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Disturbance and diversity: Lichen species richness decreases with increasing anthropogenic disturbance

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ABSTRACT

Anthropogenic disturbance is rapidly increasing through habitat degradation, development, and deforestation. Gaps remain in understanding the effects of this disturbance on diverse and ecologically important organisms such as lichens. In North America, studies have focused on epiphytic macrolichens and catastrophic disturbance, largely ignoring microlichens and less severe disturbances. The Intermediate Disturbance Hypothesis predicts these moderate disturbances will lead to higher species richness. Here we examine the effects of anthropogenic disturbance in the form of land management on overall lichen richness, including microlichens, and on the species richness of eight lichen functional groups. The study draws on a comprehensive data set of 872 species, in 208 one-hectare plots throughout the Southern Appalachian Mountains, a global biodiversity hotspot in eastern North America. A habitat quality index based on an established forestry metric was used as a proxy for anthropogenic disturbance and was quantified using a 10-part score including categories such as percent native tree canopy cover and degree of fragmentation. Linear models were used to compare habitat quality scores to overall species richness and to species richness of functional groups. Rather than following the Intermediate Disturbance Hypothesis, all groups uniformly follow a negative linear relationship: as disturbance increases, species richness decreases. This pattern held even for widely variable functional groups such as morphotype. Effective conservation of lichen richness should prioritize the maintenance of existing older, less-disturbed stands within large, contiguously forested areas.

1. Introduction

Lichens—obligate symbioses between a fungus and at least one alga or cyanobacterium—are important components of terrestrial ecosystems, regulating substrate moisture, cycling nitrogen, and sequestering carbon (Asplund and Wardle, 2017). Many lichen species are also conservation-sensitive and threatened or otherwise rare (Allen et al., 2019; Manzitto-Tripp et al., 2022). Because lichens receive all nutrients and water from atmospheric deposition, they are sensitive to air pollution, allowing them to be widely used as indicators of air quality (Hawksworth, 1970; Jovan and McCune, 2005; Will-Wolf et al., 2015) and of overall ecosystem health (Campbell and Fredeen, 2004; Nascimbene et al., 2010). Many studies have confirmed that lichens—more so than bryophytes—reflect the "naturalness" or "health" of forests (Ellis and Coppins, 2010; Arsenault and Goward, 2016; Benítez et al., 2018; Czerepko et al., 2021). More recently, lichens have been established as indicators of forest age and continuity and may provide a framework for determining which forests have the highest conservation value (McMullin and Wiersma, 2019; Miller et al., 2020; Wiersma and McMullin, 2022). Given the importance of lichens in natural systems and as tools for evaluating conservation priority, it is imperative to understand the impact of anthropogenic disturbance on these organisms.

Disturbance has long been acknowledged as a driving force for vegetative diversity (Connell, 1978; Sousa, 1984). A variety of approaches have been used to measure the impact of disturbance on

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diversity, including examining effects at different trophic levels (Wootton, 1998), intensities (Miller et al., 2011), spatial scales (Limberger and Wickham, 2012), and time scales (Svensson et al., 2007). The considerable attention paid to this complex topic has generated many hypotheses about how disturbance creates variation in the diversity and function of ecosystems (Brawn et al., 2001; Cardinale and Palmer, 2002; Pulsford et al., 2016). The Intermediate Disturbance Hypothesis (IDH; Shea et al., 2004) is one such foundational ecological hypothesis used to describe the maintenance of biodiversity in changing environments. The IDH proposes that intermediate levels of disturbance allow more species to coexist than do low or high levels (Grime, 1973; Connell, 1978). While some evidence supports the IDH for vegetative communities (e.g., Mayor et al., 2012), the hypothesis has generated controversy due to weak empirical support (reviewed in Moi et al., 2020). Despite advances in understanding the relationship between disturbance and diversity, questions remain about how disturbance impacts less studied but ecologically important and diverse groups such as lichens. While lichens are widely recognized as bioindicators, especially for air pollution, less is known about how they are affected by anthropogenic disturbance in the form of forestry practices.

Most studies of disturbance on lichen communities have investigated subsets of diversity—often epiphytic macrolichens (large, leafy species growing on trees; Esseen, 2006, Pinho et al., 2012, Benítez et al., 2012, 2018, Lundström et al., 2013, Chuquimarca et al., 2019) or a single species (Campbell and Fredeen, 2004; Esseen, 2006). Microlichens—small, primarily crustose species—have frequently been excluded from macroecological studies (though see Tripp et al., 2019, Manzitto-Tripp et al., 2022) despite comprising more than half of the lichen diversity in many systems (Ellis and Coppins, 2006; Lendemer et al., 2016; Lendemer and Coyle, 2021; Kantelinen et al., 2022). Additionally, most studies have emphasized lichen response to severe or catastrophic disturbance such as intense fire (e.g. Giordani et al., 2016) rather than mild to moderate disturbance such as trampling, regional habitat fragmentation, or selective logging (although see Pinho et al., 2012).

The few studies that have directly investigated lichen and the IDH found that lichens richness does indeed peak at intermediate disturbance. In a study examining the impact of fine-scale disturbances in southern Arizona, crustose species richness peaked at intermediate disturbance (Pastore et al., 2014). At a slightly broader spatial scale, epiphytic macrolichen richness also peaked in intermediate-aged forest stands in Canadian boreal forests (Bartels and Chen, 2015). These two studies were, however, carried out at fine spatial scales (several square meters and approximately 51 ha, respectively); they sampled limited richness (6–7 species in Pastore and 22 species in Bartels and Chen); and did not consider the full complement of lichen diversity (i.e., including all taxa regardless of size, morphology, and ecology).

Beyond the IDH, other studies of disturbance on lichens have indicated that they are generally disturbance-sensitive and in the majority of cases, species richness declines as the severity and intensity of disturbance increases (Ardelean et al., 2015; Langbehn et al., 2021; Kantelinen et al., 2022). Tripp et al. (2019) analyzed a spatially restricted subset of the data used in the current study and found that HQ score, an index of habitat quality inversely related to disturbance, showed a strong positive linear correlation with lichen species richness. The ways that lichen richness—including macro- and microlichens—respond to disturbance in *in*species-rich systems is little-studied.

This study elucidates patterns of species diversity based on functional traits. Functional traits are the measurable attributes of an organism's phenotype that account for its ecological response to a gradient (e.g., elevation, moisture, or succession; Ellis et al., 2021). Trait-based approaches have allowed community ecology to shift from a focus on identifying patterns, to a focus on uncovering the processes that create those patterns, and these approaches can provide insight into ecosystem function and response to climate change (Ellis and Coppins, 2006; Lavorel et al., 2011). Lichen functional traits in particular have the potential to increase understanding of ecological processes because lichens are sensitive to changes in the environment—in large part due to their poikilohydric properties and response to shifts in moisture content of their substrates (Ellis et al., 2021). Functional traits play an important role in understanding and assessing lichen response to environmental factors and may reveal which aspects of lichen biology link species to forest conditions. For example, the richness of epiphytic lichen functional groups shifted considerably in response to forest succession on *Populus tremula* in Scotland: early successional habitat contained more asexually-reproducing and widespread species while older forests contained more sexually-reproducing species (Ellis and Coppins, 2006). Other examples of important lichen functional traits easily determined in the field include physical protection (e.g., presence or absence of specialized structures on the upper surface) and type of photosynthesizing partner (cyanobacteria or algae; Koch et al., 2019).

Our study system, the Southern Appalachian Mountains of the southeastern USA, is among the most biologically diverse temperate habitats in the world (Yarnell, 1998). The variety of elevation, geology, and topography creates many distinct microhabitats. The absence of glaciation has allowed longer periods for species to accumulate and diversify relative to northern glaciated areas (Braun, 1989) and allowed species to persist in suitable microhabitats where they were protected from competition (Delcourt and Delcourt, 1998). Along with consistent and abundant precipitation, these biogeographical factors support a profusion of species including biodiversity hotspots for taxa including salamanders (Kozak and Wiens, 2010), crayfish (Crandall and Buhay, 2008), mussels (Parmalee and Bogan, 1998), spiders (Hedin, 1997), freshwater fishes (Lundberg et al., 2000), and of course, lichens (Allen and Lendemer, 2016; Tripp and Lendemer, 2019). The region also hosts a range of anthropogenic disturbance conditions, including extensive natural areas and public lands, interwoven with agricultural and urban/ suburban development (Rice and Emanuel, 2014). The combination of biological diversity, ecological heterogeneity, geologic history, and a robust disturbance gradient, makes the Southern Appalachians an ideal site for studying lichen response to disturbance.

This study addresses how disturbance affects total lichen diversity across a large and heterogenous landscape in a global biodiversity hotspot (Tripp and Lendemer, 2019). We performed intensive sampling across 208 plots to quantify how lichen species richness and richness of lichen functional groups respond to land-use change and forestry practices. Based on prior analyses of a spatially and taxonomically restricted subset of our data (Tripp et al., 2019), we expected that, contrary to the IDH, lichen species richness would decrease as habitat quality decreased. We hypothesized that some functional groups would not follow this trend, but rather remain neutral or increase in species richness as disturbance increased (see Table S5 for directional hypotheses). For example, sun-loving crustose species might increase with disturbance as trees are cut while foliose species that depend on moist, shaded habitat would decrease. Our results illuminate how the diversity of ecologically important organisms is impacted by land-use practices that affect the level of anthropogenic disturbance. We hope the results will inform conservation and stewardship of Southern Appalachian forests.

2. Methods

2.1. Field sampling and data collection

We studied lichen diversity across the Southern Appalachian Mountains in the eastern USA using data collected from 2015 to 2020, in 208 one-hectare sites (plots hereafter) in the mountainous regions of Alabama, Georgia, North Carolina, South Carolina and Tennessee (Fig. 1), a bioregion of approximately 15.5 million hectares (Turner et al., 2003). These plots spanned a broad range of elevations (165–2014 m) and forested sites (e.g., mixed oak forest; rich cove forest; see Table S2). Plots were selected with the goal of replication across elevation, latitude, aspect, and degree of disturbance.



Fig. 1. Map of the study area within the Southern Appalachian bioregion, USA. One-hectare plots are color-coded to reflect total lichen species richness (number of species per plot, N = 208).

At each plot, a taxonomically comprehensive inventory of lichen species was conducted, with each researcher collecting voucher specimens of all observed species during an intelligent meander using the floristic habitat sampling method (Newmaster et al., 2005). This method has been demonstrated to be more effective than transect-based or nonexpert inventories at capturing total diversity for small, sessile, microhabitat specialist organisms (Coddington et al., 1991; Sørensen et al., 2002). Inventory sampling was carried out until no new taxa were encountered. Sampling times varied from 10 min in highly degraded plots to >120 min in less disturbed plots. Geographic location, habitat, and substrate were collected for each voucher. All vouchers were identified in the field and then refined and curated in a field laboratory within one day of sampling. Identifications were error-checked and processed at The New York Botanical Garden (NY) using microscopy and chemical identification following Lendemer et al. (2013). In total, 21,819 voucher collections were generated and deposited in NY with fully georeferenced digital records available through the C.V. Starr Virtual Herbarium.

Additional biodiversity and ecological data were collected at each plot. A 10 m \times 10 m square subplot was established in the southeast corner of each one-hectare plot, and all trees >40 cm diameter at breast height (DBH) were identified, and DBH was recorded. Overall woody plant diversity (trees and shrubs) was tallied per species for the entire hectare. Aspect was determined with a compass. Slope was estimated visually, and overall rock cover was quantified on a scale of 0 to 10.

Disturbance was assessed in the field using a habitat quality score (HO) based on the vegetation assessment developed by Parkes et al. (2003) as modified by Tripp et al. (2019; Table S3 herein). This index was selected because it compares plot conditions to a typical mature forest condition, thus providing a benchmark for degree of "naturalness", or human impact. It was designed to be sensitive to anthropogenic disturbance or management activities. The HQ score combines 10 components listed in Table 1. Details of how each component was calculated can be found in Table S3. For example, a plot in the Great Smoky Mountains National Park with a high degree of habitat connectivity and a short distance to a core area, with >70 % mature canopy trees, mostly native species, little weed cover, and a high percentage of coarse woody debris would score high on the HQ scale. A plot on the edge of a national forest that had recently been logged, with many invasive species and >50 % of the debris from non-native species would receive a low HQ score (see Fig. 2 for a visual example). Despite not

Table 1

The ten components of the HQ score and their associated scores.

Habitat quality (HQ) sub-category	Score			
Percent mature canopy trees	0–10			
Percent native tree canopy cover	0–5			
Percent native understory present and degree of anthropogenic modification	0-25			
Percent weed cover	0-15			
Percent native trees recruiting	0-10			
Percent litter relative to expected mature natural site conditions	0–5			
Percent coarse woody debris relative to expected	0–5			
Degree of fragmentation of surrounding hectares				
Connectivity of the one-hectare site to natural habitat in successive radii	0–5			
Distance to nearest 50 ha core area of natural habitat	0–5			
Total	100			

being an entirely direct measure of disturbance, the index reflects the types of non-catastrophic anthropogenic disturbance that we aimed to investigate. The HQ score incorporated both site-specific conditions (e. g., percent large trees) as well as the context of the surrounding land-scape (e.g., degree of fragmentation of surrounding hectares). The HQ score was inversely related to forestry-related disturbance: the higher the HQ score in a plot, the less evidence of human-caused disturbance.

Each taxon in the dataset was then scored for eight lichen functional traits that have been demonstrated to reflect environmental conditions in previous studies and have been shown to vary with habitat quality along an urban to rural gradient (Bassler et al., 2016; Benítez et al., 2018; Koch et al., 2019, 2023; Lucheta et al., 2019; Hurtado et al., 2020; Ellis et al., 2021). The traits included: reproductive mode (sexual or asexual), photobiont type (coccoid algae, Trentepohlia, cyanobacteria), growth form (crustose, foliose, fruticose, squamulose), lobe width (narrow, < 5 mm; or wide ≥ 5 mm), epiphytic macrolichen or nonepiphytic macrolichen, substrate (calcareous rock, non-calcareous rock, bark, soil), chemical protection (presence or absence of secondary metabolites in the upper surface-cortex-of the lichen), and physical protection (presence or absence of surface pruina). After scoring for functional traits, the dataset was pruned to exclude nonlichenized fungi (e.g., Mycocaliciaceae, non-lichenized lichenicolous fungi).



Fig. 2. Examples of sites with HQ scores from low (a) to high (d). Panel a. is plot in a recent timber harvest in Oconee County, South Carolina in an area of Sumter National Forest. Panel b. is a plot in Great Smoky Mountains National Park, Sevier County, Tennessee, which has been heavily affected by *Tsuga canadensis* die-off due to the Hemlock wooly adelgid. Panel c. is a plot in Haywood County, North Carolina, on the edge of Great Smoky Mountains National Park, that had been reforested after recent agricultural use and is now an even-aged stand of *Liriodendron tulipifera*. Panel d is a mature northern hardwood forest near Bob Bald in Monroe County, Tennessee, part of Cherokee National Forest.

2.2. Statistical analysis: impact of HQ on richness

To determine whether habitat quality is an important driver of lichen diversity, we used a linear model including HQ (habitat quality) score and four geographic variables: latitude, longitude, slope, aspect. This model also included a quadratic term for HQ score (HQ²) to account for potential non-linear responses to HQ. These variables were selected based on previous studies of abiotic drivers of lichen richness (Bassler et al., 2016, Benítez et al., 2018, Koch et al., 2019, 2023, Lucheta et al., 2019, Hurtado et al., 2020, Ellis et al., 2021), and a previous analysis of a subset of our data which found these to be important geographic drivers of lichen richness in our study system (Tripp et al., 2019). Potential independent variables were evaluated for collinearity. We used a correlation coefficient threshold of <60 % removed any correlated variables. All five variables were added to create a full model to test the central hypothesis that overall lichen species richness increases as anthropogenic disturbance decreases (i.e., HQ score increases). This full model was compared to a set of alternative models (Table 2), which contained a subset of the explanatory variables, using model selection criteria (AIC, Burnham, 2002). A piecewise regression analysis was performed with total species to identify a threshold in response to HQ

(Toms and Lesperance, 2003). Prior to analysis, the independent variables were standardized to mean 0 and standard deviation of 1.0 to make regression coefficients, a measure of effect size, comparable among independent variables. All model analyses were conducted in R version 4.3.1.

3. Results

3.1. Field sampling and data collection

Over six field seasons, we collected 872 unique species across 208 one-hectare plots represented by a total of 16,337 unique species observations supported by 21,819 vouchers. Of the 872 species, 58 were non-lichen fungi (e.g., Mycocaliciaceae and lichenicolous fungi) that were then pruned from the dataset, resulting in a total of 814 lichenforming species. Among the remaining 814 lichens, 476 of these taxa were crustose, 223 were foliose (including 8 umbilicate species), 48 were fruticose and 67 were squamulose or polymorphic (43 polymorphic). Three-hundred twenty-six species were primarily asexually reproducing and 449 were primarily sexually reproducing. The remaining 39 were either polymorphic for their reproductive mode or

Table 2

AIC table including all models for total lichen richness, ranked by Δ AIC. Plots were sampled across the Southern Appalachian Mountains in southeastern North America.

Variables / equation							
-	df	AIC	ΔAIC				
$^{*}HQ + HQ^{2}$	4	1844.92	0.00				
Latitude + Slope + $HQ + HQ^2$	6	1847.20	2.28				
$Elevation + Slope + HQ + HQ^2$	6	1847.23	2.31				
Latitude + Elevation + $HQ + HQ^2$	6	1848.54	3.62				
$Slope + Latitude + Elevation + HQ + HQ^2$	7	1848.63	3.71				
HQ	3	1855.57	10.65				
Latitude $+$ Slope $+$ HQ	5	1857.38	12.46				
Latitude + Elevation + HQ	5	1857.92	13.00				
Latitude + Slope + Elevation + HQ	6	1858.25	13.33				
Elevation + Slope + HQ	5	1858.40	13.48				
Elevation + Slope	4	1939.44	94.52				
Latitude + Slope + Elevation	5	1941.18	96.26				
Elevation	3	1941.29	96.37				
Latitude + Slope	4	1941.35	96.43				
Slope	3	1941.92	96.99				
Latitude	3	1942.40	97.48				
Latitude + Elevation	4	1942.69	97.77				

*This is the model used for analysis.

reproduce primarily through fungal-only asexual propagules. Species richness was lowest at a site near a parking lot in Marshall County, Alabama (0 species), and highest at Snooks Nose in McDowell County, North Carolina (146 species). Both high and low richness plots were distributed throughout the study area, often in close spatial proximity, and not concentrated in a single area (Fig. S6). Most plots had a species richness of between 40 and 80 species (Fig. S7).

3.2. Statistical analyses

Habitat quality score (hereafter HQ) and elevation were weakly correlated (Pearson correlation coefficient, r = 0.26) as were HQ score and longitude (r = 0.178, see Table S4 for correlation matrix of all variables).

The best regression model with the lowest AIC score (Table 2) included only HQ and HQ^2 . The regression coefficients (Table 3) revealed that species richness was positively related to HQ. Increases in richness were reduced at higher levels of HQ as indicated by the negative

coefficient of the quadratic term (HQ^2) and the flattening of the curve shown in Fig. 3. This model was then used to analyze the response to disturbance for each lichen functional group.

Models for functional group richness revealed trends that mirrored those for overall lichen richness (22 functional groups; Table 3). Statistically significant variables were those in which the coefficient's confidence interval did not include zero. HQ score was positively associated with functional group richness for all groups except lichens with narrow lobes and those without a photobiont (91 % of functional groups; Table 3). The quadratic term (HQ²) was negatively associated with lichen richness in fewer functional groups (59 %, not significantly associated; Table 3). All groups increased in species richness with increasing HQ, but the strength of that relationship varied across the



Fig. 3. Total lichen species richness per plot increases as HQ score (0-100) increases. From 208 one-hectare (872 unique species) plots across the Southern Appalachian bioregion. Lower HQ score indicates higher levels of anthropogenic disturbance.

Table 3

Regression coefficient estimates (95 % CI) for all lichen species and functional groups. Confidence intervals that do not include 0 are indicated with an asterisk (*).

Eunctional Group	Functional Group	Intercent	НО	HO ²	\mathbf{p}^2
Tulctolai Group	Functional Group	intercept	ng	ΠQ	п
All	All Species	83.56	10.45 (6.66,14.24)*	-3.63 (-5.61,-1.65)*	0.384
Morphotype	Crustose	42.08	6.08 (3.8,8.36)*	-1.43 (-2.62,-0.24)*	0.31
Morphotype	Foliose	30.55	2.66 (1.22,4.1)*	-1.7 (-2.45,-0.95)*	0.331
Morphotype	Fruticose	3.74	0.67 (0.25,1.09)*	-0.12 (-0.34,0.1)	0.119
Morphotype	Squamulose	1.99	0.41 (0.08,0.74)*	-0.08 (-0.25,0.09)	0.074
Substrate	Bark	67.69	7.22 (3.81,10.63)*	-3.3 (-5.08,-1.52)*	0.315
Substrate	Noncalcareous rock	8.22	1.74 (0.19,3.29)*	-0.12 (-0.93,0.69)	0.042
Substrate	Calcareous rock	0.63	0.67 (0.19,1.15)*	0.19 (-0.06,0.44)	0.028
Substrate	Soil	3.11	0.21 (-0.27,0.69)	-0.25 (-0.5,0)	0.049
Photobiont	Cyanobacteria	3.7	1.09 (0.52,1.66)*	-0.05 (-0.35,0.25)	0.121
Photobiont	Photobiont absent	1.13	0.13 (-0.08,0.34)	-0.04 (-0.15,0.07)	0.02
Photobiont	Coccoid algae	70.84	6.83 (3.47,10.19)*	-3.78 (-5.54,-2.02)*	0.339
Photobiont	Trentepohlia	5.97	1.74 (0.79,2.69)*	0.16 (-0.34,0.66)	0.077
Reproductive Mode	Sexual	35.54	5.61 (3.47,7.75)*	-0.86 (-1.98,0.26)	0.26
Reproductive Mode	Asexual	43.44	4.46 (2.36,6.56)*	-2.46 (-3.56,-1.36)*	0.359
Epiphytic Macrolichen	Non-epiphytic macrolichens	48.36	7.05 (4.45,9.65)*	-1.73 (-3.09,-0.37)*	0.323
Epiphytic Macrolichen	Epiphytic macrolichens	33.81	3.04 (1.35,4.73)*	-1.91 (-2.79,-1.03)*	0.316
Lobe Width	Broad lobes	29.43	2.73 (1.34,4.12)*	-1.75 (-2.48,-1.02)*	0.359
Lobe Width	Narrow lobes	5.71	0.3 (-0.12,0.72)	-0.34 (-0.56,-0.12)*	0.131
Physical Protection	Pruina present	12.76	1.15 (0.32,1.98)*	-0.79 (-1.23,-0.35)*	0.228
Physical Protection	Pruina absent	68.28	8.82 (5.64,12)*	-2.8 (-4.46,-1.14)*	0.371
Chemical Protection	Cortical chemicals absent	45.07	5.27 (3.15,7.39)*	-2.05 (-3.16,-0.94)*	0.357
Chemical Protection	Cortical chem present	34.35	4.49 (2.78,6.2)*	-1.51 (-2.4,-0.62)*	0.356

functional groups (Figs. 4–6 and S9-S13). The pattern for crustose, foliose, and asexual species resembled the pattern for all lichen species (Figs. 3–4, Table 3). Within the substrate functional group, all substrates except soil were significant for HQ while only bark-dwelling species were significant for HQ² (e.g., the confidence interval for HQ coefficients included 0; Fig. 6). Figures of richness response to HQ for the remaining functional groups are provided in the supplementary material (Figs. S9-S13).

Visual examination of the regression scatterplots (Figs. 3–6) suggested that variance increases as HQ score increases and that the strength of the relationship between HQ and richness declines after a certain threshold, near the HQ score of 60. A piecewise regression confirmed this trend, illustrating a rapid increase in lichen species richness up to the level of HQ \sim 60. Above this threshold, the overall trend was still weakly positive but no longer significant (Fig. S1).

4. Discussion

Our dataset spanned the entire Southern Appalachian biodiversity hotspot and analyses demonstrated that disturbance, as measured by HQ score, was an important factor driving overall lichen species richness. This result confirms earlier analyses of a smaller, spatially restricted subset of our dataset (Tripp et al., 2019). Significant HQ^2 coefficients indicate that lichen richness response is nonlinear. The negative correlation between species richness and anthropogenic land-use disturbance (lower HQ scores) suggests that more lichen species grow in habitats that are located closer to large areas of forest (i.e., more contiguous), retain more woody debris and leaf litter, support larger trees, contain more native plants and fewer invasive species. Specific components of our index accounted for "natural" versus anthropogenic origins (Table S3), but it should be noted that the score did not directly address the impacts of recreation. An additional limitation of the HQ score is that it is a relative index used to compare sites. However, all the characteristics it incorporates are accepted measures of forest health (Parkes et al., 2003) and can be easily evaluated in the field as part of routine conservation and stewardship assessment. These characteristics directly relate to anthropogenic disturbance such that components of our index capture effects of land use, fragmentation, invasive species, and introduced pathogens.

Although not included in our best model, elevation may be an important, but weak, driver of overall species richness (Fig. S8). The relationship between elevation and species richness in montane systems is well-established, with species richness often peaking at middle elevations (McCain and Grytnes, 2010; Beck et al., 2017). Analyses of our dataset have uncovered the same trend of a middle-elevation peak in species-richness (McCain et al., under review). Our data include many plots with higher disturbance at lower elevations as well as a concentration of high diversity plots at middle and high elevations (Tripp et al., 2019). In addition, mid to high elevations also receive greater precipitation and may be less impacted by climate change (Lesser and Fridley, 2016).

Our result that less disturbed forests harbor more lichen species may seem intuitive, but other taxa do not follow this pattern, including many plants in the same Appalachian forests (Catford et al., 2012). Instead, species richness for many macroscopic taxa reaches its peak at intermediate levels of disturbance, consistent with the Intermediate Disturbance Hypothesis (IDH; Mayor et al., 2012). Two previous lichen studies have found patterns consistent with the IDH: Pastore et al. (2014), who conducted a manipulative experiment on saxicolous crusts in Arizona, USA, and Bartels and Chen (2015), who studied epiphytic macrolichens across 51 plots in Lake Nipigon, Ontario, Canada. Those studies differed significantly from ours in scale and scope, focusing on different ecosystems with much lower woody plant diversity and lower lichen species richness by an order of magnitude (783 taxa in our study, 208 of which



Fig. 4. Comparison of species richness of different lichen morphotypes: a. crustose, b. foliose, c. fruticose, and d. squamulose. The x-axis shows the habitat quality score and the y-axis species richness of each morphotype by site. All four subgroups exhibit higher richness at higher HQ scores (i.e., less disturbed).



Fig. 5. Comparison of species richness of contrasting lichen reproductive modes. The x-axis shows HQ score (low scores reflect higher anthropogenic disturbance), and the y-axis illustrates species richness of primarily sexually reproducing species (a) and primarily asexually reproducing species (b). Both groups increase in richness below a threshold of HQ \sim 60, but while sexual species richness continues to increase, asexual richness levels off as forests experience less anthropogenic disturbance.



Fig. 6. Comparison of species richness of lichens that grow on contrasting substrates: a. bark, b. humus (soil), c. non-calcareous rock, d. calcareous rock. X-axis is HQ score, and y-axis is species richness per subgroup.

were epiphytic macrolichens; vs. Pastore et al., 2014, ~6–7 spp.; Bartels and Chen, 2015, 22 epiphytic macrolichen spp.). While these previous studies indicate that some subsets of lichens follow the IDH at fine scales, our results suggest this is not the case for all lichens across regional scales. Tripp et al. (2019), analyzed a subset of our data (macro and microlichens in forest plots in Alabama) and found results that mirror ours: total lichen richness does not follow the IDH, but rather continues to increase as habitat quality increases.

The divergence from the IDH that our study and Tripp et al. (2019)

uncovered could be explained by niche availability. As habitats age and diversify, more niche space for lichens becomes available (Ellis, 2012). For example, corticolous (bark-dwelling) species benefit from the more diverse ages of trees: older trees often have more furrowed bark which offers higher diversity of microhabitats that support higher lichen richness (Rogers and Ryel, 2008). Diverse stands with variable age classes also offers greater variety in bark texture and chemistry as well as greater quantities of dead wood in a range of stages of decomposition. In addition, autochthonous (self-organizing) forests often support greater

diversity of woody plants, which in turn allows bark microhabitats that support unique lichen communities (Belinchón et al., 2017).

Few of our directional hypotheses about functional group response to disturbance were supported (see Table S5 for a list of all hypotheses). We hypothesized that relationships between richness of functional subsets and disturbance would vary, likely due to divergent responses to specific site conditions. For example, we expected that while bark-dwelling lichen richness would remain similar across plots regardless of HQ score, soil and rock-dwelling lichen richness would be neutral or decrease as disturbance decreased, because soil and rock are shaded by older trees. However, we did not find varied responses but rather found an essentially uniform response of increasing richness with decreasing habitat quality across all functional groups. This surprising trend could be explained in part by the non-independence of functional groups. Each functional group is not mutually exclusive: for example, an increase in richness of rock-dwelling crusts could mirror an increase in sexually reproducing species because many crustose species are also sexually reproducing.

However, this non-exclusivity alone does not account for the similarity of responses across functional groups. An additional explanation could be that lichen community composition shifted with changes in disturbance, even though total richness remained the same or similar. For example, at a site with a low HQ score (41), we found 33 crustose, 16 foliose, and 0 fruticose species. We found similar numbers (26 crustose and 16 foliose) in a site with much higher habitat quality (87), but an investigation of the species lists from each site revealed very little overlap: only 10 species were shared between both plots. So, though the richness of functional groups was similar, the lichen communities differed at each site. Our analyses also found that functional group richness was lower than overall richness, indicating that factors other than disturbance may also be important in driving richness of individual functional groups. Nonetheless, a positive relationship between HQ score and functional group richness can be seen in all the plots (Figs. 2-4 and Figs. S8-13), demonstrating that disturbance influences overall richness, regardless of how functional groups were delimited.

Our analyses of the disturbance responses of two functional groups, morphotype and reproductive mode, merit specific comment. Morphotype—a broad grouping based on the shape of the lichen (e.g., foliose, fruticose, crustose, etc.)—is an easily identifiable attribute of most lichens. If differently morphotypes responded dramatically differently to changes in habitat quality, they could be effectively used as ecological indicators. However, our results show that morphotype is too coarse to use alone because all groups respond to disturbance in a similar way (Fig. 3). Nonetheless, we did find that fruticose and squamulose species were much less species-rich at more disturbed plots (i.e., those with HQ score < 60). This is likely linked to the pollution and disturbance sensitivity of fruticose lichens (reviewed in Ellis et al., 2021).

Reproductive mode is an important driver of lichen species distribution because sexually reproducing species must resynthesize the symbiosis during establishment (find free-living algae), while predominately asexually reproducing species can swamp the environment with clones that do not require algae or cyanobacteria to establish (Belinchón et al., 2015). Sexual versus asexual species show similar trends however, sexually reproducing species continue to increase in richness as disturbance decreases while asexual species richness levels off at an HQ score of approximately 60 (Fig. 5). These results suggest that disturbance affects reproductive mode in similar ways up to a threshold above which sexual species richness increases and asexual species richness does not. Less disturbed forests retain more moisture (Waldrop et al., 2007) that may support microhabitats conducive to free-living algae, allowing sexually reproducing species to resynthesize and thrive.

Future studies of the relationship between disturbance and lichen biodiversity are needed to address lichen conservation issues in an era of rapid global change (Weed et al., 2013; Allen et al., 2019). Such studies should incorporate finer-scale quantification of specific disturbance

components (e.g., fragmentation, stand continuity, air pollution types, and levels) and include recreation impacts to resolve which aspects of anthropogenic disturbance most influence lichen richness. Our study focused only on species richness rather than analyzing changes in community composition. Shifts in community composition in response to disturbance should be investigated, especially because patterns of composition and richness are driven by different explanatory variables (Nöske et al., 2008; Ellis and Coppins, 2010). Community analyses of broad-scale datasets such as ours would complement the results of this richness-based analysis and could catalyze conservation efforts for lichens and other diverse, understudied groups.

5. Conclusion

Here we clarified the response of lichen species richness to disturbance across a biodiversity hotspot. The results are directly applicable to conservation and stewardship both because of the inherent value of biodiversity and because the region contains threatened ecosystems (Noss and Scott, 1995). Our central hypothesis—a strong negative relationship between disturbance and lichen species richness—was supported. However, our subsidiary hypothesis that different functional groups would respond to disturbance in different ways was not supported. Instead, all functional subgroup richness responded negatively to disturbance. None of our analyses were consistent with the IDH.

Lichens are important contributors to all ecosystems but mature forests in particular benefit from the nutrient cycling, habitat provision, and moisture regulation that lichens provide (Brodo et al., 2001). Maintaining large, contiguously forested areas with trees in multiple age classes are required to effectively protect overall lichen diversity, as well as that of lichen functional groups. Our results also illustrate that effective conservation of lichen richness should prioritize the maintenance of older, less-disturbed stands in contiguously forested areas. In addition, disturbed non-forested land should be allowed to recover to reestablish connectivity among previously fragmented stands. Active reforestation of degraded areas and allowing young forests to mature (e. g., until they reach a threshold of 60 or higher on the Habitat Quality Score) could result in significant increases in lichen species richness. We hope that the detailed understanding of the response of lichen species richness to land use-related disturbance established by this study will inform forest stewardship and enhance lichen conservation.

CRediT authorship contribution statement

Laura M. Boggess: Writing – review & editing, Writing – original draft, Visualization, Software, Methodology, Investigation, Formal analysis, Conceptualization. Christy M. McCain: Writing – review & editing, Methodology, Funding acquisition, Conceptualization. Erin A. Manzitto-Tripp: Funding acquisition, Data curation. Scott M. Pearson: Writing – review & editing, Visualization, Software, Formal analysis. James C. Lendemer: Writing – review & editing, Supervision, Resources, Project administration, Methodology, Funding acquisition, Data curation, Conceptualization.

Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: James Lendemer reports financial support was provided by National Science Foundation. Christy McCain reports financial support was provided by National Science Foundation. Erin Manzitto-Tripp reports financial support was provided by National Science Foundation. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Datasets used in this study are available on GitHub (See S2 for link). All voucher data and metadata supporting the species occurrence dataset are available through the C.V. Starr Virtual Herbarium (https://sweetgum.nybg.org/science/vh/), and the physical vouchers are publicly available through the Steere Herbarium at NY.

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Appendix A. Supplementary data

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L.M. Boggess et al.

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