RESEARCH ARTICLE

Rock-climbing shifts cliff-face vegetation community composition based on site characteristics

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Abstract

Questions: What are the effects of rock-climbing on diversity, abundance and composition of cliff-face vegetation along environmental gradients? Does site variability influence cliff vegetation more than the presence of climbing?

Location: Linville Gorge Wilderness Area, NC, USA.

Methods: We compared species richness, Shannon's diversity, abundance and species composition of lichens, bryophytes and vascular plants within 334 plots, each 1 m^2. We compared climbed plots with unclimbed plots using Non-metric Multidimensional (Distance) Scaling ordination, means comparison and regression analysis.

Results: Eighty-five species were observed within 334 m^2 of cliff-face plots, including one North Carolina state (*Canoparmelia alabamensis*) and 21 Burke County collection records. Climbing altered cliff plant communities: unclimbed cliffs supported more diverse and different species than did climbed cliffs. However, site was more important than was climbing in differentiating cliff community composition. Variation in species composition was driven mostly by variation in cliff aspect and surface heterogeneity. Cliffs with the highest surface heterogeneity had the highest species richness, diversity and abundance of all three vegetation types (lichens, bryophytes and vascular plants). Unclimbed areas had similar richness, diversity and abundance compared with easy climbing routes, whereas harder climbing routes supported lower species richness and abundance of all vegetation types.

Conclusions: Differences in cliff-face vegetation in Linville Gorge were due more to site variability than to climbing impact. Therefore, management of climbing areas and decisions for future route development should be site-specific and include a thorough biological survey.

KEYWORDS
bryophyte, cliff ecology, climbing impact, community ecology, conservation, lichen, management, recreation, rock-climbing

1 | INTRODUCTION

Cliffs support unique ecological communities and a high diversity of understudied lichens and bryophytes (Larson, 2005). Cliffs were long considered relatively devoid of life and were consequently overlooked in biotic inventories. However, cliffs are increasingly recognized for harboring rare and endemic flora and ancient forests (Larson et al., 2000; Kuntz & Larson, 2006b; Boggess et al., 2017). Many cliff-dwelling plants persist because of limited disturbance, buffered temperatures and lack of competitive exclusion. Cliff communities often vary within close geographic range: even nearby cliffs may harbor distinct vegetation (Hill, 2009; Boggess et al., 2017).

1.1 | Abiotic factors that affect cliff vegetation

Abiotic factors vary within and between cliff-faces: light, moisture, canopy cover, aspect, slope and surface heterogeneity all vary from cliff to cliff and influence species composition and diversity of cliff vegetation (Larson, 2005). Slope, aspect and surface heterogeneity drive the greatest variation in cliff communities and are most often measured in climbing impact studies (Holzschuh, 2016; Boggess et al., 2021).

Slope can serve as a proxy for moisture in some cliffs (Kuntz & Larson, 2006b; Clark & Hessl, 2015; Boggess et al., 2017). Faces with steeper slopes have less water availability than do vertical or overhanging sections. Consequently, steep slopes generally harbor more desiccation-tolerant species (Larson, 2005). Slope also affects species recruitment; shallower slopes are more likely to accumulate debris and trap propagules compared with vertical or overhanging faces (Kuntz & Larson, 2006b). Vascular plants, some bryophytes and terricolous (soil-dwelling) lichens depend on soil, and so persist on low-angle faces with high surface heterogeneity where soil readily accumulates (Kuntz & Larson, 2006b; Clark & Hessl, 2015). Species that are not dependent on soil substrates, such as rock-dwelling lichens and bryophytes, can persist on vertical, even overhanging, cliffs that have low surface heterogeneity (Brodo et al., 2001; Kuntz & Larson, 2006b).

Aspect affects insolation (Graham & Knight, 2004). North- and south-facing cliffs can have marked differences in species composition, cover and growth rate (Ursic et al., 1997; Larson et al., 2000; Larson, 2005). In the southern Appalachian Mountains, south-facing slopes receive more insolation than do north-facing slopes, and are therefore warmer and drier (Warren II, 2010).

Surface heterogeneity—the variation in the rock surface caused by ledges, cracks and pockets—can also drive the composition of cliff flora. Surface heterogeneity was the most important determinant of vegetation in a landmark study of cliff vegetation along the Niagara Escarpment in eastern Canada (Kuntz & Larson, 2006a, 2006b). As microtopographic features increase in size and frequency on cliffs, they often accumulate enough soil to support vascular plants, including ancient cedar forests (Farris, 1998; Larson, 2005; Kuntz & Larson, 2006b). These microhabitat features can also provide refugia from intense light and wind exposure, and play an important role in seed dispersal and distribution, local adaptation and microclimate diversity (Kuntz & Larson, 2006b; Opedal et al., 2015).

1.2 | Disturbance on cliffs

Natural disturbances on cliffs tend to be low frequency but high intensity, which favors the persistence of slow-growing, stress-tolerant plants and lichens (Grime, 1977; Larson et al., 2000; Larson, 2005). Natural disturbances include grazing, fire, rock fall and seasonal flooding of river gorges. Grazing and fire are both reduced on cliff-faces due to patchy distribution of vegetation (Larson, 2005). After disturbance, rock face succession begins with the establishment of crustose (crust-like) lichen species on bare rock, which are eventually overgrown by foliose (leaf-like) and fruticose (shrub-like) growth forms (Jackson, 2015; Liu et al., 2019). Larger leafier growth forms of lichen can trap more water, soil and litter than pioneer crustose lichens, facilitating the establishment of bryophytes and vascular plants (Jackson, 2015; Liu et al., 2019).

Until the past century, cliff vegetation has been largely protected from anthropogenic disturbance because of inaccessibility. Quarrying, real estate development, hiking and rock-climbing are sources of anthropogenic disturbance (Larson, 2005). Of these, rock-climbing is one of the most constant and direct (Larson, 2005; Holzschuh, 2016). There are at least 35 million rock climbers worldwide, and that number is growing (Cordell, 2012; The American Alpine Club, 2019). Increased popularity has resulted in higher use of established routes, as well as a proliferation of new routes and climbing areas (Cordell, 2012). There are several, distinct styles of rock-climbing, which include aid, traditional and sport climbing (Child, 1997). Traditional and aid routes rely on the use of microtopographic features for the placement of safety devices, whereas sport climbing routes follow paths of permanent bolts drilled into the rock face (Child, 1997). There are inherent differences in microtopographic features and slope between climbing routes of different styles and difficulty levels (Kuntz & Larson, 2006a; Clark & Hessl, 2015).

Holzschuh (2016) and Boggess et al. (2021) reviewed the impact of rock-climbing on cliff biodiversity and concluded that findings are usually specific to the study area. Studies on climbing impact are sparse—only 17 peer-review papers about climbing impact on vegetation have been published in English (Boggess et al., 2021). The research that does exist has inconsistent survey methodologies and often inconclusive and conflicting results. Some studies report that rock-climbing activities negatively impact cliff-face vegetation (Nuzzo, 1995; McMillan & Larson, 2002; Rusterholz et al., 2004; Adams & Zaniewski, 2012; Clark & Hessl, 2015), whereas others conclude that climbing has no effect (Nuzzo, 1996; Kuntz & Larson, 2006a; Baur & Fröberg, 2007; Adams & Zaniewski, 2012; Boggess et al., 2017). Climbing impact may be taxon specific to only lichens (Nuzzo, 1996; Adams & Zaniewski, 2012; Clark & Hessl, 2015), bryophytes (McMillan & Larson, 2002; Kuntz & Larson, 2006a) or

FIGURE 1 Diagram of a cliff-face sampling design modified from Boggess et al. (2017). (a) Survey plots (1 m²) were placed on both sides of the transect centerline (rappel line). Plots were placed at the edge and talus of each transect, as well as every 5 m down the cliff-face. (b) Photograph of 1 m² survey plot used, including nine subplots
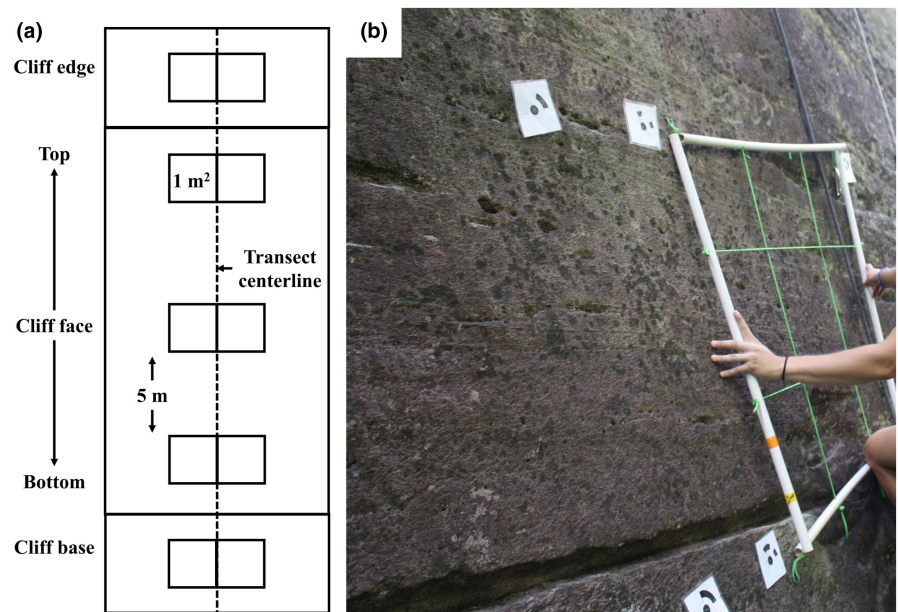
vascular plants (Kelly & Larson 1997; Farris, 1998). Further, impact can depend on levels of climbing use (Clark & Hessl, 2015; Tessler & Clark, 2016; Boggess et al., 2017).

Many gaps remain in our understanding of climbing impact on vegetation. Most climbing impact research has focused on impacts on vascular plants, often excluding bryophytes and lichens. Lichens and bryophytes dominate cliff ecosystems, so they must be included to accurately quantify climbing impact (Boggess et al., 2021). No studies consider the impact of multi-pitch routes. Multi-pitch routes are many rope lengths tall and thus usually on taller cliffs than single-pitch routes. Climbing impact can vary by style, as highlighted by Kuntz and Larson (2006a) and Tessler and Clark (2016). Multi-pitch routes make up one-third of the climbing in the Linville Gorge Wilderness Area (LGWA), so it is important to include these routes in a climbing impact study. No studies have sampled in a designated wilderness area (Boggess et al., 2021). Over one-third of climbing in the USA takes place on public lands. In wilderness areas, climbing is restricted by requiring registration, permitting, limiting bolt placement and route development, and only allowing hand tools for bolt placement (The American Alpine Club, 2019). Understanding climbing impact in areas with limited development and varied climbing use is critical to managing both climbing access and cliff communities.

We need to understand climbing impact to inform management decisions that ensure the conservation of cliff ecosystems. To address this need, we examine the effects of rock-climbing on diversity, abundance and species composition of cliff-face vegetation along environmental gradients including slope, aspect and surface features. Specifically, we assess climbing impact in a designated US Forest Service Wilderness Area with previously unstudied rock-climbing styles, including traditional style climbs and multi-pitch routes (Boggess et al., 2021). We compare climbed and unclimbed cliff-face communities to assess potential differences caused by climbing, site and abiotic variables (slope, aspect and surface heterogeneity). Further, we characterize the diversity of LGWA cliff-faces

by surveying the lichens, bryophytes and vascular plants. Altogether, we provide valuable insights into the cliff vegetation species assemblages, which can guide site-specific management recommendations for this popular climbing area.

2 | METHODS

2.1 | Site description

The LGWA is a steep gorge along the Linville River within the Pisgah National Forest in North Carolina, USA (Burke County, 35.8910°N, 81.8829°W, 1,250 m elevation). The LGWA contains numerous rock outcroppings and cliffs along the Jonas and Linville Ridge on either side of the gorge, and is 47.7 km² in size. Rock-climbing in the LGWA has been popular for at least 50 years, with over 250 routes (Lambert & Harrison, 2002). We sampled two sites: Table Rock and Hawksbill Mountain which contain 94 climbing routes. Most of the routes at Table Rock are traditional style, multi-pitch climbs with permanent anchors at the top of the climb. Large parties and guiding agencies frequent Table Rock because of the short approach and routes of moderate difficulty. Hawksbill has abundant challenging, single-pitch sport climbs in the LGWA, and is a popular destination for summer day trips (Lambert & Harrison, 2002). Both areas contain both sport and traditional rock-climbing routes, ranging from easy (5.4 Yosemite Decimal System [YDS]: a climbing system of grading difficulty of a route) to challenging (5.13 YDS; Lambert & Harrison, 2002).

All transects were over 13 m high with continuous cliffs extending 2 m on either side. If a climbing route was multiple pitches long, every pitch in the route was surveyed. Unclimbed transects had no evidence of climbing (no chalk or permanent equipment), were not mentioned in local guidebooks and occurred at least 2 m from established climbing routes (Lambert & Harrison, 2002).

2.2 | Field collection methods

Field sampling took place from May to August 2019. Vegetation was sampled along a vertical transect, which ran down the center of each climbed or unclimbed area, and was marked by a rappel line. Survey plots were placed to the left and right of a survey (rappel) line, starting 2 m below the cliff edge or climbing anchor and subsequently plots were placed every 5 m at Table Rock and 3 m at Hawksbill to account for differences in cliff height, descending the cliff-face (Figure 1a). The presence or absence of each lichen, bryophyte and vascular plant was recorded within 1 x 1 m quadrats, broken into nine sub-quadrats as indicated by tape or paracord rope on the plot frame (Figure 1b; Kuntz & Larson, 2006a). Each species in each plot received a value from 0 to 9 to reflect abundance. We focused on cliff-face vegetation, excluding talus and cliff edge, because of the multi-pitch nature of most of our transects.

In the field, lichens and bryophytes were described and placed into "morphospecies" based on morphological features. Bryophytes, fruticose and foliose lichens, and vascular plants were collected by hand from within 1 x 1 m quadrats. Crustose lichens were removed using a hammer and chisel at least 1 m from established climbing routes and known rare and endemic species were not collected. Lichens and bryophytes were identified to species in the laboratory using the dichotomous keys and nomenclature of Brodo et al. (2001, 2016) and the Flora of North American Editorial Committee (2007, 2014), respectively, such that morphospecies were converted to a species-level determination whenever possible. Vascular plants were identified using the nomenclature of Weakley (2015). Specimens were deposited in the University of Tennessee Herbarium (TENN) (bryophytes and a few vascular plants, Appendix S1) and Appalachian State University Herbarium (BOON) (lichens and a majority of vascular plants, Appendix S1). Degree of sampling completeness by site and presence of climbing (either climbed or unclimbed) was determined using function "iNext" from the R package *iNext* (version 2.0.20; R Core Team, R Foundation for Statistical Computing, Vienna, AT), which interpolates and extrapolates diversity using Hill numbers.

Continuous environmental variables were recorded for each survey plot and transect. Aspect was recorded once per transect using a compass and decomposed into two linear components, north–south (northness) and east–west (eastness) (Beers et al., 1966). Slope was recorded at the center of each plot using an inclinometer to capture site variability. The area (length × width) of ledges and volume (length, width and depth into the rock face) of pockets and crevices within the survey plot were measured as described by Kuntz and Larson (2006a, 2006b).

2.3 | Statistical analyses

Species composition of cliff-face plots was explored using Non-metric Multidimensional (Distance) Scaling (NMDS) ordination produced with "metaMDS" function in package *vegan* version 2.5-7 (R Core Team, R version 4.0.3 Foundation for Statistical Computing,

Vienna, AT). Cover values (0–9 for each species) were used, and data were transformed using Wisconsin double standardization to account for variation in species abundance. A three-dimensional solution was chosen to reduce stress. We visualized the impact of climbing and site on community composition by placing 95% confidence ellipses on the first two NMDS axes. A permutational multivariate analysis of variance was used to compare communities across sites and climbing exposure. Surface features for each plot were summarized using a two-dimensional NMDS. We performed non-parametric linear regression of environmental variables (slope, aspect and two surface heterogeneity values) against the ordination axes using function "envfit" (*vegan*). Vectors proportional to regression coefficients were plotted on the ordination to illustrate the strength and direction of their relationship with each axis.

For all further analysis, data were partitioned into four groups: all taxa, vascular plants, bryophytes and lichens. Species richness and Shannon's Diversity Index (H') were calculated for each plot using the *vegan* package (R Core Team, R Foundation for Statistical Computing, Vienna, AT). Species abundance was calculated by summing all cover values for each species in a plot to obtain a relative abundance estimate. Differences among richness, diversity, and abundance by site (Hawksbill or Table Rock) and presence of climbing were tested using a Kruskal–Wallis test. We further compared species richness and diversity by climbing route difficulty. Climbed survey transects were classified into three groups based on their grade (Clark & Hessl, 2015), as reported by Lambert and Harrison (2002): ≤ 5.6, beginner; 5.7–5.9, moderate; 5.10–5.12, advanced; and ≥ 5.13, professional. Generalized Linear Mixed Models were used to estimate relationships between species richness, diversity and abundance to transect (eastness, northness) and plot (slope, values from first two surface heterogeneity NMDS axes) abiotic variables.

Lichens were divided into five functional groups based on their morphological features: powder, crustose, umbilicate foliose, lobed foliose and fruticose. Species richness, Shannon's Diversity Index and total cover of each functional group was calculated per plot. We compared average richness, diversity and cover for each lichen functional group by site and presence of climbing using a Kruskal–Wallis test Dunn post-hoc test. Significance was assumed for α ≤ 0.05 for all tests. Whenever appropriate, data were tested for normality using a Shapiro–Wilk test. All statistical analyses were conducted in R (version 4.0.3; R Core Team, R Foundation for Statistical Computing, Vienna, AT).

3 | RESULTS

We surveyed 39 transects with 334 survey plots (each 1 m²). Most of the surveys took place at Table Rock, with 19 climbed and 12 unclimbed transects (*n* = 272 plots). Hawksbill had four climbed and four unclimbed transects (*n* = 62 plots). Appendix S2 contains a list of all climbing routes surveyed including grade and length.

We observed 85 species, including 42 lichens within 29 genera, 22 vascular plants within 21 genera and 22 bryophyte species within

17 genera. Appendix S3 contains a complete species list, including naming authority, in rank abundance order. Lichens were the most abundant taxa group at both sites. *Aspicilia cinerea*, *Lasallia papulosa*, *Physcia subtilis*, *Lepraria neglecta* and *Acarospora fuscata* were the five most common species in climbed plots, and *Lasallia papulosa*, *Lepraria neglecta*, *Umbilicaria mammulata*, *Aspicilia cinerea* and *Physcia subtilis* were the most abundant in unclimbed plots. The most common species at Table Rock were *Lasallia papulosa*, *Aspicilia cinerea*, *Lepraria neglecta*, *Physcia subtilis* and *Umbilicaria mammulata*. The most common species at Hawksbill were *Lasallia papulosa*, *Acarospora fuscata*, *Lepraria neglecta* and *Diploschistes actinostomous*. *Selaginella tortipila*, followed by *Hydatica petiolaris* (syn. *Saxifraga michauxii*), were the most abundant vascular plants and are characteristic of cliff-faces in the LGWA (Newell & Peet, 1998). The most abundant bryophyte was a field-described morphospecies common in seeps, followed by *Campylopus tallulensis* and *Weissia controversa*.

Table 1 displays degree of sampling completeness by comparison observed and estimated species richness and diversity by site and presence of climbing. This demonstrates adequate sample coverage at both sites and by climbing presence, with similar coverage among both site and climbing groups.

3.1 | Community composition

Site ($F_{1,324} = 42.44$, $p = 0.001$, $R^2 = 0.11$) was a more important factor than climbing presence ($F_{1,334} = 15.97$, $p = 0.001$, $R^2 = 0.04$) for differentiating cliff-face communities (Figure 2). The interaction between climbing and site was significant but with a low R^2 value ($F_{1,334} = 2.21$, $p = 0.026$, $R^2 = 0.005$, Figure 2). Climbed plots were not clustered as a subset within unclimbed sites (Figure 2). Vectors of slope, northness, eastness and surface heterogeneity were all a highly significant ($p < 0.001$) environmental fit to the cliff-face community NMDS (Figure 2).

3.2 | Climbing and site impact

Table Rock plots contained more species than did Hawksbill plots, regardless of climbing status, with unclimbed plots having more species than did climbed plots ($p < 0.001$, Table 2; Figure 3). Across all climbed and unclimbed plots, Table Rock had the highest lichen richness ($p < 0.001$, Table 2; Figure 3). Vascular plant and bryophyte richness were low, especially at Hawksbill. Bryophyte richness was highest at Table Rock ($p < 0.01$, Table 2; Figure 3). Following the pattern of all taxa grouped together, vascular plant richness was highest in unclimbed, followed by climbed plots at Table Rock, both of which were richer than Hawksbill ($p = 0.004$, Table 2; Figure 3). Diversity trends mirrored richness trends (Table 2; Figure 4).

Table Rock plots had higher total cover than did Hawksbill plots ($p < 0.001$, Table 2; Figure 5). Lichens ($p = 0.002$) and bryophytes ($p < 0.001$) were most abundant at Table Rock, but there were no differences by climbing (Table 2; Figure 5). Vascular plants were also most abundant at Table Rock but had highest cover in unclimbed plots ($p = 0.002$).

Most of the climbed cliff-face plots surveyed were easy climbing grade ($n = 122$), compared to moderate ($n = 14$), advanced ($n = 70$) and unclimbed areas ($n = 138$). Easy climbing routes had the same species richness ($F_{3,328} = 11.44$, $p < 0.001$) and diversity ($F_{3,328} = 14.24$, $p < 0.001$) as unclimbed areas, both of which were more species rich and diverse than moderate and advanced climbed plots (Figure 6). Relative abundance was lower on moderate routes ($F_{3,328} = 7.38$, $p < 0.001$), but there were no other differences in abundance between easy, advanced and unclimbed routes (Figure 6).

3.3 | Abiotic influence

Size and abundance of surface features varied by site and climbing presence. Unclimbed plots at Table Rock had the most features (ledges, crevices, pockets), followed by climbed Table Rock plots, which had more than Hawksbill plots ($F_{1,328} = 4.93$, $p < 0.05$). Table Rock had higher total feature surface area ($F_{1,328} = 3.03$, $p < 0.1$), more ledges ($F_{1,328} = 35.16$, $p < 0.001$), higher ledge surface area ($F_{1,328} = 28.6$, $p < 0.001$) and more crevices ($F_{1,328} = 7.93$, $p < 0.01$) per plot than Hawksbill. Pockets were rare at both sites and there were no differences in their abundance or surface area by site or climbing.

Linear models of species richness, diversity and cover with transect and plot abiotic variables indicated species richness and diversity were most often related to aspect and surface heterogeneity,

TABLE 1 Comparing observed and estimated species richness and diversity by site and presence of climbing using Hill numbers

Factor	Site	Diversity	Observed	Estimator	*SE*	LCL	UCL
Site	Hawksbill	Species richness	36.0	36.0	0.62	36.00	37.65
		Shannon diversity	18.1	18.4	0.53	18.13	19.46
	Table Rock	Species richness	122.0	160.1	16.88	138.62	209.34
		Shannon diversity	33.6	35.0	1.09	33.63	37.09
Climbing	Climbed	Species richness	89.0	115.4	14.76	98.52	162.34
		Shannon diversity	31.2	31.4	1.01	30.18	33.36
	Unclimbed	Species richness	88.0	108.6	11.01	95.68	142.99
		Shannon diversity	34.7	36.8	1.42	34.70	39.54

Abbreviations: LCL: lower confidence limit; UCL: upper confidence limit.
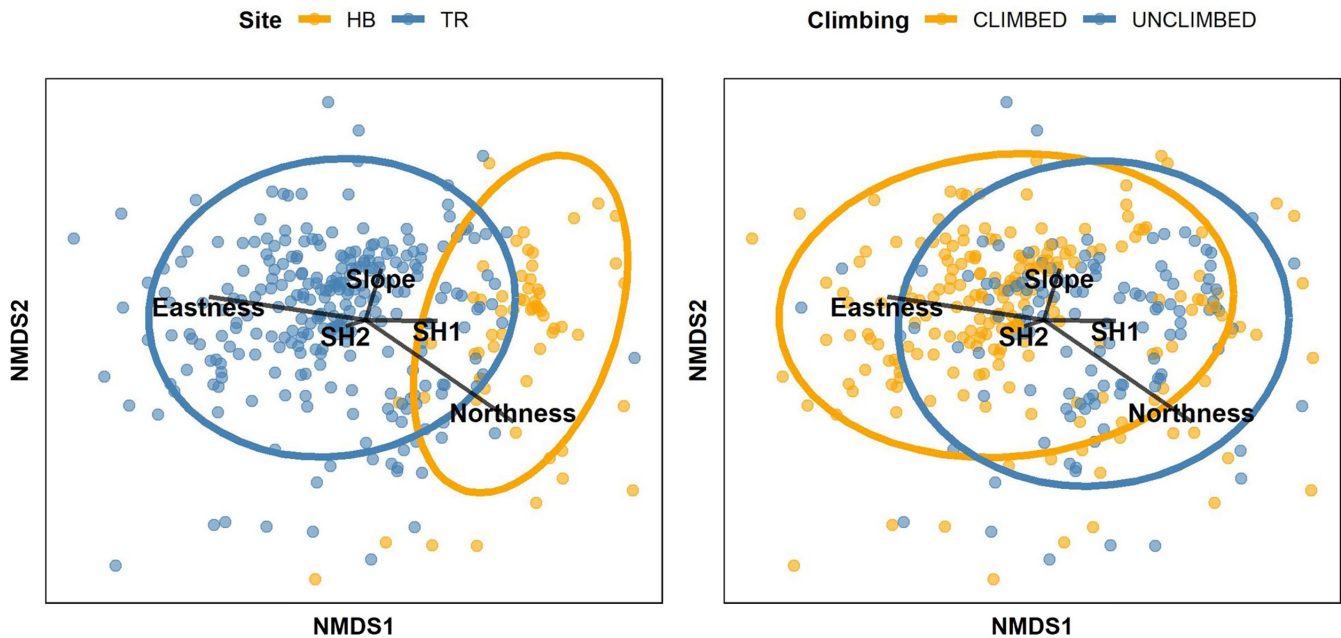
FIGURE 2 Non-metric Multidimensional (Distance) Scaling (NMDS) plots of vegetation community (all taxa) when grouped by site (left) and by climbing (right). HB: Hawksbill; TR: Table Rock. SH1 and SH2 are the first two surface heterogeneity axes from NMDS compression. Climbed plots were not clustered as a subset within unclimbed sites

although the predictive power of the models was low (Appendix S4; maximum adjusted $R^2 = 0.15$). Richness and diversity of all taxa grouped together was influenced by slope, eastness and surface heterogeneity (Appendix S4). Eastness was important for all groups except vascular plants ($p < 0.05$), and the more east-facing a cliff was, the higher the diversity of lichen, bryophyte and their combined taxa richness and diversity (Appendix S4). Lichen richness was related to both components of aspect and surface heterogeneity ($p < 0.05$; Appendix S4). Linear models for vascular plant species richness and diversity had the weakest explanatory power of all the taxonomic groups, but were related to slope ($p < 0.01$; Appendix S4). Generally, trends were consistent for both richness and diversity (Appendix S4). Relative abundance of the all-taxa group was related to plot eastness and surface heterogeneity (Appendix S4). Lichen abundance was influenced only by eastness and bryophyte abundance was influenced only by northness (Appendix S4).

3.4 | Lichen functional groups

Lichen functional group cover (crustose, powder, umbilicate foliose, lobed foliose and fruticose) varied by site and presence of climbing (Figure 7). Crustose and fruticose lichens exhibited opposite coverage patterns (Figure 7): Hawksbill plots, which contained small, sparse surface features, had higher crustose cover than did Table Rock plots ($p < 0.001$). Table Rock, which had high surface heterogeneity, supported higher fruticose cover than did Hawksbill ($p < 0.001$). Umbilicate and lobed foliose cover was also higher ($p < 0.001$) in unclimbed Table Rock plots than in Hawksbill and climbed Table Rock plots (Figure 7). Powder lichens have

higher cover in unclimbed plots than climbed plots at both sites ($p < 0.001$).

4 | DISCUSSION

4.1 | Cliff community species assemblages

Lichens were the most common taxonomic group on LGWA cliffs, and the most common species were *Lasallia papulosa*, *Lepraria neglecta*, *Physcia subtilis*, *Aspicilia cinerea* and *Xanthoparmelia conspersa*. Many of these common species are characteristic of southern Appalachian high-elevation rock outcrops and cliffs (Newell & Peet, 1998). Many of the most common lichens encountered by Clark and Hessl (2015) in New River Gorge, West Virginia, such as *Aspicilia cinerea*, *Dimelaena oreina*, *Lasallia papulosa*, *Lasallia. pennsylvanica*, *Lepraria neglecta*, *Lepraria. nomandinioides*, *Phlyctis. petraea*, *Physcia subtilis* and *Umbilicaria mammulata*, were also observed in the LGWA. Many genera common to this study were also observed by Smith (1998), and Boggess et al. (2017) during their survey of cliff communities in the LGWA and Big South Fork National River and Recreation Area, respectively.

The most common of the bryophyte species were *Campylopus tallulensis*, *Weissia controversa* and *Dicranum montanum*. Smith (1998) also observed *Dicranum montanum*, *Dicranum. scoparium* and *Dicranella heteromalla* on LGWA cliffs. Additionally, *Dicranum montanum* was one of the most common bryophytes recorded by Boggess et al. (2017). Another epipetric (rock-dwelling) bryophyte, *Andreaea rothii*, was characteristic of seeps on climbed and unclimbed cliffs in this study, and was also a common bryophyte in Boggess et al. (2017). The most common bryophytes in Clark and Hessl (2015),

TABLE 2 Species richness, diversity and abundance by site, presence of climbing and the interaction of site and climbing using a Kruskal–Wallis test. Degrees of freedom for all tests was 1,328. Diff is difference of Table Rock - Hawksbill for site and Unclimbed - climbed for climbing. Significance code: $p < 0.001$ ***, $p < 0.01$ **, $p < 0.05$*

Indicator	Taxa group	Factor	χ^2	p value	Significance	Diff.
Richness	All	Climbing	3.23	0.072		0.56
		Site	43.51	0.000	***	2.26
	Lichen	Climbing	1.64	0.200		0.25
		Site	17.43	0.000	***	1.25
	Bryophyte	Climbing	0.00	0.962		0.12
		Site	36.56	0.000	***	0.70
	Vascular plants	Climbing	7.38	0.007	**	0.19
		Site	10.56	0.001	**	0.32
Diversity	All	Climbing	2.77	0.096		0.07
		Site	47.59	0.000	***	0.30
	Lichen	Climbing	1.82	0.178		0.05
		Site	19.95	0.000	***	0.18
	Bryophyte	Climbing	4.49	0.034	*	0.09
		Site	10.43	0.001	**	0.13
	Vascular plants	Climbing	0.54	0.463		0.02
		Site	4.75	0.029	*	0.07
Abundance	All	Climbing	2.35	0.125		1.74
		Site	24.18	0.000	***	7.47
	Lichen	Climbing	1.49	0.223		1.14
		Site	9.37	0.002	**	4.51
	Bryophyte	Climbing	1.06	0.303		−0.13
		Site	35.94	0.000	***	2.28
	Vascular plants	Climbing	8.13	0.004	**	0.73
		Site	9.73	0.002	**	0.68

Campylopus tallulensis, *Dicranella heteromalla*, *Leucobryum glaucum* and *Pseudotaxiphyllum elegans*, were all also observed in this study.

Selaginella tortipila was the most common vascular plant and is a primary inhabitant of exposed rocky cliffs in the southern Appalachians (Smith, 1998). This species is functionally important for cliff succession because it forms dense mats over exposed rock, until the weight is too great, causing them to break loose and tumble down the cliff-face, either naturally or because of rock-climbing. *Selaginella* mats often also contain fruticose and foliose lichens. The second most common vascular plant, *Hydatica petiolaris* (syn. *Saxifraga michauxii*), is a rock outcrop specialist in the southern Appalachians. *Hydatica petiolaris* was present predominantly on ledges and within crevices on both climbed and unclimbed cliff-faces at Table Rock, but was also present on the cliff top in thin soil pockets. Many of the vascular plants observed in this study were also recorded by Smith (1998) during his survey of cliff plants in the LGWA, including *Galax urceolata*, *Hydatica petiolaris*, *Kalmia latifolia*, *Rhododendron minus* and *Vaccinium corymbosum*,

Several bryophyte and lichen species collected in this study were noteworthy because of their rarity of collection. *Bucklandiella venusta* (= *Racomitrium venustum* Frisvoll) has not been collected

in Burke County, North Carolina since 1964 (L.E. Anderson, Hawk's Bill Mountain), based on the specimens documented by the Consortium of North American Bryophyte Herbaria (CNABH; bryophyteportal.org) as of 9 March 2022. Tessler et al. (2017) also observed *Bucklandiella venusta* in the Shawangunk Mountains of New York on boulders used for rock-climbing. Records indicate that *Dicranella varia*, *Polytrichum strictum* and *Polytrichum. juniperinum* are Burke County records and *Dicranella varia* has not been collected in North Carolina since 1988 (CNABH accessed on 9 March 2022). *Canoparmelia alabamensis*, a foliose lichen species found on non-calcareous outcrops in Alabama, was collected on an unclimbed transect at Table Rock, and represents the first report of this species in North Carolina according to the CNABH (lichenportal.org) as of 9 March 2022. Seventeen other lichen species have no record of collection in Burke County, NC (Appendix S5). Burke County has a long history of bryophyte collecting, starting in 1891, with over 1,000 herbarium specimens collected from the county (CNABH accessed on 12 May 2021). Similarly, there are over 550 lichen collections in Burke County which date back to 1920 (CNALH accessed on 30 June 2021). Both lichens and bryophytes have rarely been collected from cliff environments, with only three bryophyte specimens collected
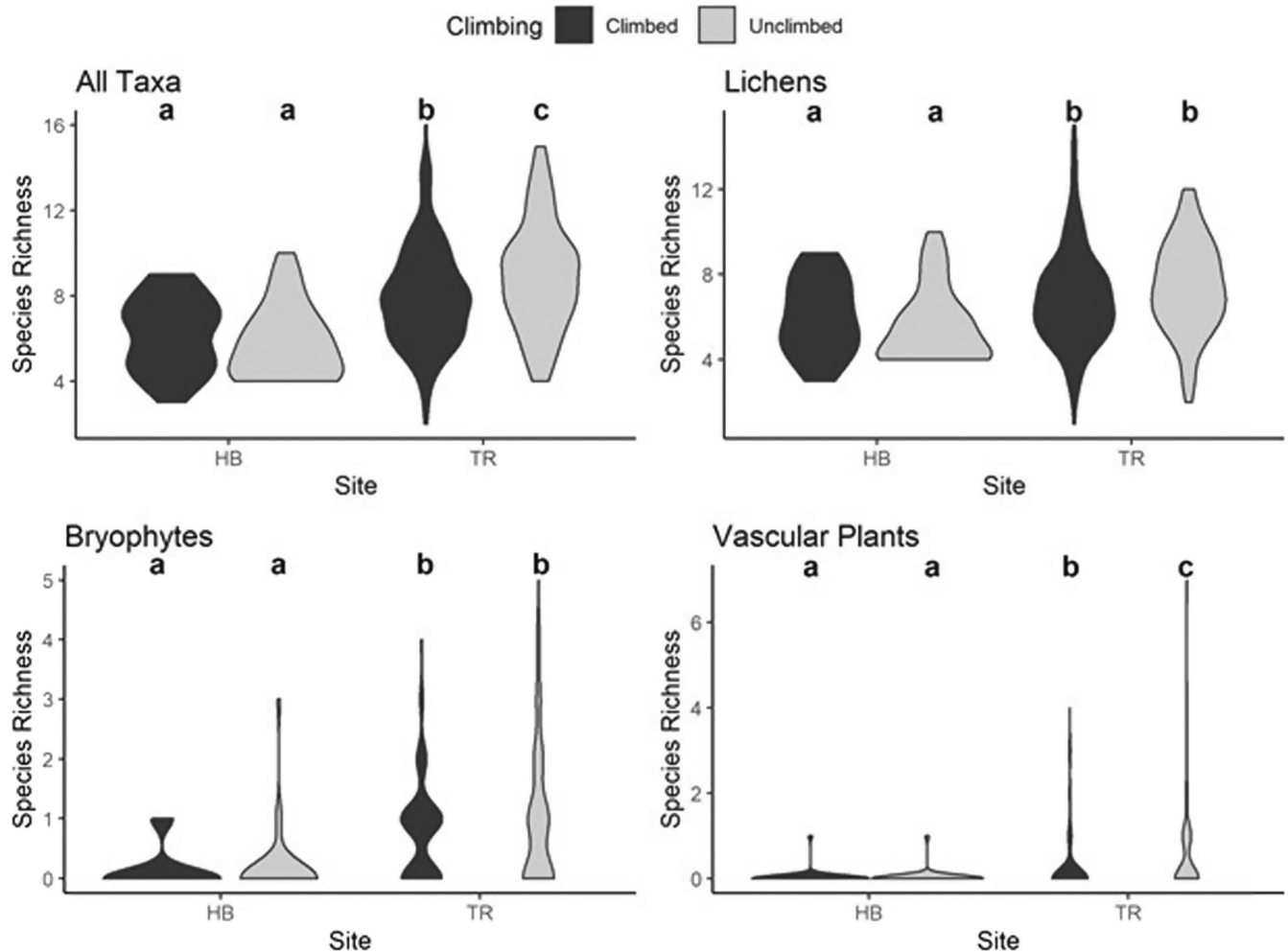
FIGURE 3 Species richness of all taxa and groups by climbing and site factors, statistically significant differences are indicated by letters. Unclimbed plots at Table Rock had the highest richness, followed by climbed plots at Table Rock, both of which were more rich than Hawksbill ($p = 0.04$). Lichens were the most abundant species

from cliffs (CNABH accessed on 12 May 2021). This lack of sampling points toward the need for additional surveying to continue to deepen our understanding of these elusive ecosystems.

4.2 | Climbing impact

Cliff vegetation often develops under minimal disturbance. It follows a typical successional pattern of species establishment, beginning with crustose lichens, followed by leafy lichens and ending with bryophytes and plants (Jackson, 2015; Liu et al., 2019). Transitions between successional stages are mediated by environmental factors, especially surface heterogeneity and slope. For example, high surface heterogeneity directly facilitates transitions to climax communities by trapping water, propagules and soil that allow the growth of climax successional species. In addition, large leafy lichens can further facilitate the transition to later successional stages that include the establishment of bryophyte and vascular plant species by trapping water, soil and litter (Jackson, 2015). However, with direct disturbance from climbing, cliff communities may be retarded

in primary successional stages. Pioneer crustose species can persist through disturbance and can have high species richness on climbed routes (Smith, 1998). Climbed routes, like early successional cliff vegetation, are characterized by abundant crustose lichens and few umbilicate, foliose and fruticose lichens. Transitional successional stage foliose and fruticose lichens are less closely anchored to their substrate than are crustose lichens and therefore more easily removed by climbers. The unclimbed cliffs at Table Rock supported higher fruticose lichen and vascular plant richness than did climbed areas, which supports this "retarded by climbing" hypothesis.

Site-level characteristics drove differences in vegetation diversity and abundance. Specifically, variation in cliff-face microtopography between the Table Rock and Hawksbill contributed to a majority of site-level variation. Table Rock, which had high richness and diversity for all taxa, also had the most microtopographic features and surface area. Habitat variables also interact with climbing disturbance to shape the community response to disturbance: in other words, site characteristics govern climbing impact. Climbing impacts were greatest on cliffs with the highest surface heterogeneity (Table Rock) because unclimbed areas on these cliffs had
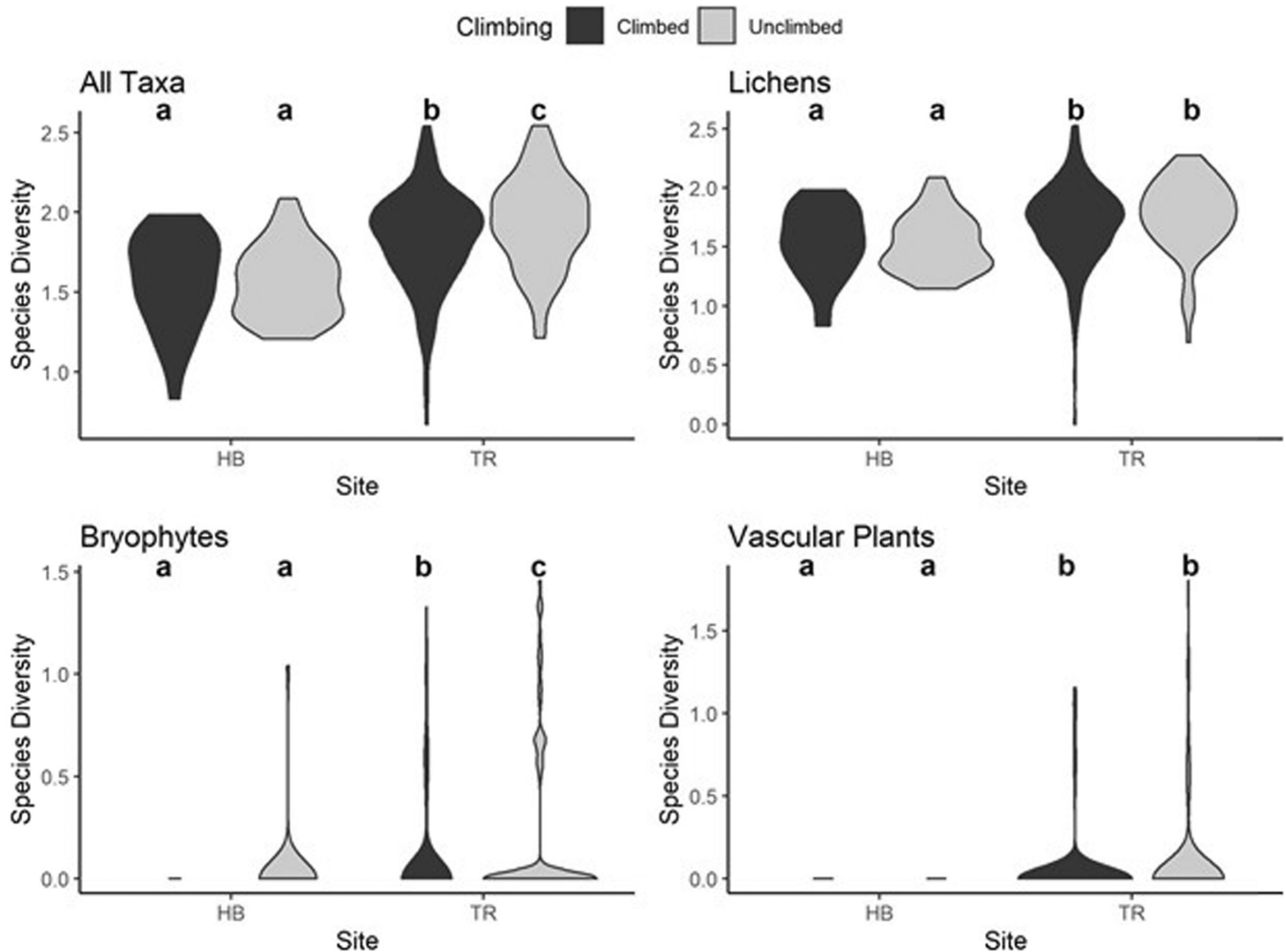
FIGURE 4 Shannon Diversity Index of all vegetation and taxa groups by climbing and site factors, statistically significant differences are indicated by letters. Overall, Table Rock had higher species diversity than Hawksbill ($p < 0.001$). Lichens accounted for most of the diversity because of their abundance

the highest diversity and richness, especially of vascular plants and bryophytes. In addition, climbed communities at both sites were distinctly different, not just subsets, from their unclimbed counterparts. Kuntz and Larson (2006) and Adams and Zaniewski (2012) observed a similar phenomenon: climbed areas support different community composition compared with unclimbed areas rather than supporting a subset of those in unclimbed areas. In our study, climbing caused shifts to different, less diverse and less species-rich cliff plant communities.

Species richness and diversity differed by route difficulty in the climbed areas. Easy climbing grade areas were the most diverse and species rich. These results are consistent with assumptions by Clark and Hessl (2015) and Kuntz and Larson (2006) of inherent abiotic variability of climbing routes depending on grade. Harder climbing routes are steeper, sometimes overhanging, and have less surface heterogeneity than do easier routes (both feature size and abundance), which are associated with decreased diversity and less species-rich communities. However, in the LGWA, the distribution of climbing grades surveyed was not equivalent by site. Hawksbill is a relatively small climbing area, made up of moderate and advanced

difficulty climbing routes (Lambert & Harrison, 2002). By contrast, Table Rock is a larger climbing area with more routes overall, which are well distributed across climbing grades. Our study corroborates findings by Clark and Hessl (2015) and Kuntz and Larson (2006) that route difficulty is a predictor of cliff species richness and diversity.

The difficulty of a climb influences how often it is climbed (climbing intensity). To quantify this phenomenon, Clark and Hessl (2015) created a climbing use index using a climbing route's popularity and approach time to gauge relative use by climbers. The climbing use index is not relative to a route's difficulty and can be applied to routes of any grade. Thus, at Table Rock Mountain, routes of easy difficulty receive high traffic, especially from large groups and guiding agencies, whereas at Hawksbill, the opposite is true. Moderate and challenging routes are higher quality and thus receive higher traffic than easier climbs. Local climbing organizations and guiding agencies may be able to classify routes by climbing use intensity. When combined with route difficulty and site-specific knowledge from local climbing organizations, climbing use intensity can be used to inform levels of climbing disturbance for future research and management.
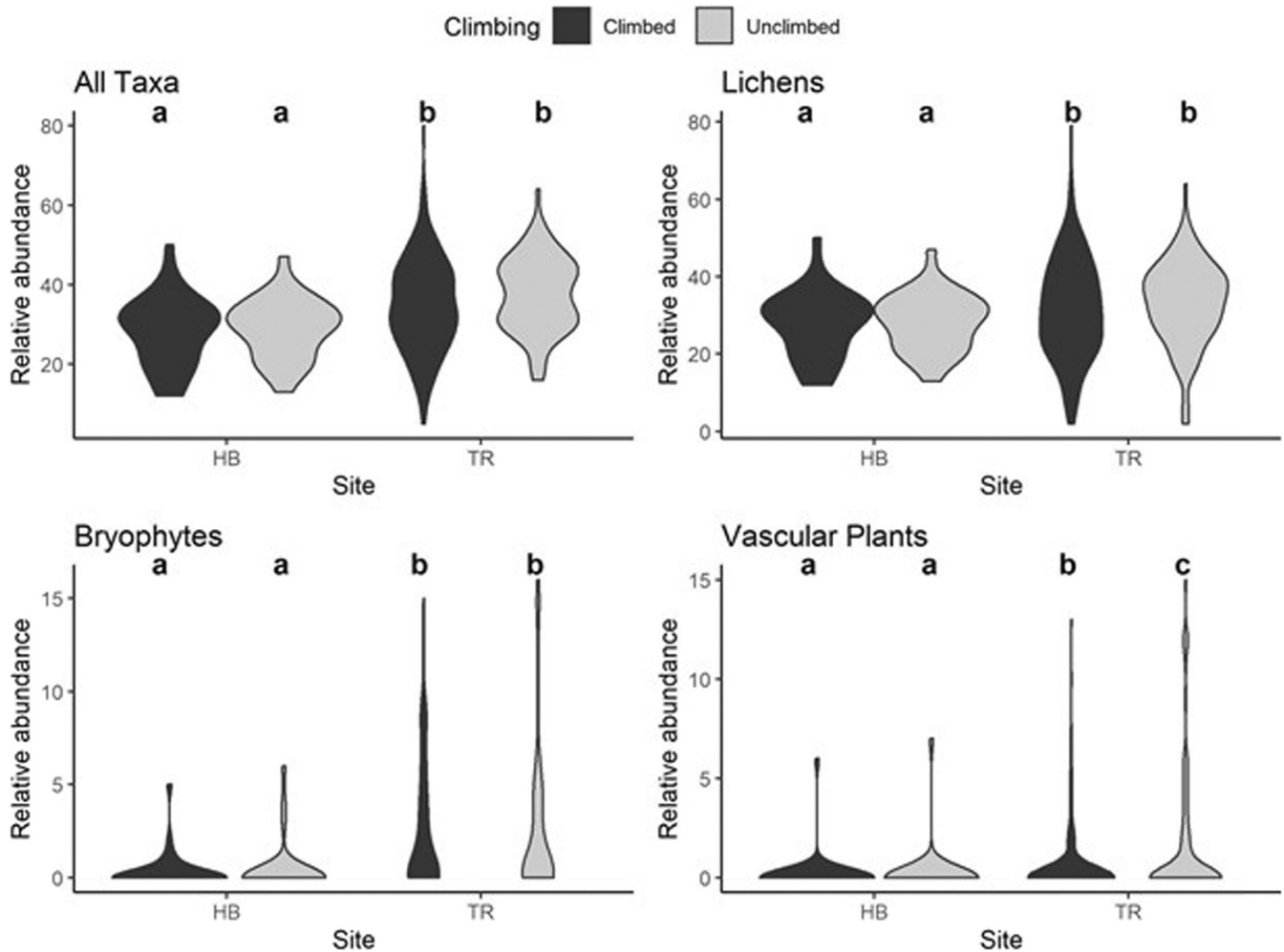
Climbing ■ Climbed ▢ Unclimbed

FIGURE 5 Relative abundance of all taxa and groups within cliff-face plots by climbing and site factors, statistically significant differences are indicated by letters. Table Rock had the highest cover of all taxa, and lichens were the most abundant taxa. Vascular plants at Table Rock were the most abundant, and unclimbed Table Rock plots had higher cover than climbed plots

4.3 | Lichen functional groups

Climbing impacts lichen functional groups in different ways. In this study, crustose lichens were the most abundant functional group, with highest cover in climbed plots with smaller and fewer surface features. Crustose lichens also dominated climbed faces in both species richness and percent cover in Boggess et al. (2017) and Clark and Hessl (2015). Unclimbed areas at both sites had increased cover of non-crustose functional groups, especially umbilicate foliose. Smith (1998) also observed high crustose cover on disturbed cliffs and high foliose and fruticose cover on undisturbed cliffs in the LGWA. Climbing-induced shifts in lichen morphotypes were also demonstrated by Adams and Zaniewski (2012) on the north shore of Lake Superior. Because climbing impacts groups of lichens in different ways, functional groups should be included in analysis of climbing impact.

4.4 | Management of cliff ecosystems

Cliff-face vegetation communities in the LGWA are unique, even given their close geographical proximity. They also contain rare and understudied lichens and bryophytes. It is critical to perform an ecological survey to understand site-specific diversity before making management decisions for cliff systems. In general, a survey before a site is disturbed would be ideal, but areas already established as climbing sites would still benefit from assessment and monitoring. Newly proposed climbing areas should be surveyed prior to development and monitored for changes if climbed. Each cliff and climbing area should be assessed independently of each other, even when sites are near each other due to site-specific differences in species composition.

Surveys allow for the identification of fragile areas or hotspots of diversity that may be protected by restricting access. Such restrictions have been successful at the Obed Wild and Scenic River, TN, USA, where the National Park Service has successfully implemented a "no-top out" policy which prevents climbers from walking on sensitive cliff-edge habitat while still allowing route access to climbers (Walker et al., 2004). Rock climbers should play a key role in ecological monitoring, as highlighted by Clark and Hessl (2015). Inclusion of recreational users can benefit researchers and climbers alike through selecting and accessing study sites, informing climbing use intensity and increasing engagement from local climbers to conservation practices.
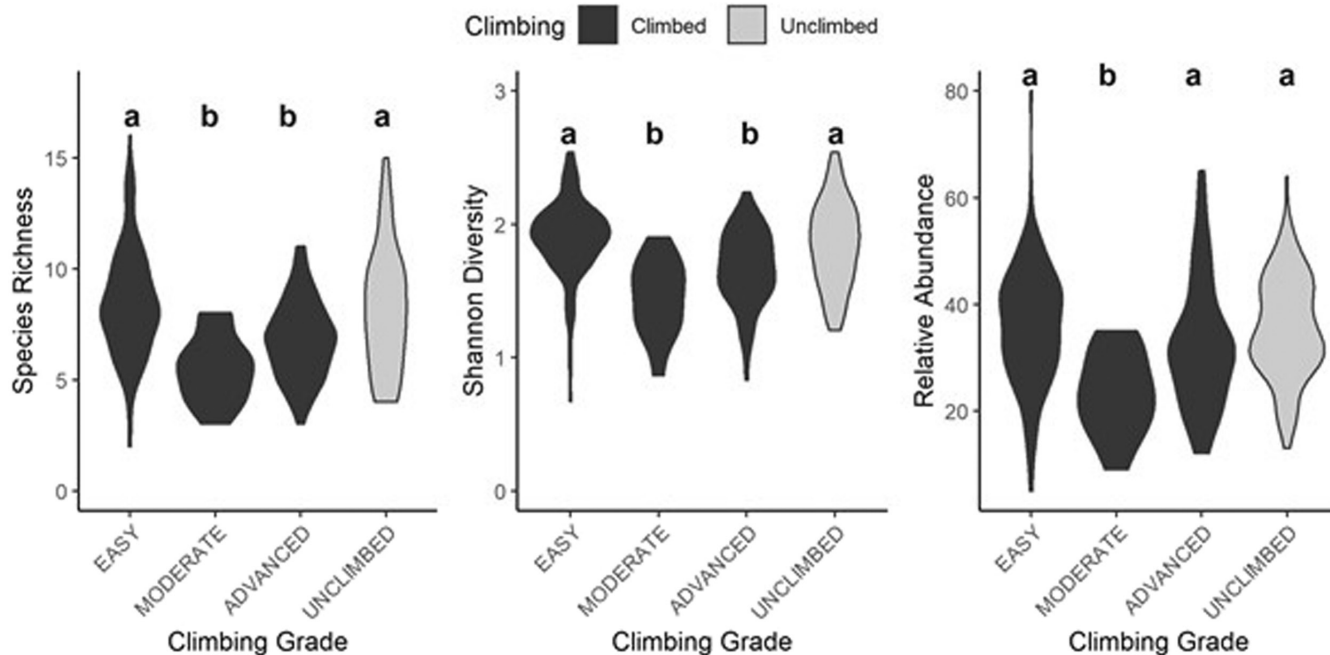
FIGURE 6 Species richness, Shannon Diversity Index, and relative abundance of all species by climbing grade. Significance is shown by letters. Climbing routes were classified into three groups based on their Yosemite Decimal System grade as reported by Lambert and Harrison (2002): ≤ 5.6, beginner; 5.7–5.9, moderate; 5.10–5.12, advanced; ≥ 5.13, professional. Climbing routes grouped into the "easy" grade, as well as unclimbed areas, had significantly higher species richness ($p < 0.001$), Shannon Diversity Index ($p < 0.001$) and relative abundance ($p < 0.001$) than moderate and advanced climbing routes
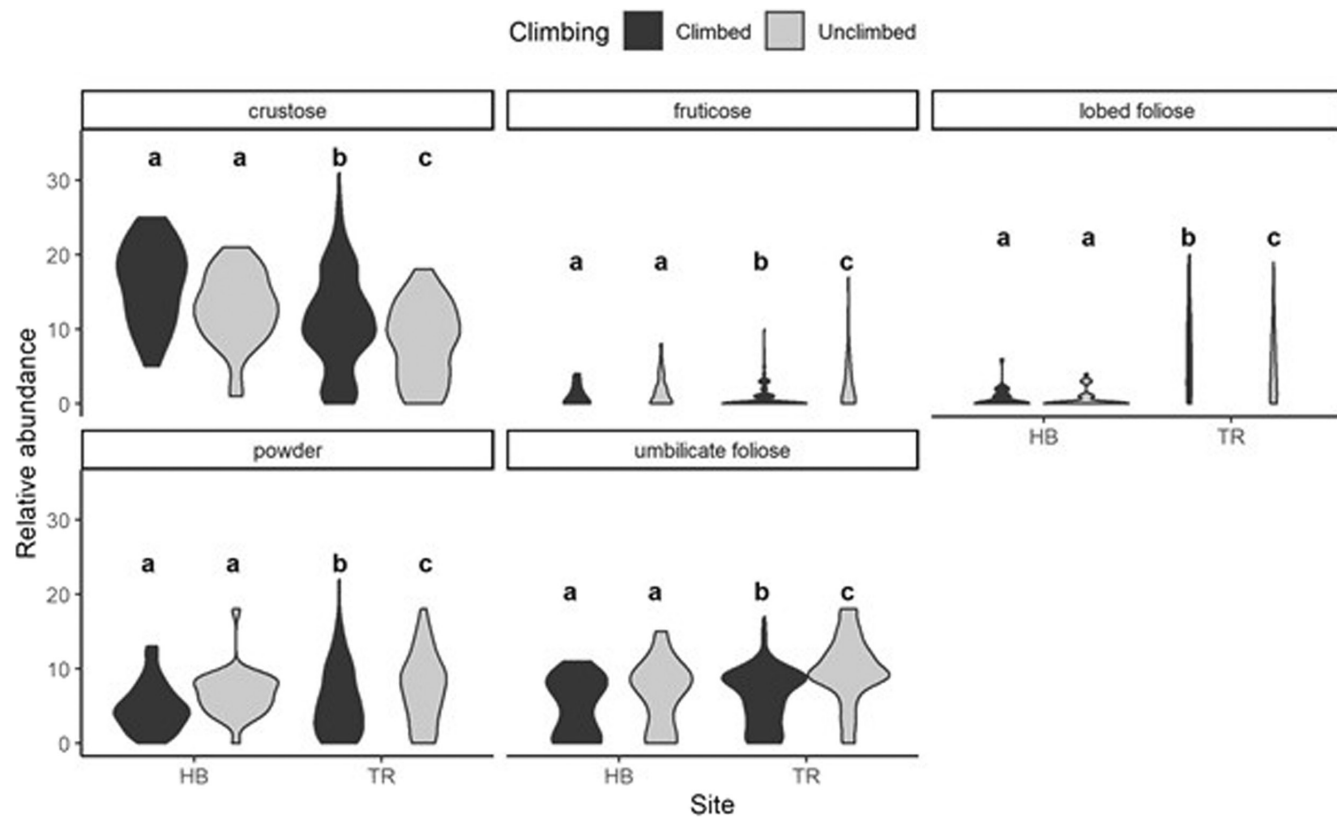
FIGURE 7 Relative abundance lichen functional groups on cliff-face plots by climbing and site factors, statistically significant differences are indicated by letters. Cover of all lichen functional groups was highest on unclimbed plots at Table Rock, followed by climbed Table Rock plots. There were no differences in lichen functional cover between climbed and unclimbed plots at Hawksbill

Although climbing in Linville Gorge did not have as great of an impact on cliff communities as did site variability, climbing still decreased species richness and diversity for all taxonomic groups at Table Rock. Climbing was most impactful in low-angle cliffs with abundant surface features, consistent with easier climbing routes, because these were the most diverse and species rich prior to disturbance. Conversely, harder climbing areas, which are frequently steep or overhanging and have sparse features, are less diverse and thus climbing has less of an impact. If management aims to conserve overall species richness and diversity, easier climbing routes should be targets for survey and monitoring. Cliff surveys should also inform whether unclimbed areas can open or need to remain closed to the development of future routes. Based on the results of this study, unclimbed areas that contain harder routes could still be developed with minimal impact on cliff vegetation. However, areas with easier climbing routes were more impacted, suggesting that development of easy climbing routes should be limited. Altogether, biological surveys, which factor in climbing route difficulty and potential use intensity, along with site-specific habitat variables, should inform climbing area management.

Given the limited resources available for ecosystem monitoring and the difficulty of accessing cliff-faces, many successful management projects focusing on cliff communities have incorporated collaborative stewardship, including vegetation monitoring by climbers (Clark & Hessl, 2015; Tessler & Clark, 2016; Boggess et al., 2017). Management of cliff-face communities will require difficult decisions about existing climbing routes and the development of new routes. Collaborative stewardship directly involving climbers allows for more regular monitoring to determine the full range of ecological conditions and management options available for these cliff ecosystems.

AUTHOR CONTRIBUTIONS
Georgia R. Harrison and Michael D. Madritch designed the study, carried out fieldwork and conducted data analysis. Laura M. Boggess and Jessica M. Budke identified lichen and bryophyte specimens, respectively. Georgia R. Harrison wrote the manuscript and all authors provided comments on and approved the final manuscript.

DATA AVAILABILITY STATEMENT
Primary data are submitted as electronic Supporting Information (Appendix S6).

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

Appendix S1. Bryophyte and some vascular plant specimen records deposited in the TENN herbarium.

Appendices S2. Climbing routes surveyed.

Appendices S3. Species list by taxa group in rank abundance order by taxa.

Appendices S4. Generalized linear mixed regression models of richness, Shannon diversity Index, and relative abundance to transect (northness and eastness) and plot (slope, first two NMDS values of surface heterogeneity) environmental factors.

Appendices S5. Burke County records of lichen species.

Appendix S6. Primary data for this study.