<sup>-2</sup> yr<sup>-1</sup>). We question whether lichens may be less subject to classic tradeoffs (Connell 1978; Wilson 1994; Violle et al. 2010) and more strongly driven by availability of resources (Death 2002).

Lichens are by definition autotrophic organisms, and thus are not primarily limited by carbon availability in their environments (Honegger 1998; Cornelissen et al. 2007). Rather than abiotic limitations, the single most important resource required for lichens to colonize a new landscape is likely the availability of suitable symbiotic partners. Due to the diverse reproductive modes of lichens, these partners can be transmitted vertically, horizontally, or via a combination of means depending on species-specific factors (Dal Grande et al. 2012; Muggia et al. 2014; Tripp and Lendemer 2018; see also Chagnon et al. 2016). While many lichens produce asexual propagules that co-disperse the complement of symbionts required to form a lichen, a larger proportion reproduce sexually and must establish new contact with at minimum a suitable photobiont to yield further development (Tripp and Lendemer 2018). For example, in the present study, 40% of lichen species co-disperse their symbionts asexually while 58% disperse sexual ascospores. This mirrors broader continental scale patterns in North America

[> 70% of all North American lichens reproduce sexually (E. Tripp and J. Lendemer, ms in prep.)].

Following symbiont availability, lichen colonization is expected to be limited by substrate availability and variety (i.e., presence and type of woody substrates or rocks) given that substrate preferences of many lichens relate to a narrow range of chemical and physical characters (Barkman 1958; Wolf 1994; Wolseley and Aguirre-Hudson 1997; Cáceres et al. 2007; Nelson et al. 2015; Tripp 2015; Jüriado et al. 2017; McDonald et al. 2017; Resl et al. 2018). Subsequent to initial colonization and establishment, the most important factors governing later stages of lichen development are likely to involve physiological constraints and tolerance of the abiotic environment and microclimates including temperature, precipitation, airborne (or waterborne) nutrients, and air quality (McCune et al. 1997; Dynesius and Zinko 2006; Ellis and Coppins 2010; Nelson et al. 2015), in addition to ongoing biotic interactions experienced by a given individual throughout its lifetime (e.g., competition, disease dynamics).

Taken together, it seems likely that two broad classes of factors, biotic and abiotic, impact lichen biodiversity at different life stages: colonization (dependent on symbiont availability and density; see Tretiach et al. 2013) and subsequent development (dependent on abiotic factors in addition to ongoing biotic interactions). If true, this complexity presents challenges to the hypothesis that any single resource may set an upper limit on lichen diversity. In the present study, symbiont availability was not examined, but this ‘biotic limitation’ hypothesis presents an exciting avenue for further study (K. Keepers et al., ms in prep.).

### Limited additional factors predict lichen diversity

Our key finding that habitat quality and disturbance drive patterns of lichen diversity was tempered by limited demonstration of the potential relevance of additional variables modulating natural lichen diversity. For instance, we found precipitation and rock cover impacted sexual lichens, and rock or tree cover helped explain species richness of taxa with fruticose and squamulose growth forms.

That sexual species diversity increased with precipitation at low rock cover but declined with precipitation for higher rock cover suggests an interesting tradeoff that may involve several different contributing factors including habitat diversity (with or without rocks) and competitive exclusion imposed by bryophytes (typically more abundant at higher, wetter elevations, e.g., Dynesius and Zinko 2006). This, however, does not lend insight into why such a tradeoff should impact sexual but not asexually reproducing lichens. This tradeoff, if accurate, may involve limitations of sexual spore dispersal or colonization in rocky, wetter habitats compared to the mitotic diaspores of asexually reproducing



species that are dispersed together with the full complement of symbionts (Tripp and Lendemer 2018).

Although not yet empirically demonstrated, there likely exist correlations between (1) mode of reproduction and growth form for the two most species-rich groups of lichens, foliose and crustose lichens, as well as (2) competitive interactions between these two growth forms as a function of precipitation and substrate. Results from ongoing research (E. Tripp and J. Lendemer, ms in prep.) have already revealed that foliose species are overrepresented in regions of North America with extensive hardwood forest cover (such as the Appalachian Mountains) whereas crustose species are overrepresented in regions with extensive rock cover (such as the Rocky Mountains). At the same time, crustose species tend to reproduce sexually whereas foliose species tend to reproduce asexually. Thus, high and typically wet elevations in eastern North America may be dominated by foliose species because of physiological constraints such as higher water demands (larger, thicker thalli) to the exclusion of crustose species. Correspondingly, lower and drier environments in this region may be more conducive to the establishment and development of crustose species that have lower water demands, especially considering that crustose lichens tend to be overrepresented on rocks. Better understanding of functional traits (cf. Nelson et al. 2015) across a large complement of North American lichens would likely shed new light on distributions of species and their traits at regional and local scales.

For fruticose species, the best model for predicting richness included disturbance as well as high rock cover whereas for squamulose species, the best model incorporated disturbance together with a low number of large trees. This may reflect open habitat associations, but note that both models were weaker on average than were all models for other lichen groups that included only disturbance. Additionally, these two growth forms together comprise only a small fraction (13%) of our overall dataset of 509 species, which was dominated by crustose (59%) and foliose (25%) species.

We also failed to find evidence that tree diversity, total number of trees per plot, average tree DBH per plot, plot elevation, slope, temperature, or net primary productivity impacted lichen biodiversity. But as noted above, the tree variables are also positively and linearly related to habitat quality, thus decline with disturbance as do lichens (Fig. 2; Appendix 2). They alone are not better explanatory variables than disturbance, but are casually linked to disturbance, and thus lichen diversity patterns. In contrast, our analyses did recover a significant effect of plot orientation: flat plots were less diverse than those on slopes facing any cardinal orientation. Flat plots were, however, also the most disturbed, suggesting a correlation: flat areas are more readily disturbed by humans and a need to incorporate more data from disturbed plots on slopes. That so many of the above factors did not

explain patterns of species richness at first seems puzzling given the preponderance of studies that have highlighted their importance, especially that of temperature, elevation, and productivity (Currie 1991; McCain and Grytnes 2010; García-López et al. 2012). However, variability in most of these abiotic environmental factors was limited in the present dataset due to the spatial proximity of the plots in northern Alabama. An expanded study that spans larger gradients in temperature, precipitation and NPP is needed to more fully understand their relative importance to patterns of lichen diversity (e.g., Ellis and Coppins 2010), such study is currently underway by the authors (C. McCain et al., in progress).

### Ecological thresholds

Data from the present study provide an opportunity to understand specific attributes of lichens such as tolerance to disturbance, commonality, and rarity. A total of seven lichen species were found both multiple times in our study and consistently occupied only the most disturbed habitats (i.e., HQ < 50%, Table 1; Electronic Supplemental Material Appendix 1). Of these, all reproduce asexually except one and all are crustose except one, which is microfoliose. This suggests that both traits, asexual reproduction and a crustose growth form, are conducive to disturbance tolerance. Other disturbance-tolerant species were found only in the most disturbed plots but found only once in our study, and finally an assemblage of additional species was found in highly disturbed plots in addition to relatively undisturbed plots (Table 1; Electronic Supplemental Material Appendix 1).

Seventeen species comprised the most common taxa (i.e., present in 25 or more plots), and these are a mix of foliose, crustose, sexual and asexual lichens. They are, however, considered among the most common lichens in eastern North America (Table 1; Electronic Supplemental Material Appendix 1). These taxa are characterized by broad ecological thresholds and are found frequently as a cohort in a wide variety of habitats (Brodo 1961; Dibben 1980; Brodo et al. 2001; Hinds and Hinds 2007; Lendemer et al. 2013; Muscavitch et al. 2017). In contrast, nearly a third of lichens in our dataset (144 of 509 species, or 28%) were found and collected in the field only once. This percentage is on par with numbers derived from other lichen biodiversity hotspots, such as The Greater Sonoran Desert, Great Smoky Mountains National Park, and the Dare Regional Biodiversity Hotspot (Nash 2002; Lendemer et al. 2013; Lendemer and Allen 2014; Lendemer et al. 2016; Tripp and Lendemer 2019a, b in press). The species that were located only once included several that are either at the edges of their biogeographical ranges, are rare to begin with, or both (Table 1; Electronic Supplemental Material Appendix 1; Brodo et al.

2001; Knudsen 2007; Breuss 2016; Lendemer et al. 2014, 2017; Tripp and Lendemer 2019a, b, in press).

## Conclusions

Results from this study demonstrate clearly that a conspicuous class of obligate symbiotic organisms—lichens—are highly and negatively impacted by disturbance. The present investigation explored patterns not only across a full complement of lichen diversity, but also in a region already characterized by its exceptional overall biodiversity, especially for temperate latitudes. This has important implications for conservation and management, particularly in the southeastern United States—a recognized biodiversity hotspot.

That nearly a third of all lichens in northern Alabama can be considered to be rare in this study (found in few plots) but yet 30 of 47 1 ha plots (64%) contained 50 or more species conveys overall high lichen biodiversity (and high alpha diversity) present in the southernmost portion of southern Appalachian Mountains. These data and the regional species accumulation curve indicate that the region as a whole warrants extensive future study. Optimally, future research should include broader environmental gradients as well as incorporate impacts from biotic factors, especially a clearer understanding of photobiont diversity and distributions. More specifically, it seems likely that biotic and abiotic factors limit different stages of lichen development and, once more fully investigated, this will yield a highly complex and temporally dynamic set of ecological processes that govern lichen biodiversity.

**Acknowledgements** We are grateful for permission to conduct fieldwork on federal and state lands including the U.S. National Park Service (particularly, Mary Shew, Little River Canyon N.P.), U.S. Forest Service, U.S. Fish and Wildlife Service, and Alabama Department of Conservation and Natural Resources (particularly, Jo Lewis, Chief of Natural Heritage). We thank Carly Anderson Stewart and Jordan Hoffman for contributions to fieldwork and Nolan Kane, Kyle Keepers, Cloe Pogoda, and Kristin White for additional conversation. We additionally are grateful to two anonymous reviewers as well as Anne Pringle whose comments improved an earlier version of the manuscript. This research was made possible by a National Science Foundation Dimensions of Biodiversity Award to University of Colorado (Award #1542629) and New York Botanical Garden (Award #1432629).

**Author contribution statement** EAT, JCL, and CMM conceived the study, collected the data, conducted the analyses, and wrote the manuscript.

**Data accessibility** The entirety of the dataset used herein is included in Electronic Supplemental Material Appendix 1, including the georeferenced locality, elevation, aspect, slope, the number of lichens (total, micro- and macrolichens, sexual and asexual lichens, and four growth forms), disturbances scores (HQ), rock coverage, number of trees, sum of tree diameters, average annual temperature, precipitation, and net primary productivity (NPP) for each of the 47 sites. GIS layers

from which the average annual temperature, precipitation, NPP were extracted are publicly available at <http://www.worldclim.org/bioclim> and <http://www.nts.gov/umt.edu/project/modis/default.php>. OTU tables with taxonomic information, fasta files with representative sequences for each OTU, a metadata file and mapping file are available for download at <http://dx.doi.org/10.6084/m9.figshare.1270900>. All taxonomic and inventory data are freely available at <http://sweetgum.nybg.org/science/vh/>.

## Compliance with ethical standards

**Conflict of interest** The authors report no conflicts of interests. The work was funded by the US National Science Foundation (see award numbers in acknowledgements).

## References

- Ardelean IV, Keller C, Scheidegger C (2015) Effects of management on lichen species richness, ecological traits and community structure in the Rodnei Mountains National Park (Romania). *PLoS One* 10:e0145808
- Arnold AE, Miadlikowska J, Higgins KL, Sarvate SD, Gugger P, Way A, Hofstetter V, Kauff F, Lutzoni F (2009) A phylogenetic estimation of trophic transition networks for ascomycetous fungi: are lichens cradles of symbiotrophic fungal diversification? *Syst Biol* 58:283–297
- 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 Ind* 69:730–738
- Asplund J, Wardle DA (2017) How lichens impact on a terrestrial community and ecosystem properties. *Biol Rev* 92:1720–1738
- Balasundaram SV, Engh IB, Skrede I, Kausserud H (2015) How many DNA markers are needed to reveal cryptic fungal species? *Fungal Biol* 119:940–945
- Barkman JJ (1958) Phytosociology and ecology of cryptogamic epiphytes. Van Gorcum, Assen
- Barry M, McMullin RT, Horn A (2015) Edge effects on the lichen genus *Lobaria* in Atlantic Canadian Forests. *For Chron* 91:534–540
- Bartels SF, Chen HYH (2014) Dynamics of epiphytic macrolichen abundance, diversity, and composition in boreal forest. *J Appl Ecol* 52:181–189
- Bartels SF, Chen HYH (2015) Species dynamics of epiphytic macrolichens in relation to time since fire and host tree species in boreal forest. *J Veg Sci* 26:1124–1133
- Bates ST, Berg-Lyons D, Lauber CL, Walters WA, Knight R, Fierer N (2012) A preliminary survey of lichen associated eukaryotes using pyrosequencing. *Lichenologist* 44:137–146
- Benítez Á, Prieto M, González Y, Aragón G (2012) Effects of tropical montane forest disturbance on epiphytic macrolichens. *Sci Total Environ* 441:169–175
- Biswas SR, Mallik AU (2010) Disturbance effects on species diversity and functional diversity in riparian and upland plant communities. *Ecology* 91:28–35
- Breuss O (2016) *Byssolema maderense* is not endemic to Macaronesia. *Evansia* 33:54–62
- Brodie J, Ball SG, Bouget FY, Chan CX, Clerk O et al (2017) Biotic interactions as drivers of algal origin and evolution. *New Phytol* 216:670–681
- Brodo IM (1961) A study of lichen ecology in central Long Island, New York. *Am Midl Nat* 65:290–310

- Brodo IM, Sharnoff SD, Sharnoff S (2001) Lichens of north America. Yale University Press, New Haven
- Cáceres MES, Lücking R, Rambold G (2007) Phorophyte specificity and environmental parameters versus stochasticity as determinants for species composition of corticolous lichen communities in the Atlantic rain forest of northeastern Brazil. *Mycol Prog* 6(3):117–136
- Chagnon PL, U'Ren JM, Miadlikowska J, Lutzoni F, Arnold AE (2016) Interaction type influences ecological network structure more than local abiotic conditions: evidence from endophytic and endolichenic fungi at a continental scale. *Oecologia* 180:181–191
- Coddington JA, Griswold CE, Dávila SD, Peñaranda E, Larcher SF (1991) Designing and testing sampling protocols to estimate biodiversity in tropical ecosystems. In: Dudley EC (ed) The unity of evolutionary biology: proceedings of the fourth international congress of systematic and evolutionary biology. Dioscorides Press, Portland
- Connell JH (1978) Diversity in tropical rain forests and coral reefs. *Science* 199:1302–1310
- Cornelissen JH, Lang SI, Soudzilovskaia NA, During HJ (2007) Comparative cryptogam ecology: a review of bryophyte and lichen traits that drive biogeochemistry. *Ann Bot* 99:987–1001
- Currie DJ (1991) Energy and large-scale patterns of animal- and plant-species richness. *Am Nat* 137:27–49
- Currie DJ, Mittelbach GG, Cornell HV, Field R, Guégan JF, Hawkins BA, Kaufman DM, Kerr JT, Oberdorff T, O'Brien E, Turner JRG (2004) Predictions and tests of climate-based hypotheses of broad-scale variation in taxonomic richness. *Ecol Lett* 7:1121–1134
- Dal Grande F, Widmer I, Wagner HH, Scheidegger C (2012) Vertical and horizontal photobiont transmission within populations of a lichen symbiosis. *Mol Ecol* 21:3159–3172
- Death RG (2002) Predicting invertebrate diversity from disturbance regimes in forest streams. *Oikos* 97:18–30
- Dibben MJ (1980) The Chemosystematics of the Lichen Genus *Pertusaria* in North America North of Mexico. Milwaukee Public Museum, Milwaukee
- DLIA (Discover Life in America) (2017) Smokies species tally. <http://dlia.org/smokies-species-tally/>. Accessed 4 Sep 2017
- Dynesius M, Zinko U (2006) Species richness correlations among primary producers in boreal forests. *Divers Distrib* 12:703–713
- Ellis CJ, Coppins BJ (2010) Integrating multiple landscape-scale drivers in the lichen epiphyte response: climatic setting, pollution regime and woodland spatial-temporal structure. *Divers Distrib* 16:43–52
- Esslinger TL (2016) A cumulative checklist for the lichen-forming, lichenicolous and allied fungi of the continental United States and Canada, Version 21. *Opusc Phil* 15:136–390
- Fernandez-Mendoza F, Kopun T, Fleischhacker A, Grube M, Muggia L (2017) ITS1 metabarcoding highlights low specificity of lichen mycobiomes at a local scale. *Mol Ecol* 26:4811–4830
- Fierer N, McCain CM, Meir P, Zimmermann M, Rapp JM, Silman MR, Knight R (2011) Microbes do not follow the elevational diversity patterns of plants and animals. *Ecology* 92:797–804
- Fleischhacker A, Grube M, Kopun T, Hafellner J, Muggia L (2015) Community analyses uncover high diversity of lichenicolous fungi in alpine habitats. *Microb Ecol* 70:348–360
- Flock JW (1978) Lichen-bryophyte distribution along a snow-covered-soil-moisture gradient, Niwot Ridge, Colorado. *Arct Alp Res* 10:31–47
- García-López A, Micó E, Galante E (2012) From lowlands to highlands: searching for elevational patterns of species richness and distribution of scarab beetles in Costa Rica. *Divers Distrib* 18:543–553
- Hawkins BA, Field R, Cornell HV, Currie DJ, Guegan JF, Kaufman DM, Kerr JT, Mittelbach GG, Oberdorff T, O'Brien EM, Porter EE, Turner JRG (2003) Energy, water, and broad-scale geographic patterns of species richness. *Ecology* 84:3105–3117
- Henson A, Lea C, Bates ST (2013) Lichens of granitic rocks in Rocky Mountain National Park Larimer County, Colorado, U.S.A. *Evansia* 30:17–23
- Hestmark G, Skogedal O, Skullerud Ø (2007) Early recruitment equals long-term relative abundance in an alpine saxicolous lichen guild. *Mycologia* 99:207–214
- Hinds JW, Hinds PL (2007) The macrolichens of New England. *Memoirs of the New York botanical garden*, vol 96. The New York Botanical Garden Press, Bronx
- Honegger R (1998) The lichen symbiosis—what is so spectacular about it? *Lichenologist* 30:193–212
- Honegger R (2012) The symbiotic phenotype of lichen-forming ascomycetes and their endo- and epibionts. In: Esser K, Lemke PA, Melton AC (eds) *The mycota: a comprehensive treatise on fungi as experimental systems for basic and applied research*. Springer, New York
- Honegger R (1991) Functional aspects of the lichen symbiosis. *Annu Rev Plant Physiol Plant Mol Biol* 42:553–578
- Huston M (1979) A general hypothesis of species diversity. *Am Nat* 113:81–100
- Huston M (1994) Biological diversity: the coexistence of species on changing landscapes. Cambridge University Press, Cambridge
- Huston MA (2014) Disturbance, productivity, and species diversity: empiricism vs. logic in ecological theory. *Ecology* 95:2382–2396
- Hutchinson GE (1953) The concept of pattern in ecology. *Proc Acad Nat Sci Phila* 105:1–12
- Johansson V, Ranius T, Snäll T (2012) Epiphyte metapopulation dynamics are explained by species traits, connectivity, and patch dynamics. *Ecology* 93(2):235–241
- Johansson V, Snäll T, Ranius T (2013) Estimates of connectivity reveal non-equilibrium epiphyte occurrence patterns almost 180 years after habitat decline. *Oecologia* 172(2):607–615
- Johnst K, Huth A (2005) Testing the intermediate disturbance hypothesis: when will there be two peaks of diversity? *Divers Distrib* 11:111–120
- Jürriado I, Kaasalainen U, Rikkinen J (2017) Specialist taxa restricted to threatened habitats contribute significantly to the regional diversity of *Peltigera* (Lecanoromycetes, Ascomycota) in Estonia. *Fungal Ecol* 30:76–87
- Kessler M, Kluge J, Hemp A, Ohlemüller R (2011) A global comparative analysis of elevational species richness patterns of ferns. *Global Ecol Biogeogr* 20(6):868–880. <https://doi.org/10.1111/1/j.1466-8238.2011.00653.x>. (Cited by: 96)
- Knudsen K (2007) *Acarospora*. In: Nash TH III, Gries C, Bungartz F (eds) *Lichen flora of the greater sonoran desert region*, vol 3. Lichens Unlimited, Tempe
- Leavitt SD, Esslinger TL, Divakar PK, Crespo A, Lumbsch HT (2016) Hidden diversity before our eyes: delimiting and describing cryptic lichen-forming fungal species in camouflage lichens (Parmeliaceae, Ascomycota). *Fungal Biol* 120(11):1374–1391
- Lendemer JC (2011) A taxonomic revision of the North American species of *Lepraria* s.l. that produce divaricatic acid, with notes on the type species of the genus *L. incana*. *Mycologia* 103:1216–1229
- Lendemer JC, Allen JL (2014) Lichen biodiversity under threat from sea-level rise in the Atlantic Coastal Plain. *Bioscience* 64:923–931
- Lendemer JC, Harris RC, Tripp EA (2013) The lichens and allied fungi of Great Smoky Mountains National Park: an annotated checklist with comprehensive keys. *Memoirs of the New York Botanical Garden*. New York Botanical Garden Press, Bronx
- Lendemer JC, Tripp EA, Sheard JW (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
- 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
- Lendemer JC, Stone HB, Tripp EA (2017) Taxonomic delimitation of the rare, eastern North American endemic lichen *Santessonniella crossophylla* (Pannariaceae). *J Torrey Bot Soc* 144:459–468
- Limberger R, Wickham SA (2012) Disturbance and diversity at two spatial scales. *Oecologia* 168:785–795
- Lücking R (1995) Biodiversity and conservation of foliicolous lichens in Costa Rica. *Mitt Eidgenöss Forsch Anst Wald Schnee Landsch* 70:63–92
- Lücking R, dal Forno M, Moncada B, Coca LF, Vargas-Mendoza LY, Aptroot A, Arias LJ, Besal B, Bungartz F, Cabrera-Amaya DM, Cáceres MES, Chaves JL, Eliasaro S, Gutiérrez MC, Marin JEH, Herrera-Campos MA, Holgado-Rojas ME, Jonitz H, Kukwa M, Lucheta F, Madriñán S, Marcelli MP, Martins SMA, Mercado-Díaz JA, Molina JA, Morales EA, Nelson PR, Nugra F, Ortega F, Paredes T, Patiño AL, Peláez-Pulido RN, Pérez REP, Perlmutter GB, Rivas-Plata E, Robayo J, Rodríguez C, Simijaca DF, Soto-Medina E, Spielmann AA, Suárez-Corredor A, Torres J-M, Vargas CA, Yáñez-Ayabaca A, Weerakoon G, Wilk K, Pacheco MC, Diazgranados M, Brokamp G, Borsch T, Gillevet PM, Sikaroodi M, Lawrey JD (2017) Turbo-taxonomy to assemble a megadiverse lichen genus: seventy new species of *Cora* (Basidiomycota: Agaricales: Hygrophoraceae), honouring David Leslie Hawksworth’s seventieth birthday. *Fungal Divers* 84(1):139–207
- Lundström J, Jonsson F, Perhans K, Gustafsson L (2013) Lichen species richness on retained aspens increases with time since clear-cutting. *For Ecol Manag* 293:49–56
- Lutzoni F, Pagel M, Reeb V (2001) Major fungal lineages are derived from lichen symbiotic ancestors. *Nature* 411:937–940
- MacArthur RH (1972) Geographical ecology: patterns in the distribution of species. Harper and Row, New York
- Mackey RJ, Currie DJ (2001) The diversity–disturbance relationship: is it generally strong and peaked? *Ecology* 82:3479–3492
- Magain N, Truong C, Goward T, Niu D, Goffinet B, Sérusiaux E, Vitikainen O, Lutzoni F, Miadlikowska J (2018) Species delimitation at a global scale reveals high species richness with complex biogeography and patterns of symbiont association in *Peltigera* section *Peltigera* (lichenized Ascomycota: Lecanoromycetes). *Taxon* 67:836–870
- McCain CM (2004) The mid-domain effect applied to elevational gradients: species richness of small mammals in Costa Rica. *J Biogeogr* 31:19–31
- McCain CM (2009) Global analysis of bird elevational diversity. *Glob Ecol Biogeogr* 18:346–360
- McCain CM, Grytnes JA (2010) Elevational gradients in species richness. In: *Encyclopedia of life sciences*. Chichester: Wiley
- McCune B, Dey J, Peck J, Heiman K, Will-Wolf S (1997) Regional gradients in lichen communities of the southeast United States. *Bryologist* 100:145–158
- McDonald L, Van Woundenberg M, Dorin B, Adcock AM, McMullin RT, Cottenie K (2017) The effects of bark quality on corticolous lichen community composition in urban parks of southern Ontario. *Botany* 95(12):1141–1149
- McMullin RT, Duinker PN, Cameron RP, Richardson DHS, Brodo IM (2008) Lichens of coniferous old-growth forests of southwestern Nova Scotia, Canada: diversity and present status. *Bryologist* 111:620–637
- Miadlikowska J, Magain N, Pardo-De la Hoz CJ, Niu D, Goward T, Sérusiaux E, Lutzoni F (2018) Species in section *Peltidea* (aphthosa group) of the genus *Peltigera* remain cryptic after molecular phylogenetic revision. *Plant Fungal Syst* 63:45–64
- Mistry J (1998) Population dynamics of the lichen genus *Bulbothrix* Hale as potential bioindicators of ‘time-since-last-fire’ in the cerrado of the Distrito Federal, central Brazil. *Divers Distrib* 4:155–165
- Muggia L, Pérez-Ortega S, Kopun T, Zellnig G, Grube M (2014) Photobiont selectivity leads to ecological tolerance and evolutionary divergence in a polymorphic complex of lichenized fungi. *Ann Bot* 114:463–475
- Muggia L, Fleischhacker A, Kopun T, Grube M (2016) Extremotolerant fungi from alpine rock lichens and their phylogenetic relationships. *Fungal Divers* 76:119–142
- Muscavitch ZM, Lendemer JC, Harris RC (2017) A review of the lichen genus *Phlyctis* in North America (Phlyctidaceae) including the description of a new widespread saxicolous species from eastern North America. *Bryologist* 120:388–417
- Nash TH (2002) Lichen Flora of the Greater Sonoran Desert region. Arizona State University, Tempe
- Nelson PR, McCune B, Roland C, Stehn S (2015) Non-parametric methods reveal non-linear functional trait variation of lichens along environmental and fire age gradients. *J Veg Sci* 26:848–865
- Nylén T, Luoto M (2015) Primary succession, disturbance and productivity drive complex species richness patterns on land uplift beaches. *J Veg Sci* 26:267–277
- O’Bryan KE, Prober SM, Lunt ID, Eldridge DJ (2009) Frequent fire promotes diversity and cover of biological soil crusts in a derived temperate grassland. *Oecologia* 159:827–838
- Ossowska M, Guzow-Krzemińska B, Dudek M, Oset M, Kukwa M (2018) Evaluation of diagnostic chemical and morphological characters in five *Parmelia* species (Parmeliaceae, lichenized Ascomycota) with special emphasis on the thallus pruinosity. *Phytotaxa* 383(2):165–180
- Parkes D, Newell G, Cheal D (2003) Assessing the quality of native vegetation: the ‘habitat hectares’ approach. *Ecol Manag Restor* 4:S29–S38
- Pastore AI, Prather CM, Gornish ES, Ryan WH, Ellis RD, Miller TE (2014) Testing the competition–colonization trade-off with a 32-year study of a saxicolous lichen community. *Ecology* 95:306–315
- Ray DG, Barton JW, Lendemer JC (2015) Lichen community response to prescribed burning and thinning in southern pine forests of the Mid-Atlantic coastal plain, USA. *Fire Ecol* 11:14–33
- Resl P, Fernández-Mendoza F, Mayrhofer H, Spribille T (2018) The evolution of fungal substrate specificity in a widespread group of crustose lichens. *Proc R Soc B* 285:20180640
- Rivas Plata E, Lücking R, Lumbsch HT (2008) When family matters: an analysis of Thelotremales (lichenized Ascomycota: Ostropales) as bioindicators of ecological continuity in tropical forests. *Biodivers Conserv* 17:1319–1351
- Röthig T, Costa RM, Simona F, Baumgarten S, Torres AF, Radhakrishnan A, Aranda M, Voolstra CR (2016) Distinct bacterial communities associated with the coral model *Aiptasia* in aposymbiotic and symbiotic states with *Symbiodinium*. *Front Mar Sci*. <https://doi.org/10.3389/fmars.2016.00234>
- Shea K, Roxburgh SH, Rauscher ESJ (2004) Moving from pattern to process: coexistence mechanisms under intermediate disturbance regimes. *Ecol Lett* 7:491–508
- Sheil D, Burslem DFRP (2013) Defining and defending Connell’s intermediate disturbance hypothesis: a response to Fox. *Trends Ecol Evol* 28:571–572
- Shrestha G, St. Clair LL (2011) A comparison of the lichen floras of four locations in the Intermountain Western United States. *N Am Fungi* 6:1–20
- Sørensen LL, Coddington JA, Scharff N (2012) Inventorying and estimating subcanopy spider diversity using semiquantitative sampling methods in an afro-montane forest. *Pest Manag Sampl* 31:319–330

- Svensson JR, Lindegarth M, Siccha M, Lenz M, Molis M, Wahl M, Pavia H (2007) Maximum species richness at intermediate frequencies of disturbance: consistency among levels of productivity. *Ecology* 88:830–838
- Szczepaniak K, Biziuk M (2003) Aspects of the biomonitoring studies using mosses and lichens as indicators of metal pollution. *Environ Res* 93:221–230
- Tarasova VN, Obabko RP, Himelbrant DE, Boychuk MA, Stepanchikova IS, Borovichev EA (2017) Diversity and distribution of epiphytic lichens and bryophytes on aspen (*Populus tremula*) in the middle boreal forests of Republic of Karelia (Russia). *Folia Cryptogam Estonica* 54:125–141
- Thom D, Seidl R (2016) Natural disturbance impacts on ecosystem services and biodiversity in temperate and boreal forests. *Biol Rev* 91:760–781
- Tretiach M, Bertuzzi S, Carniel FC, Virgilio D (2013) Seasonal acclimation in the epiphytic lichen *Parmelia sulcata* is influenced by change in photobiont population density. *Oecologia* 173:649–663
- Tripp EA (2015) Lichen inventory of White Rocks Open Space (City of Boulder, Colorado). *West N Am Nat* 75:301–310
- Tripp EA, Lendemer JC (2018) Twenty-seven modes of reproduction in the obligate lichen symbiosis. *Brittonia* 70:1–14
- Tripp EA, Lendemer JC (2019a) Field guide to the lichens of Great Smoky Mountains National Park. University of Tennessee Press, Knoxville (in press)
- Tripp EA, Lendemer JC (2019b) Lichenology in great smoky mountains National Park: highlights from 10 years of research. *Syst Bot*. (in press)
- Tripp EA, Lendemer JC, Barberán A, Dunn RR, Fierer N (2016) Biodiversity gradients in obligate symbiotic organisms: exploring the diversity and traits of lichen propagules across the United States. *J Biogeogr* 45:1667–1678
- Tripp EA, Zhang N, Schneider H, Huang Y, Mueller GM, Hu ZH, Haggblom M, Bhattacharya D (2017) Reshaping Darwin's tree: impact of the symbiome. *Trends Ecol Evol* 32:552–555
- U'Ren JM, Lutzoni F, Miadlikowska J, Laetsch AD, Arnold AE (2012) Host and geographic structure of endophytic and endolichenic fungi at a continental scale. *Am J Bot* 99:898–914
- Violle C, Pu Z, Jiang L (2010) Experimental demonstration of the importance of competition under disturbance. *Proc Natl Acad Sci USA* 107:12925–12929
- Weakley AS (2015) Flora of the southern and mid-Atlantic States. Working Draft 21 May 2015. [http://www.herbarium.unc.edu/FloraArchives/WeakleyFlora\\_2015-05-29.pdf](http://www.herbarium.unc.edu/FloraArchives/WeakleyFlora_2015-05-29.pdf)
- Wilson JB (1994) The 'Intermediate Disturbance Hypothesis' of species coexistence is based on patch dynamics. *N Z J Ecol* 18:176–181
- Witman JD, Cusson M, Archambault P, Pershing AJ, Mieskowska N (2008) The relationship between productivity and species diversity in temperate-arctic marine ecosystems. *Ecology* 89:S66–S80
- Wolf JHD (1994) Factors controlling the distribution of vascular and non-vascular epiphytes in the northern Andes. *Vegetatio* 112:15–28
- Wolseley PA, Aguirre-Hudson B (1997) The ecology and distribution of lichens in tropical deciduous and evergreen forests of northern Thailand. *J Biogeogr* 24:327–343
- Wootton JT (1998) Effects of disturbance on species diversity: a multitrophic perspective. *Am Nat* 152:803–825
- Yahr R, Schoch CL, Dentinger BTM (2016) Scaling up discovery of hidden diversity in fungi: impacts of barcoding approaches. *Philos Trans R Soc B* 371:20150336
- Zemanová L, Trotsiuk V, Morrissey RC, Bace R, Mikolás M, Svoboda M (2017) Old trees as a key source of epiphytic lichen persistence and spatial distribution in mountain Norway spruce forests. *Biodivers Conserv* 26:1943–1958