THE IMPACT OF ROCK-CLIMBING DISTURBANCE ON CLIFF COMMUNITIES OF THE LINVILLE GORGE WILDERNESS AREA

A Thesis
by
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Abstract

THE IMPACT OF ROCK-CLIMBING DISTURBANCE ON CLIFF COMMUNITIES OF THE LINVILLE GORGE WILDERNESS AREA

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Cliff communities are dominated by stress-tolerant, often cryptic lichens, bryophytes, and vascular plants whose abundance is controlled by harsh abiotic conditions. These taxa vary in their requirement for soil substrate, water, and sunlight and ability to withstand disturbance. Rock climbing is a major source of anthropogenic disturbance to cliff ecosystems. To assess the impact of climbing and habitat variability, climbed and unclimbed areas at Table Rock and Hawksbill Mountain in the Linville Gorge Wilderness area in North Carolina were surveyed for lichens, bryophytes, and vascular plants across 39 vertical transects.

I observed 42 lichen, 21 bryophyte, and 22 vascular plant species. *Canoparmelia alabamensis* was a new record for the state of North Carolina while 21 other species (17 lichens, four bryophytes) were Burke County records. Linear models indicated species richness and diversity were most strongly related to ledge and crack surface area for all three taxonomic groups. Climbed plots were less diverse and less species rich than their unclimbed counterparts at Table Rock. Climbing impacted lichen growth forms differently, causing decreased foliose and fruticose cover, and increased crustose cover. Climbing impacts cliffs by holding back ecological succession to the pioneer stage, with abundant crustose lichens, while removing larger, later successional stage lichens. Soil development, a critical step in vascular plant establishment, is also hindered. Since cliff vegetation varies by site due to differences in surface heterogeneity, each potential climbing area should be surveyed, especially for cryptic species, before management decisions are made. Since unclimbed cliffs were the most species rich and diverse, it should be a priority for these areas to remain undisturbed.

Surface heterogeneity is an important habitat variable for cliff ecosystems, but has not been consistently measured. Structure-from-Motion (SfM) techniques could afford a standardized method for measuring surface heterogeneity. We used color photographs and SfM to create 3D models of cliff faces that were surveyed for vegetation. Surface heterogeneity was calculated as average, standard deviation, and coefficient of variation of each plots' average elevation, Terrain Ruggedness Index (TRI), Topographic Position Index (TPI), and roughness at four different focal statistic neighborhood sizes. Roughness and average elevation at larger neighborhood cell sizes weakly correlated with all features and crevice surface area. Vascular plant richness and diversity were correlated with a few measures of remotely modeled surface heterogeneity. The methodology developed in this study will help lay the ground-work for developing a novel technique to quantify structural spatial variability on cliff faces, which could lead to an increase in measurement consistency among cliff ecology researchers.

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Dedication

“When times are easy and there’s plenty to go around, individual species can go it alone. But when conditions are harsh and life is tenuous, it takes a team sworn to reciprocity to keep life going forward. In a world of scarcity, interconnection and mutual aid become critical for survival. So say the lichens.”

– Robin Wall Kimmerer, Braiding Sweetgrass

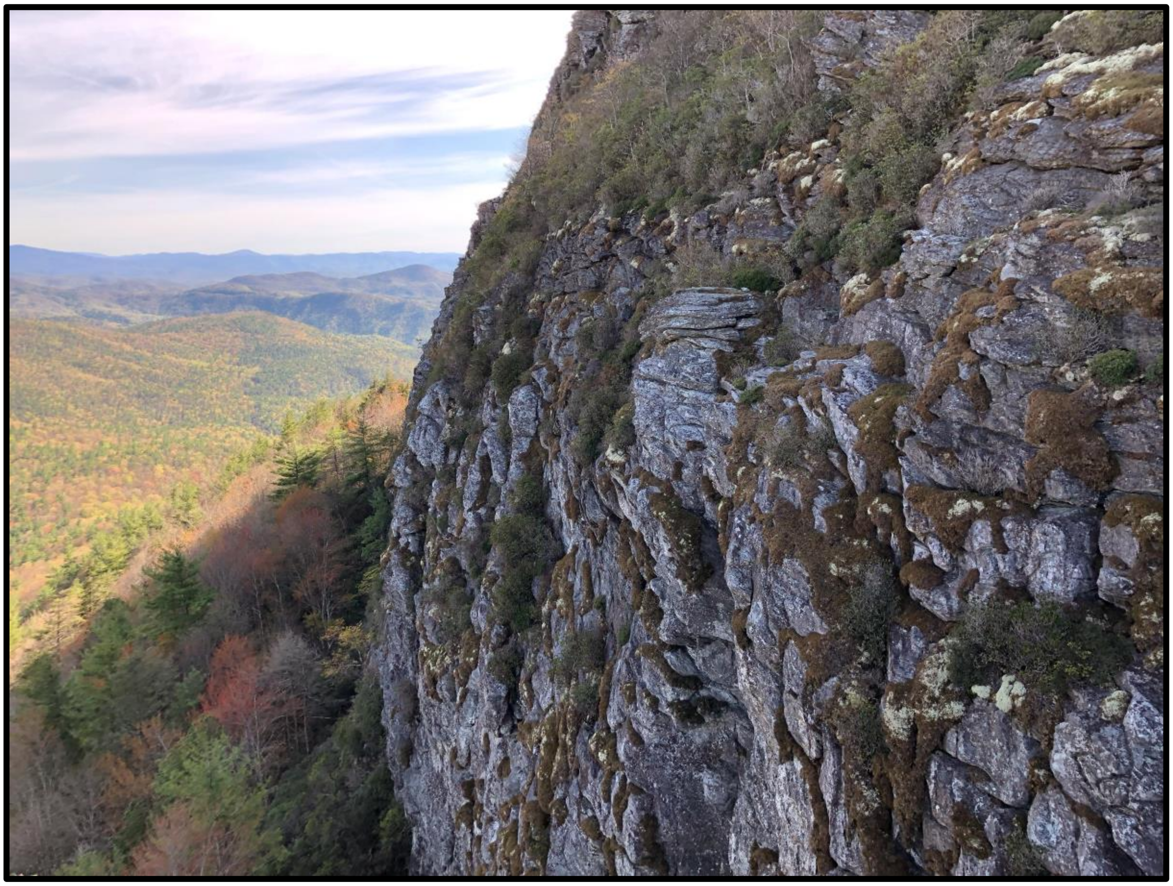

Table Rock Mountain, Linville Gorge Wilderness Area. Photo by Georgia Harrison, 2019.

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CHAPTER 2

Foreword

Chapter 1 of this thesis will be submitted to *Natural Areas Journal*, and is formatted in accordance to the style guide for that journal. Chapter 2 is formatted in the same style.

CHAPTER 1:

THE IMPACT OF ROCK-CLIMBING DISTURBANCE ON CLIFF COMMUNITIES OF THE LINVILLE GORGE WILDERNESS AREA

ABSTRACT

Cliff communities are dominated by stress-tolerant, often cryptic lichens, bryophytes, and vascular plants whose abundance is controlled by harsh abiotic conditions. These taxa vary in their requirement for soil substrate, water, and sunlight and in their ability to withstand disturbance. Rock climbing is a major source of anthropogenic disturbance to cliff ecosystems, but can vary in impact relative to surface heterogeneity. To assess the impact of climbing, cliffs at Table Rock and Hawksbill Mountain in the Linville Gorge Wilderness area in North Carolina were surveyed for lichens, bryophytes, and vascular plants. I observed 42 lichen, 22 vascular plant, and 21 bryophyte species within 382 1 m^2 survey plots. The most common species were lichens *Lasallia papulosa, Lepraria neglecta, Physcia subtilis, Aspicilia cinerea*, *Xanthoparmelia conspersa*, and *Umbilicaria mammulata;* vascular plants *Selaginella tortipila and Hydatica petiolaris;* and bryophytes *Campylopus tallulensis* and *Weissia controversa. Canoparmelia alabamensis* was the first collection in North Carolina and 21 other species (17 lichens, four bryophytes) were county records. Species richness and diversity were most strongly related to ledge and crack surface area for all three taxonomic groups. Climbed plots were different and less diverse than their unclimbed counterparts. Surface features (ledges, cracks, and pockets) differed in their abundance and size between sites and contributed to differences in richness and diversity. Climbing impacted lichen cover differently according to functional type, causing decreased foliose and fruticose, but

increased crustose lichen cover. Climbing impacts cliffs by retarding ecological succession, resulting in abundant crustose lichens, and depauperate umbilicate foliose and fruticose lichens. Potential climbing area should be thoroughly surveyed before management decisions are made since cliff communities vary by site.

INTRODUCTION

Cliff Communities

Cliffs contain unique ecological communities which can harbor high biodiversity of understudied taxa. Cliff communities have a typically depauperate vascular flora and are instead dominated by lichens and bryophytes (Smith 1998, Larson et al. 2000b). Cliffs were long considered to have low diversity and were consequently overlooked in biotic inventories, but are increasingly recognized for harboring numerous rare and endemic plants and lichens (Boggess et al. 2017). Cliff-dwelling plants persist due to limited disturbance, buffered temperatures, and a lack of competitive exclusion. Ancient forests have been discovered on the cliffs throughout North America (Larson et al. 2000a, Walker 1987). Cliff faces can also sustain high pockets of floral diversity, especially along microhabitat features such as ledges and crevices (Kuntz and Larson 2006). Many of the rare species present on cliffs are restricted exclusively to these areas (Boggess et al. 2017).

Among terrestrial ecosystems there are few gradients more distinct than those at the edge of rock outcrops and escarpments (Larson et al. 1989). In transitions from intact woodland (or grassland) to exposed rock over distances of a few meters, changes in physical aspects of the habitat can be greater than those found when comparing deciduous forest with open tundra thousands of kilometers away (Larson et al. 1989). In addition, plant communities on cliffs are fragmented, allowing small pockets to support a similar levels of plant biodiversity as do large, continuous sections (Haig et al. 2000). Cliff species are high-light and high-stress specialists that can tolerate dramatic temperatures shifts, drought, and high winds. The harsh environmental conditions, limited disturbance, and limited competition allow southern cliffs to serve as climatic refugia for disjunct populations of glacial relict species, such as *Cladonia* *pocillum* and ancient stands of *Thuja occidentalis* (Walker 1987, Kelly and Larson 1997, Tessler and Clark 2016).

Cliffs as an Ecosystem

Typically, a cliff system includes edge, face, and talus habitats. The cliff edge is the area of relatively level ground above the cliff face, while the talus is the area below, which often contains fallen rocks (Larson et al. 2000b). Numerous, related abiotic factors including light, moisture, vertical zonation (height), aspect, slope, and surface heterogeneity vary between the cliff face, edge, and talus, allowing them to contain distinct plant communities.

Baskin and Baskin (1988) found that a requirement for high light levels was the most important characteristic common to endemic herbaceous rock outcrop species in the eastern United States. In addition, variation in light (Coates and Kirkpatrick 1992) and moisture (Kuntz and Larson 2006) among microsites on cliff faces are correlated with the presence or absence of plant species in Tasmania and Canada, respectively. However, there are exceptions to the high light requirement. For example, a southern Appalachian endemic *Hymenophyllum tayloriae* grows only in extremely low light, high moisture environments such as spray cliffs and caves near waterfalls (Weakley 2007).

Moisture gradients impact plant community composition and distribution on cliff sites and are governed by the climate, presence of permanent seeps, surface heterogeneity of the rock, and exposure to incident radiation. Higher surface temperatures and windy conditions on exposed rocks may increase evaporative rates, resulting in dry conditions and a strong selection for desiccation-tolerant species (Kuntz and Larson 2006). However, some cliff habitats buffer plants from drought because they retain moisture in deep cracks in the rock and provide habitats that experience no direct insolation (Kelly and Larson 1997).

Cliff plant community structure varies with cliff face position. The lower portions of cliffs, particularly those in narrow river gorges, are less exposed than are the upper cliff faces, and thus less likely to experience stressful wind, temperature, and moisture regimes. For instance, Smith (1998) determined that species composition varied along a vertical gradient in the Linville Gorge Wilderness Area, NC, an area characterized by steep slopes in a narrow river gorge.

Aspect also influences the distribution of mountain and cliff vegetation, and can be used as a proxy for insolation (Graham and Knight 2004). In mountainous areas in the southern Appalachian Mountains, south-facing slopes receive more insolation than north-facing slopes, and are therefore warmer and drier (Cottle 1932, Cantlon 1953, Warren 2010, 2008, Lafon et al. 2019). On cliffs systems, north- and south-facing areas can have marked differences in species composition (Walker 1987, Ursic et al. 1997, Larson et al. 2000b) and in overall vegetation cover. Walker (1987) found *Thuja occidentalis* on north-facing cliffs grew faster than those on south-facing cliffs.

Surface heterogeneity—the variation in the rock surface caused by ledges, cracks, and pockets—can also drive the composition of cliff flora and was the most important determinant of vegetation on the Niagara Escarpment (Kuntz and Larson 2006). As microtopographic features increase in size and frequency on cliffs they can accumulate soil and retain propagules thereby supporting vascular plants, including pockets of old growth forest (Farris 1998, Kuntz and Larson 2006, Walker 1987, Farris 1998, Larson et al. 2000a). These microhabitat features can also provide refugia from intense light and wind exposure and play an important role in seed dispersal, distribution, local adaptation, and microclimate diversity (Kuntz and Larson 2006b, Opedal et al. 2015). Species are exposed to a wide variety of environmental conditions on cliffs due to high microclimate diversity, which can create optimal growth opportunities for many species that also have a resilience to a changing climate (Larson et al. 2000b).

Slope also drives variation in cliff plant communities, and can serve as a proxy for moisture level in some systems (Kuntz and Larson 2006; Clark and Hessl 2015; Boggess et al. 2017). The steeper the slope, the less water is available to vegetation because most of it quickly runs off the cliff face; thus, steep slopes generally harbor more desiccation-tolerant flora (Larson 2000). Trees which grow on cliffs can develop sectorial transport, where sections of the tree which are dead to still be used for water and nutrient transport, allowing portions of the tree to still thrive (Larson et al. 1993). Slope also affects species recruitment, since shallower slopes are more likely to accumulate debris that can trap propagules (Kuntz and Larson 2006).Vascular plants, and some bryophytes and terricolous (soil-dwelling) lichens are dependent on a soil substrate, and thus persist on cliff faces of low angle and high surface heterogeneity where soil readily accumulates (Kuntz and Larson 2006; Clark and Hessl 2015). Species which are not dependent on soil substrates, such as saxicolous lichens and epipetric bryophytes, do not depend on soil accumulation and thus can persist on vertical, even overhanging, cliffs with low surface heterogeneity (Brodo et al. 2001, Kuntz and Larson 2006).

In many cliff systems, the presence of large canopy trees on the cliff top or talus can drive important differences in plant communities. For example, Ursic et al. (1997) observed a community shift toward shade-tolerant plants near the base of cliffs when canopy trees were present just beyond the talus. Large trees on cliff tops retain moisture and provide shade, and creates tops of cliff faces with higher plant abundance than lower, more exposed regions (Boggess et al. 2017, Smith 1998). Cliffs with canopied edges have more diverse and heterogeneous plant communities than those with bare edges (Boggess et al. 2017). However, cliff tops lacking canopy cover provide an important opportunity for high-light plants without the competitive challenges associated with growing in nearby terrestrial systems. The threatened, endemic shrub *Hudsonia montana* requires high amounts of light, but is shaded and outcompeted in forested areas with suppressed fire regimes (Gross et al. 1998). *Hudsonia montana* is able to persist on cliff edges with high light conditions in the Linville Gorge Wilderness Area because it is free from competition with faster and taller growing species that occur in forests (Gross et al. 1998).

Cliff Ecological Succession

Cliff systems historically have low amounts of disturbance that allow the persistence of slow-growing, stress-tolerant plants and lichens (Grime 1977). Systems with high disturbance and severe stress, such as climbed cliff faces, prevent the recovery and reestablishment of vegetation (Grime 1977). The succession of rocky faces starts with the establishment of bare rock by crustose lichen species, which are eventually overgrown by foliose and fruticose growth forms (Liu et al. 2019, Jackson 2015). Larger and leafier growth forms are able to trap water, soil, and litter better than pioneer crustose lichens, which facilitates succession toward bryophyte and vascular plant establishment (Liu et al. 2019, Jackson 2015).

Cliff Disturbance

Natural disturbances are usually low in both frequency and intensity on cliffs. (Larson et al. 2000b). Gravity consistently induces rock fall and drives adaptations such as sectoral transport and specialized root structures that anchor woody trees to the face (Larson et al. 1993). Cliff-dwelling old growth forests often display gnarled and twisted trunks and can grow in inverted directions to withstand the force of gravity and avoid hazardous rock fall (Walker 1987; Larson et al. 2000a). Grazing is reduced on cliff faces due to their inaccessibility (Larson et al. 2000b). Fire frequency and intensity is low on cliffs, primarily due to the patch distribution of vegetation and thus lack of fuel (Larson et al. 2000b). However, when fire burns the cliff talus and top, it can decrease plant and bryophyte diversity by removing canopy layers.

Cliffs have also historically been inaccessible to humans, but in recent years, they have been increasingly subject to human disturbances, including quarrying, real estate development, hiking, and rock climbing (Larson et al. 2000b; Boggess et al. 2017). Of these disturbances, rock climbing is one of the most constant and direct sources of disturbance (Larson et al. 2000b). The impacts of climbing are multifaceted and can change as climbing routes are developed. When a cliff face is climbed for the first time, it must be “cleaned,” which includes removing plants and lichens to clear hand and foot placements, sometimes using wire scrub brushes (Tessler and Clark 2016, Kuntz and Larson 2006). Over time, the route is established and receives increased traffic, and the deleterious impacts of trail creation on the cliff top and base include trampling plants and compacting the soil (Tessler and Clark 2016, McMillan and Larson 2000).

Previous studies on the impact of rock climbing on cliff communities have reported conflicting results. Some report that rock climbing activities negatively impact cliff face vegetation (Nuzzo 1995, McMillan and Larson 2002, Rusterholz et al. 2004, Adams and Zaniewski 2012, Clark and Hessl 2015, Carmo et al. 2016) while others conclude that climbing has no effect (Nuzzo 1996, Kuntz and Larson 2006, Baur et al. 2007, Adams and Zaniewski 2012, Boggess et al. 2017). Holzschuh (2016) reviewed the threat of rock climbing to cliff biodiversity and concluded that evidence of impacts are largely inconclusive, limited in geographic range, and ultimately that more research is required.

Impacts on vegetation can differ by cliff region (base, face, or top; Adams and Zaniewski 2012, Clark and Hessl 2015, McMillan and Larson 2002, Kuntz and Larson 2006, Kelly and Larson 1997, Camp and Knight 1998, Farris 1998). Generally, species which are closely anchored to their substrate, such as crustose lichens or well-rooted trees, are challenging to remove and thus persist under disturbance, while loosely attached taxa, such as bryophytes, small vascular plants, and umbilicate and fruticose lichens, are more easily removed (Clark and Hessl 2015). Trails on the top and base of cliffs generally suffer greater impacts on vascular plants and mosses more so than on lichens, whereas clearing the cliff face usually impacts lichens the most since they are the dominant life form on this surface (Boggess et al. 2017).

Rock Climbing

There are several, distinct classifications of rock climbing, which include aid, traditional, and sport climbing (Child 1998). Traditional and aid routes rely on the use of microtopographic features for the placement of safety devices whereas sport climbing routes follow paths of preinstalled, permanent bolts, drilled into the rock face (Child 1998). Thus, there are inherent differences in microtopographic features and slope between climbing routes of different style and difficulty (Kuntz and Larson 2006, Clark and Hessl 2015).

Rock climbing is increasing in popularity, with at least 10 million rock climbers in the US alone (Cordell 2012). Increased popularity has resulted in higher use of historically established routes, as well as developing new routes and climbing areas (Cordell 2012). Not all climbed cliffs are subject to the same levels of climber traffic and development. Route traffic can be affected by difficulty, style, and hiking trail distance to reach the cliff (Clark and Hessl 2015). Overall quality and popularity of routes are listed by stars in climbing guide books, which can serve as a vector for traffic (Clark and Hessl 2015). Unfortunately, a majority of studies on the impact of rock climbing do not consider the style, difficulty, popularity, or traffic of climbing routes, limiting their usefulness for management decisions (Holzschuh 2016, Clark and Hessl 2015).

Climbed cliff faces should be compared to unclimbed areas that exhibit comparable environmental conditions due to the impact of local- and fine-scale factors on cliff-dwelling species. In practice, quantifying surface heterogeneity can prove challenging (Kuntz and Larsen 2006; Clark and Hessl 2015). Much of the early research into the impact of climbing on cliff communities did not control for abiotic variation (Nuzzo 1995, Kelly and Larson 1997, Camp and Knight 1998, McMillan and Larson 2002). Farris (1998) was the first to quantify microtopographic feature size, occurrence, and frequency in order to determine the probability of features supporting vascular plants. Cliff ecologists have implemented different techniques to assess cliff face heterogeneity (i.e. Nuzzo 1996, Spitale and Nascimbene 2012, Carmo et al. 2016, March-Salas et al. 2018). The most extensive approach was conducted by Kuntz and Larson (2006), who measured surface area and abundance of every ledge, crevice, and pocket within their survey plots. Similarly, Clark and Hessl (2015) measured feature abundance, and classified them as macro (>1 m) or micro (<1 m) features. Boggess et al. (2017) simplified this approach by visually assigning a surface heterogeneity rating from 0-10 to each plot. However, since methods for quantifying surface heterogeneity are not consistent, how rock climbing combined with fine scale environmental variation impacts cliff communities among broad climatic and geologic distributions cannot be confidently compared.

Cliff face studies in the southern Appalachian Mountains have demonstrated that each cliff, even in close geographic range, can harbor unique communities (Boggess et al. 2017, Hill 2009). It is critical that we better understand the impact of climbing on cliff community ecology in order to inform sound management decisions for public lands and ensure the conservation of these rare and fragile ecosystems.

MATERIALS AND METHODS

Study Site

My study took place in the Linville Gorge Wilderness Area (LGWA) in northwestern North Carolina (Burke County, 35.8910° N, 81.8829° W, 1,250 m elevation). Rock climbing in the LGWA dates back to 1970, with over 250 established routes (Lambert and Harrison 2002). Cliff sampling took place at Table Rock and Hawksbill Mountains due to accessibility and abundance of sport and traditional rock-climbing routes. Hawksbill and Table Rock combined contain 94 established climbing routes, 66 traditional and 28 either sport or “mixed” style (sport and traditional style), ranging from 5.4 (easy) – 5.13 (challenging) on the Yosemite Decimal System (YDS, a measure of a route’s difficulty, Lambert and Harrison

2002). Most of the routes at Table Rock are traditional style, multi-pitch climbs with permanent bolts at the top of the climb. Large groups, including the North Carolina Outward Bound School, frequently use Table Rock due to the short approach and plentiful routes of moderate difficulty. Hawksbill Mountain contains the highest concentration of challenging, single-pitch sport climbs in the LGWA, and is a popular destination for day trips (Lambert and Harrison 2002).

Field sampling took place from May to August 2019. All transects, climbed and unclimbed, were over 13 meters in height and had continuous cliffs extending two meters on either side. Unclimbed transects had no evidence of climbing (no chalk or equipment) or mention in local guide books, and occurred at least two meters away from climbing routes (Lambert and Harrison 2002).

Cliff Field Sampling

Cliff face field sampling following a modified protocol described by Boggess et al. (2017). Each cliff transect was sampled in three areas: top (plateau), face, and base (talus). Along a vertical transect, lichens, bryophytes, and vascular plants were described within 1 m^2 quadrats, each subdivided into nine sub-quadrats (Figure 1, Boggess et al. 2017). Survey plots were placed to the left and right of a survey (rappel) line, starting 2 m below the cliff top 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 1). Top and talus plots were placed horizontally within two meters of the cliff top or base. In some cases, it was not possible to survey top and base transects since transects occurred mid-cliff face (Table Rock) and did not end at the top of the cliff (Hawksbill).

Within each plot, I recorded how many of the nine sub-quadrats each species occurred in (Kuntz and Larson 2006). Species were collected and described in the field. Crustose lichens were removed with hammer and chisel away from established climbing routes to maintain the route's integrity, and known rare and endemic species were not collected. Vascular plants were identified by Ethan Hughes (Appalachian State University), bryophyte samples by Jessica Budke and Eric Shershen (University of Tennessee) and lichen samples by Georgia Harrison and S. Coleman McCleneghan (Appalachian State University) and verified by Laura Boggess and James C. Lendemer (New York Botanical Garden) using the nomenclature of Brodo et al. (2001). All specimens were catalogued in the Appalachian State University (BOON) herbarium, and duplicates of bryophyte samples were deposited at the University of Tennessee at Knoxville (TENN).

Local physical factors of each transect were recorded, including: (1) cliff height (2) transect slope, and (3) aspect. Canopy cover and large features above each transect were also noted. Area (length x 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 (2006 a, b). Aspect was decomposed into two linear components, north-south (northness) and east-west (eastness) before further analysis (Beers et al. 1966).

Statistical Analysis

All statistical analyses were conducted in R (v3.5.1). I partitioned vegetation data into four groups: total taxa, vascular plants, bryophytes, and lichens. Species richness and Shannon's Diversity Index (H′) were calculated for each plot. Species accumulation curves were created to determine if sampling adequately captured cliff species richness using the *specaccum* function in package vegan (v2.0-10, http:// CRAN.R-project.org/package=vegan). I explored if there were any indicator species between climbed and unclimbed plots for all taxa and a subset of only lichens using function *mulipatt* across 999 paramutations in package indic.species (v1.7.8, http:// CRAN.R-project.org/package=indic.species). This function creates combinations of clusters within groups (climbed and unclimbed) of all input species. For each species, the combination with the highest association value is selected and tested for statistical significance. For indicator species analysis, I assumed $\alpha \leq 0.1$.

To test for differences due to climbing and site, I used a two-way ANOVA and Tukey's post-hoc test. Significance was assumed for $\alpha \leq 0.05$. First, I tested for differences in species richness and diversity. I also compared richness and diversity by plot location (top, face, or base). To explore the effect of climbing on community composition, I used non-metric multidimensional scaling (NMDS) based on Bray-Curtis similarity in package vegan. NMDS was performed for all taxa as well as a subset of only lichens, since lichens were the most abundant taxa and occurred in all but one plot. I used permutational multivariate analysis of variance (PERMANOVA) to compare community clustering by site and climbing.

I compared species richness and diversity by climbing grade difficulty. Climbed survey transects were classified into three groups based on their YDS grade (Clark and 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.

I used linear models to estimate relationships between species richness and diversity to transect (eastness, northness) and plot (slope, feature abundance, and feature area) abiotic variables. Variables were included in the linear model if independent effects from hierarchical partitioning explained >10% of the total variance using package hier.part (v1.0-6). Hierarchical partitioning estimates the independent contribution of each variable given all possible models in a multiple regression setting and is well suited for multivariate data (Mac Nally 2002, Murray and Conner 2009).

I compared differences in lichen cover by functional group. Lichens were classified into five functional groups: powder, crustose, umbilicate foliose, lobed foliose, and fruticose. Functional group richness and average cover was calculated for each plot by combining all the morphospecies within each group. Cover estimates were converted from field cover value (1-9) to percent.

To explore differences in surface features of each plot, I employed an NMDS using Bray-Curtis similarity on a matrix of feature area (length x width for ledges) or volume (length x width x depth for crevices and pockets, Kuntz and Larson 2006) by plot. I compared clustering by climbing and site using a PERMANOVA and tested for differences in frequency and total area for all ledges, crevices, and pockets.

RESULTS

We surveyed a total of 39 transects with 382 1 m^2 survey plots. At Table Rock Mountain, we surveyed 19 climbed and 12 unclimbed transects with 24 base plots, 272 face plots, and 14 cliff top plots. Many of the survey transects at Table Rock occurred mid-cliff and thus did not contain top or base plots. At Hawksbill Mountain, we surveyed four climbed and four unclimbed transects with 10 base plots and 62 cliff face plots. Hawksbill did not contain any top plots since climbing routes ended below the cliff top and unclimbed areas were only accessed via climbing routes.

Cliff species composition

We observed 85 species, including 42 lichens within 29 genera, 22 vascular plants within 21 genera, and 21 bryophyte species within 17 genera. *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 and Peet 1998, Table 1). The most abundant bryophyte was a field-described morphospecies common in seeps, followed by *Campylopus tallulensis* and *Weissia controversa* (Table 2). The most abundant lichens were *Lasallia papulosa*, *Lepraria neglecta*, *Physcia subtilis*, *Aspicilia cinerea*, *Xanthoparmelia conspersa*, a green powder (*Lepraria* spp.), and *Umbilicaria mammulata* (Table 3).

Species accumulation curves indicate sampling captured most of the site diversity (Figure 2). Indicator species analysis revealed lichens *Acarospora fuscata, Diploschistes actinostomus, Rhizocarpon* sp.*, L. neglecta, another Lepraria* sp., vascular plant *Agrostis parennans,* and two bryophyte field morphospecies were indicator species for unclimbed plots (Table 4). Lichens *Canoparmelia alabamensis, Xanthoparmelia conspersa, Rhizocarpon geographicum, Lepraria neglecta, Acarospora fuscata, Lepraria* sp., and bryophytes *Weissia controversa*, *Andreaea rothii, Bryum* sp., as well as two different bryophyte field morphospecies were indicative of climbed plots (Table 4). An indicator species analysis on only lichens revealed *Cladonia pleurota, C. chlorophaea, Fuscidea recensa, Cladonia* sp.*, C. arbuscula, C. furcate, Diploschistes actinostomus,* and *Hypotrachyna imbricatula* were indicative of unclimbed plots (Table 5) and *Canoparmelia* *alabamensis, Lepraria* sp. 1*, R. geographicum, Lepraria* sp. 2*,* and *A. fuscata* as indicators of climbed plots (Table 5).

Plot abiotic conditions and impact on cliff communities

Plot abiotic, including micro- and macro-site conditions, 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 ($F_{1,330} = 4.93$, $P < 0.05$, Figure 3). Table Rock had higher total feature surface area ($F_{1,330} = 3.03$, $P < 0.1$), more ledges ($F_{1,330} = 35.16$, $P < 0.001$), higher ledge surface area ($F_{1,330} = 28.6$, $P < 0.001$), and more crevices ($F_{1,330} = 7.93$, $P < 0.01$) per plot than Hawksbill (Figure 4). There was no difference in abundance or surface area of pockets due to their rarity. A PERMANOVA detected no differences in abiotic features clustering by climbing ($F_{1,299} = 1.41$, $P = 0.15$, $R^2 = 0.004$). However, there were significant differences in the clustering of abiotic feature area by site ($F_{1,299} = 2.48$, $P = 0.013$, $R^2 = 0.008$) and the interaction between both factors ($F_{1,299} = 1.96$, $P = 0.036$, $R^2 = 0.006$, Figure 5).

Linear models and hierarchical partitioning using abiotic variables indicated species richness and diversity was most strongly related to ledge and crack surface area for all three taxonomic groups (Figures 6, 7), although the predictive power of the models was low (Table 6; maximum adjusted $R^2 = 0.18$). Eastness was important for diversity of all taxa groups except vascular plants ($P < 0.05$). The more east-facing a cliff was, the higher were all taxa and bryophyte richness and diversity (Table 6). Linear models for lichen species richness and diversity had the weakest explanatory power of all the taxa groups, but lichen richness increased with greater ledge abundance ($P < 0.05$, Table 6). Vascular plants were the only taxa groups whose richness and diversity were strongly related to slope ($P < 0.01$, Table 6). Crevice abundance explained over 15% of independent effects on vascular plant richness and diversity, but was not statistically significant in linear models (Figures 6, 7). Generally, trends were consistent among taxa for both richness and diversity (Figures 6, 7, Table 6).

Climbing and site impact

Table Rock plots contained more species than did Hawksbill, regardless of climbing status, with unclimbed plots having more species than climbing plots ($F_{1,330} = 4.42$, $P = 0.036$, Figure 8). Across all climbing and unclimbed plots, Table Rock had the highest lichen richness ($F_{1,330} = 16.08$, $P < 0.001$, Figure 8). Vascular plant and bryophyte richness were low, especially at Hawksbill. Bryophyte richness was highest at Table Rock ($F_{1,330} = 29.41$, $P < 0.001$, Figure 8). 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 ($F_{1,330} = 8.95$, $P = 0.003$, Figure 8). Diversity mirrored richness (Figure 9).

Site ($F_{1,333} = 45.21$, $P = 0.001$, $R^2 = 0.12$) was a more important factor than was climbing presence ($F_{1,333} = 17.21$, $P = 0.001$, $R^2 = 0.036$) in shifting to a different cliff face community (Figure 10). The interaction between climbing and site was statistically significant but with a low R^2 value ($F_{1,333} = 2.14$, $P = 0.025$, $R^2 = 0.005$) and demonstrated that climbed plots at both sites were the most different from each other (Figure 10). Climbed plots were not clustered as a subset within unclimbed sites. NMDS on only lichen data revealed similar patterns, but with weaker R^2 and lower significance values (Figure 11).

Climbed routes varied in their richness and diversity by difficulty. Easy climbing routes and unclimbed areas were more species rich ($F_{3,330} = 11.44$, $P < 0.001$) and diverse ($F_{3,330} = 14.24$, $P < 0.001$) than were moderate and advanced climbing routes (Figure 12). Lichen species richness ($F_{3,330} = 5.91$, $P < 0.001$) and diversity ($F_{3,330} = 6.69$, $P < 0.001$) were significantly lower on moderate climbing routes than on easy and advanced climbing routes, as well as unclimbed areas (Figure 12).

Lichen functional group (crustose, powder, umbilicate foliose, lobed foliose, and fruticose) cover varied by site and climbing impact (Figure 13). Crustose and fruticose lichens exhibited opposite coverage patterns (Figure 13). Hawksbill, which had low surface heterogeneity, had higher crustose cover than Table Rock ($P < 0.001$). Table Rock, which had high surface heterogeneity, had higher fruticose cover than Hawksbill ($P < 0.001$). Umbilicate and lobed foliose cover was also higher ($P < 0.001$) at Table Rock, though there were differences by climbing presence (Figure 13). Powder lichens had higher cover at unclimbed areas at both sites ($P < 0.001$).

DISCUSSION

Rock climbing disturbance decreased lichen, bryophyte, and vascular plant richness and species diversity on cliffs in the Linville Gorge Wilderness Area. Differences in cliff-face microtopography explained much of the site variation between Table Rock and Hawksbill. Site habitat variables were instrumental in shaping the composition of cliff communities and they also interacted with climbing disturbance. Table Rock, which had high richness and diversity, also had the most microtopographic features and surface area. The same pattern of high richness and diversity in the most heterogeneous areas was observed by Kuntz and Larson (2006) on cliffs in Canada. Climbing impacts were greatest on cliffs with the highest surface heterogeneity (Table Rock), because unclimbed areas on these cliffs already have high diversity and richness to begin with, especially of vascular plants and mosses. Additionally, cliff communities at both sites were different, not just subsets, of unclimbed areas. Kuntz and Larson (2006) and Adams and Zaniewski (2012) also observed climbing areas with different community composition than climbed areas that were also not just a subset of those in undisturbed areas. Climbing caused shifts to different, less diverse and less species rich cliff communities.

Species richness and diversity differed by route difficulty in the climbed area. Unclimbed and easily climbed plots 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 (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 and Harrison 2002). In contrast, Table Rock is a larger climbing area with more routes overall, which are well distributed among climbing grades.

Climbing impact may also depend on climbing intensity, which is more challenging to quantify. Clark and Hessl (2015) created a Climbing Use Index (CUI) using a climbing route’s popularity and approach time in order to gauge relative use by climbers. CUI must be considered relative to climbing route since increasing difficulty grade does not necessarily mean less traffic. The opposite may be true, where routes of intermediate grade are climbed more frequently. At Table Rock Mountain, routes of easy difficulty receive high traffic, especially from large groups and guiding agencies. Within well established and large climbing areas, climbing grade and style are readily available in local guide books and may provide managers with a quick assessment of potential differences in species richness and diversity among the numerous climbing areas. Clark and Hessl (2015) stated in the New River Gorge National River, an area with over 1,500 climbing routes, CUI could highlight which cliffs were the most threatened by high traffic. Further, routes of the lowest popularity (stars) may receive low to intermediate traffic. This intermediate disturbance may be frequent enough to hinder ecological succession, but these routes are not popular enough to be completely "cleaned", hence the impact is less than might be expected.

Cliff Community Species Assemblages

Selaginella tortipila A. Baun was the most common vascular plant and is a primary inhabitant on exposed rocky cliffs in the southern Appalachians (Wofford 1989). This species is functionally important for cliff succession as it forms dense mats over exposed rock, often associated with fruticose reindeer lichens (*Cladonia* spp.). These mats grow on ledges or on the cliff top until the weight is too great, causing them to break loose and tumble down the cliff face. These mats are often a hotspot for other fruticose and foliose lichens, which often grow with and directly on *S. tortipila*. They naturally fall when they become too heavy but can also be removed directly or indirectly by rock climbing. Since *S. tortipila* is a club moss, it requires water in order for the bi-flagellated sperm to reach the eggs.

Consequently, it is typically found towards the top of cliffs, where it can take advantage of direct rain and water run-off (Wofford 1989, Smith 1998).

The second most common vascular plant, *Hydatica petiolaris (*syn. *Saxifraga michauxii*) (Raf.) Small, 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* (Poir.) Brummitt, *Rhododendron minus* Michx., *Vaccinium corymbosum* L., *Hydatica petiolaris*, and *Kalmia latifolia* L.

Many of the most common lichens in this study are characteristic of southern Appalachian high elevation rock outcrops (Newell and Peet 1998). Lichens that were most common in Clark and Hessl (2015) include *Aspicilia cinerea* (L.) Körb., *Dimelaena oreina* (Ach.) Norman, *Lasallia papulose* (Ach.) Llano, *L. pennsylvanica* (Hoffm.) Llano, *Lepraria neglecta* (Nyl.) Erichsen, *L. nomandinioides* Lendemer & R.C. Harris, *Phlyctis petraea* R.C. Harris, Musc. Ladd & Lendemer, *Physcia subtilis* Degel., and *Umbilicaria mammulata* (Ach.) Tuck., were also observed in the LGWA. Many genera were also common among this study, Smith (1998), and Boggess et al. (2017) during her survey of cliff communities in the Big South Fork National River and Recreation Area. Lichen distribution and ranges, especially those of crustose and powder lichens, are poorly understood. I checked these identified specimens with the records available through the Consortium of North American Lichen Herbaria (lichenportal.org) as of 20 April 2020. *Canoparmelia alabamensis* (Hale & McCull.) Elix, a foliose species on non-calcareous outcrops in Alabama, was collected on an unclimbed transect at Table Rock, and to my knowledge represents the first report for this species in North Carolina. Seventeen other lichen species have no record of collection in Burke County (Table 7).

The most common bryophytes were *Campylopus tallulensis* Sull. & Lesq., *Weissia controversa* Hedw., and *Dicranum montanum* Hedw. Smith (1998) also observed *D. montanum, Dicranella heteromalla* (Hedw.) Schimp., and *D. scoparium* Hedw. on LGWA cliffs. *D. montanum* was also one of the most common bryophytes in Boggess et al. (2017). Another epipetric (rock-dwelling) bryophyte, *Andreaea rothii* F. Weber & D. Mohr, 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), *C. tallulensis*, *Dicranella heteromalla, Leucobryum glaucum* (Hedw.) Angstr., and *Pseudotaxiphyllum elegans* (Brid.) Z. Iwats. were all observed in this study. I checked these identified specimens with the records available through the Consortium of North American Bryophyte Herbaria (bryophyteportal.org) as of 20 April 2020and compared this bryophyte collection to others using the Consortium of North American Bryophyte Herbaria (bryophyteportal.org). *Bucklandiella venusta* (Fisvoll) Bedn.-Ochyra & Ochyra has not been collected in North Carolina since 1936 (P. O. Shallert, Roan Mountain) and is a Burke County Record. Tessler et al. (2016) also observed *B. venusta* in the Shawangunk Mountains of New York on boulders used for rock climbing. *Dicranella varia* (Hedw.) Schimp. has not been collected in North Carolina since 1988 and is a Burke County record. Two species within the genus *Polytrichum*, *P. strictum* Menzies ex Bird. and *P. juniperinum* Hedw. were also Burke County Records. These first-time documentations of bryophyte species in Burke

County are most likely due to the lack of bryophyte collecting in the county, rather than range expansions for these species.

Species accumulation curves (Figure 2) indicated that my sampling efforts captured most of the cliff diversity at both Table Rock and Hawksbill Mountains. Lichens and bryophytes species richness was sampled more thoroughly than vascular plants. Species richness in the LGWA was lower than found in other surveys of cliff communities in the Southeastern US (Table 8). These studies varied broadly in their geologic and geographic distribution, as well as survey methodologies (Table 8). In addition, cliff ecology studies within the past five to ten years have dramatically increased the number of transects and total area sampled, which should result in a higher species capture rate. For example, Boggess et al. (2017) sampled 50 transects in the Big South Fork (TN) and Clark and Hessl (2015) sampled 111 transects in the New River Gorge (WV).

Transect count may not always be the best way to assess sampling effort, since plots can be placed at different frequencies down the cliff face, resulting in variation of the total surface area sampled. For instance, Clark and Hessl (2015) surveyed 441 m^2 across 111 transects (un-paired plots which were placed every 6 meters), compared to my study, which sampled 382 m^2 across only 39 transects. Greater transect abundance may allow for broader abiotic variation and increasing species richness (Clark and Hessl 2015, Boggess et al. 2017), but more densely placed sample plots within transects may yield a better picture of species diversity and richness. In addition, the amount of area surveyed at different cliff areas (top, base) can greatly impact the estimate of species richness, especially that of vascular plants. A majority of surveying in this study was on the cliff face, since many transects at Table Rock occurred mid-cliff and did not have a top or talus region. This is in contrast to Smith's (1998) survey of cliff areas in the Linville Gorge, which sampled more extensively on cliff top and bases to assess trampling effects by hikers and climbers.

Shifts in ecological succession

The presence of climbing has the potential to alter cliff vegetation dynamics, which are built on a history of minimal disturbance. With climbing disturbance, cliff communities are held back in primary successional stages with abundant crustose lichens, and few umbilicate foliose and fruticose lichens. Pioneer crustose species are able to persist through high disturbance and have been observed to have high species richness on climbing routes (Smith 1998). Transitional successional stage foliose and fruticose lichens are less closely anchored to their substrate and therefore more easily removed by climbers. These larger and leafier growth forms are better able to trap water, soil, and litter, which, can facilitate the transition to later successional stages that include the establishment of bryophyte and plant species (Jackson 2015). This process can be inferred from the fact that unclimbed cliffs at Table Rock did have higher fruticose lichen and vascular plant richness and were, by definition, in a later successional sere.

Indicator species analysis on lichens also revealed a divide influenced by climbing presence. In climbed areas, most indicator lichens were crustose or powder forms. In unclimbed areas, they were fruticose and foliose species. Smith (1998) also observed high crustose percent cover on disturbed cliffs and high foliose and fruticose cover on undisturbed cliffs in the LGWA. Crustose lichen genera also dominated climbed cliff faces in both species’ richness and percent cover in Boggess et al. (2017) and Clark and Hessl (2015). Climbing-induced shifts in lichen morphotypes were also demonstrated by Adams and

Zaniewski (2012) on the North shore of Lake Superior. But lichen morphotype may provide a greater understanding of ecosystem functioning on cliffs, because this attribute is closely linked to lichen physiology and hence cliff ecological succession

Management of Cliff Ecosystems

Cliff communities in the LGWA are unique to each site, even compared to nearby cliffs within the same area. In order to understand this diversity, each potential climbing area should be surveyed before management decisions are made because blanket management plans may not sufficiently protect these fragile ecosystems. Although climbing does not have as large of an impact on cliff communities as does site variability, there is still a careful balance between climbing frequency and cliff community impacts (Tessler and Clark 2016). In remote areas, small changes, such as the addition of a parking lot to trailheads, could lead to greater climbing route traffic and overwhelming disturbance (Tessler and Clark 2016; Schmera et al. 2018). In climbing areas that are well established and accessible, large groups may use the area, which can spread impacts at the cliff base. Education and enforcement surrounding best practices for climbing should be implemented and maintained in remote and popular climbing areas alike to mitigate the environmental impact on these sensitive and unique natural areas (Tessler and Clark 2016, Clark and Hessl 2015). More generally, the fragile edge habitats should be protected via appropriate trail routing, which should access overlooks via trails perpendicular to the cliff edge.

Successful management of cliff communities in the past has incorporated stakeholder influence and collaborative stewardship, including vegetation monitoring by climbers (Clark and Hessl 2015, Tessler and Clark 2016, Boggess et al. 2017). Given limited resources available for ecosystem monitoring and the difficulty of accessing cliff faces, collaborative stewardship directly involving climbers is more likely to include the full range of ecological conditions present and management options available. Careful management of cliff-face communities will require difficult decisions about both existing climbing routes and the development of new routes, but local environmental factors must be taken into account.

Conclusions

Cliffs are fragile ecosystems, which contain high abundances of understudied and often cryptic lichens and bryophytes as well as many rare vascular plant taxa. These high-stress, light-light specialist communities are built on a history of minimal disturbance, but rock climbing is acting as a major source of anthropogenic disturbance. Cliff communities vary varies by site due to differences in surface heterogeneity, even within the same geographic area. Each potential climbing area should be surveyed, especially for cryptic and understudied species, before management decisions are made. Since unclimbed cliffs were the most species rich and diverse, it should be a priority for these areas to remain undisturbed.

LITERATURE CITED

Adams, M. D., and K. Zaniewski. 2012. Effects of recreational rock climbing and environmental variation on a sandstone cliff-face lichen community. Botany 90:253–259.

Beers, T.W., P.E. Cress, and L.C. Wensel. 1966. Aspect transformation in site productivity research. Journal of Forestry 64:691-692.

Boggess, L. M., G. L. Walker, and M. D. Madritch. 2017. Cliff flora of the Big South Fork National River and Recreation Area. Natural Areas Journal 37:200–211.

Brodo, I. M., S. D. Sharnoff, and S. Sharnoff. 2001. Lichens of North America. First Printing edition. Yale University Press, New Haven.

Camp, R. J., and R. L. Knight. 1998. Effects of rock climbing on cliff plant communities at Joshua Tree National Park, California. Conservation Biology 12:1302–1306.

Carmo, F. F. do, I. C. de Campos, and C. M. Jacobi. 2016. Effects of fine-scale surface heterogeneity on rock outcrop plant community structure. Journal of Vegetation Science 27:50–59.

Child, G. 1998. Climbing: the complete reference to rock, ice and indoor climbing. Facts on File Inc., New York.

Clark, P., and A. Hessl. 2015. The effects of rock climbing on cliff-face vegetation. Applied Vegetation Science 18:705–715.

Coates, F., and J. B. Kirkpatrick. 1992. Environmental relations and ecological responses of some higher plant species on rock cliffs in northern Tasmania. Australian Journal of Ecology 17:441–449.

Cordell, H. K. 2012. Outdoor recreation trends and futures: a technical document supporting the Forest Service 2010 RPA Assessment. Gen. Tech. Rep. SRS-150. Asheville, NC: U.S. Department of Agriculture Forest Service, Southern Research Station, 167 p. 150:1–167.

Farris, M. A. 1998. The effects of rock climbing on the vegetation of three Minnesota cliff systems. Canadian Journal of Botany 76:1981–1990.

Walker, Gary L. 1987. Ecology and population biology of *Thuja occidentalis* L. in its southern disjunct range. Ph. D. thesis, University of Tennessee, Knoxville.

Grime, J. P. 1977. Evidence for the Existence of Three Primary Strategies in Plants and Its Relevance to Ecological and Evolutionary Theory. The American Naturalist 111:1169–1194.

Gross, K., J. R. Lockwood, C. C. Frost, and W. F. Morris. 1998. Modeling controlled burning and trampling reduction for conservation of *Hudsonia montana*. Conservation Biology 12:1291–1301.

Haig, A. R., U. Matthes, and D. W. Larson. 2000. Effects of natural habitat fragmentation on the species richness, diversity, and composition of cliff vegetation. Canadian Journal of Botany 78:786–797.

Harkey, J. 2013. Species-area relationships on cliff system vegetational communities in Cumberland Gap National Historical Park. M.S. thesis, Appalachian State University, Boone, North Carolina.

Hill, E. P. 2009. Characterization of plant community structure and abiotic conditions on climbed and unclimbed cliff faces in the Obed River Gorge. M.S. thesis, Appalachian State University, Boone, North Carolina.

Holzschuh, A. 2016. Does rock climbing threaten cliff biodiversity? - A critical review. Biological Conservation 204:153–162.

Jackson, T. A. 2015. Weathering, secondary mineral genesis, and soil formation caused by lichens and mosses growing on granitic gneiss in a boreal forest environment. Geoderma 251-251:78-91.

Kelly, P. E., and D. W. Larson. 1997. Effects of rock climbing on populations of presettlement Eastern White Cedar (*Thuja occidentalis*) on cliffs of the Niagara Escarpment, Canada. Conservation Biology 11:1125–1132.

Kuntz, K. L., and D. W. Larson. 2006. Influences of microhabitat constraints and rock-climbing disturbance on cliff-face vegetation communities. Conservation Biology 20:821–832.

Lafon, C. W., Hanson, A. A., & Dwight, R. A. (2019). Geographic variations in fine-scale vegetation patterns: aspect preferences of montane pine stands over Southern Appalachian landscapes. Physical Geography, 40(5), 433.

Lambert, Y., and S. Harrison. 2002. Selected climbs North Carolina. The Mountaineers Books.

Larson, D. W., U. Matthes, J. A. Gerrath, N. W. K. Larson, J. M. Gerrath, J. C. Nekola, G. L. Walker, S. Porembski, and A. Charlton. 2000a. Evidence for the Widespread Occurrence of Ancient Forests on Cliffs. Journal of Biogeography 27:319–331.

Larson, D. W., U. Matthes, and P. E. Kelly. 2000b. Cliff ecology: pattern and process in cliff ecosystems. Cambridge University Press, Cambridge, UK ; New York.

Liu, Y, M. Lu, X. Zhang, O. Sun, Qibiao, R. Liu, B. Lian, Bin. 2019. Shift of the microbial communities from exposed sandstone rocks to forest soils during pedogenesis. International Biodeterioration & Biodegradation 140:21-28.

Mac Nally, R. 2002. Multiple regression and inference in ecology and conservation biology: further comments on identifying important predictor variables. Biodiversity and Conservation 11:1397-1401.

March-Salas, M., M. Moreno-Moya, G. Palomar, P. Tejero-Ibarra, E. Haeuser, and L. R. Pertierra. 2018. An innovative vegetation survey design in Mediterranean cliffs shows evidence of higher tolerance of specialized rock plants to rock climbing activity. Applied Vegetation Science 21:289–297.

McMillan, M. A., and D. W. Larson. 2002. Effects of rock climbing on the vegetation of the Niagara Escarpment in Southern Ontario, Canada. Conservation Biology 16:389–398.

Murray, K, M. M. Conner. 2009. Methods to quantify variable importance: implications for the analysis of noisy ecological data. Ecology 90: 348-355.

Newell, C. L., and R. K. Peet. 1998. Vegetation of Linville Gorge Wilderness, North Carolina. Castanea 63:275–322.

Nuzzo, V. A. 1995. Effects of rock climbing on Cliff Goldenrod (*Solidago sciaphila* Steele) in Northwest Illinois. The American Midland Naturalist 133:229–241.

Nuzzo, V. A. 1996. Structure of cliff vegetation on exposed cliffs and the effect of rock climbing. Canadian Journal of Botany 74:607–617.

Opedal, Ø. H., W. S. Armbruster, and B. J. Graae. 2015. Linking small-scale topography with microclimate, plant species diversity and intra-specific trait variation in an alpine landscape. Plant Ecology & Diversity 8:305–315.

Rusterholz, H.-P., S. W. Miiller, and B. Baur. 2004. Effects of rock climbing on plant communities on exposed limestone cliffs in the Swiss Jura mountains. Applied Vegetation Science 7:35–40.

Smith, P. 1998. A vegetational characterization of cliff faces in the Linville Gorge Wilderness Area. M.S. thesis, Appalachian State University, Boone, North Carolina.

Spitale, D., and J. Nascimbene. 2012. Spatial structure, rock type, and local environmental conditions drive moss and lichen distribution on calcareous boulders. Ecological Research 27:633–638.

Tessler, M., and T. A. Clark. 2016. The impact of bouldering on rock-associated vegetation. Biological Conservation 204:426–433.

Tessler, M., T. A. Clark, S. W. Cunningham. 2016. An updated checklist of bryophytes of the Shawangunk Mountains, New York. Evansia 33(4):154-164.

Ursic, K. A., N. C. Kenkel, and D. W. Larson. 1997. Revegetation dynamics of cliff faces in abandoned limestone quarries. Journal of applied ecology:289.

Weakley, A. 2007. Flora of the Carolinas, Virginia and Surrounding Area. University of North Carolina Herbarium, N.C. Botanical Garden, Chapel Hill, NC.

Cottle, H. J. 1932. Vegetation on north and south slopes of mountains in southwestern Texas. Ecology 13: 121-134

Cantlon, J. E. 1953. Vegetation and microclimates on north and south slopes of Cushetunk Mountain, New Jersey. Ecological Monographs 23(3):241-270.

Warren, R. J. 2010. An experimental test of well-described vegetation patterns across slope aspects using woodland herb transplants and manipulated abiotic drivers. New Phytologist 185(4): 1038-1049.

Warren, R. J. 2008. Mechanisms driving understory evergreen herb distributions across slope aspects: as derived from landscape position. Plant Ecology 198(2): 297-308.

Larson, D. W., U. Mattes-Sears, P. E. Kelly. 1993. Cambial dieback and partial shoot mortality in cliff-face *Thuja occidentalis*: evidence for sectored radial architecture. International Journal of Plant Sciences 154(4): 496-505.

Baur, B., L. Fröberg, and S. W. Müller. 2007, November. Effect of rock climbing on the calcicolous lichen community of limestone cliffs in the northern Swiss Jura Mountains. Nova Hedwigia 85(3-4):429-444.

Table 1. Vascular plant species in rank order beginning with the most abundant species. Abundance is presence in survey plots.

Species	Naming Authority
Selaginella tortipila	A.Baun
Hydatica petiolaris	(Raf.) Small
Sporobolus sp.	
Agrostis perennans	(Walter) Tuck.
Carex umbellata	Schkuhr ex Willd
Dicanthelium accumulatum	
Betula alleghaniensis	Britton
Carex sp. 3	
Carex sp. 2	
Galax urceolata	(Poir.) Brummitt
Graminoid #1	
Kalmia latifolia	L.
Oxydendrum arboreum	(L.) DC
Rhododendron maximum	L.
Solidago spp.	
Acer saccharum	Marshall
Andropogon virginicus var virginicus	Fernald & Griscom
Carex sp. 4	
Carex sp. 5	
Carex sp. 6	
Carex sp. 7	
Coreopsis major	Walter
Dennstaedtia punctilobula	(Michx.) T.Moore
Krigia dandelion	Nutt.
Nyssa sylvatica	Marshall
Pinus rigida	Porcher
Vascular Plant #3	
Vascular Plant #4	
Vascular Plant #5	
Rhododendron minus	Michx.
Rubus allegheniensis	Porter
Symphyotrichum sp.	
Vaccinium corymbosum	L.

Table 2. Bryophyte species in rank order beginning with the most abundant. Abundance is presence in survey plots.

Species	Naming Authority
Bryophyte #6	
Campylopus tallulensis	Sull. & Lesq.
Weissia controversa	Hedw.
Bryophyte #5	
Bryophyte #8	
Dicranum montanum	Hedw.
Bryophyte #7	
Bryophyte #15	
Bryophyte #2	
Bryophyte #11	
Andreaea rothii	F. Weber & D. Mohr
Bryum spp.	
Leucobryum albidum	(Brid. ex. P. Beauv.) Lindb.
Bryophyte #10	
Dicranella varia	(Hedw.) Schimp.
Polytrichum commune	Hedw.
Bucklandiella venusta	(Fisvoll) Bedn.-Ochyra & Ochyra
Dicranum scoparium	Hedw
Bryophyte #12	
Polytrichum strictum	Menzies ex Brid.
Leucobryum glaucum	(Hedw.) Angstr.
Atrichum angustatum	(Brid.) Bruch & Schimp.
Dicranella heteromalla	(Hedw.) Schimp.
Ditrichum lineare	(Sw.)Lindb.
Bryophyte #13	
Ditrichum pusillum	(Hedwe.) Hampe
Bryophyte #16	
Pohlia nutans	(Hedw.) Lindb.
Polytrichum juniperinum	Hedw.
Ceratodon purpureus	(Hedw.) Brid.
Diplophyllum apiculatum	(A. Evans) Steph.
Bryophyte #14	
Bryophyte #4	
Bryophyte #9	
Polytrichum piliferum	Hedw.
Pseudotaxiphyllum elegans	(Brid.) Z. Iwats.
Racomitrium heterostichum	(Hedw.) Brid.

Table 3. Lichen species in rank order of abundance. Species are listed with the highest known biologic species classification based on Brodo et al. 2001. Most common species listed at the top. Functional groups include: powder, crustose (CRUST), umbilicate foliose (FOL_UMB), lobed foliose (FOL_LOBE, and fruticose lichens (FRUIT). Morphospecies is listed based off field description and was used for analysis.

Morpho Species	Functional Group	Species	Naming Authority
TOADSK	FOL_UMB	*Lasallia papulosa*	(Ach.) Llano
WHPDR	POWDER	*Lepraria neglecta*	(Nyl.) Erichsen
TNYBRNCH	FOL_LOBE	*Physcia subtilis*	Degel.
MINGREY	CRUST	*Aspicilia cinerea*	(L.) Körb.
GRNSQB	FOL_LOBE	*Xanthoparmelia conspersa*	(Ehrh. ex Ach.) Hale
GRNPDR	POWDER	*Lepraria neglecta*	(Nyl.) Erichsen
ROCKTRP	FOL_UMB	*Umbilicaria mammulata*	(Ach.) Tuck.
BLBRDOT	CRUST	*Acarospora fuscata*	(Nyl.) Arnold
CLADSQ	FRUIT	*Cladonia coniocraea*	(Flörke) Sprengel
BRGCRUST	CRUST	*Rhizocarpon geographicum*	(L.) DC.
BRBLKBDR	CRUST	*Acarospora fuscata*	(Nyl.) Arnold
PAPER	POWDER	*Phlyctis petraea*	R.C. Harris, Musc. Ladd & Lendemer
BRBLKCRST	CRUST	*Acarospora fuscata*	(Nyl.) Arnold
WHITBUB	CRUST	*Phlyctis* sp.	(Wallr.) Flot
GRMEDSQ	FOL_LOBE	*Xanthoparmelia conspersa*	(Ehrh. ex Ach.) Hale
USNEA	FRUIT	*Usnea* sp.	Dill. ex Adans.
BLWHDOT	CRUST	*Diploschistes actinostomus*	(Ach.) Zalhbr.
GRWIDE	FOL_LOBE	*Canoparmelia alabamensis*	(Hale & McCull.) Elix
CLADSTLK	FRUIT	*Cladonia* sp.	P. Browne
CLADPIX	FRUIT	*Cladonia chlorophaea*	(Flörke ex. Sommerf.) Sprengel
GRNWDE	FOL_LOBE	*Canoparmelia alabamensis*	(Hale & McCull.) Elix
CLADBRS	FRUIT	*Cladonia pleurota*	(Flörke) Schaer.
BLGRDOT	CRUST	*Diploschistes actinostomus*	(Ach.) Zalhbr.
GRNCRST	CRUST	*Rhizocarpon geographicum*	(L.) DC.
BRBLDOT	CRUST	*Fuscidea recensa*	(Stirton) Hertel, V. Wirth & Vězda
GREYPDR	POWDER	*Lepraria* sp.	Ach.
GRNWART	CRUST	*Lepraria neglecta*	(Nyl.) Erichsen
BLKPDR	POWDER	*Lepraria* sp.	Ach.
BRNWART	CRUST	*Acarospora fuscata*	(Nyl.) Arnold
GRNFOL	FOL_LOBE	*Canoparmelia alabamensis*	(Hale & McCull.) Elix
GREEREIN	FRUIT	*Cladonia arbuscula subsp. arbuscula*	(Wallr.) Flot.

Table 3 (Continued)

Morpho Species	Functional Group	Species	Naming Authority
YELLWART	CRUST	*Chrysothrix candelaris*	(L.) J. R. Laundon
WHITREIN	FRUIT	*Cladonia furcata*	(Hudson) Schrader
BLASQ	FOL_LOBE		
JETBLK	CRUST	*Diploschistes actinostomus*	(Ach.) Zalhbr.
GRBBRD	CRUST	*Rhizocarpon* sp.	Ramond ex DC.
WHBLDOT	CRUST	*Rhizocarpon* sp.	Ramond ex DC.
GREYREIN	FRUIT	*Cladonia rangiferina*	(L.) F. H. Wigg.
GREMED	FOL_LOBE	*Xanthoparmelia conspersa*	(Ehrh. ex Ach.) Hale
BUBLGUM	CRUST		
GRESMSQ	FOL_LOBE	*Hypotrachyna imbricatula*	(Zahlbr.) Hale
GRMED	FOL_LOBE	*Hypotrachyna imbricatula*	(Zahlbr.) Hale
MINTPDR	POWDER	*Lepraria* sp.	Ach.
PNKCRST	CRUST	*Trapelia glebulosa*	(Sm.) J. R. Laundon
YELPDR	POWDER	*Lepraria* sp.	Ach.
BLAFLA	FOL_LOBE		
GRNSM	FOL_LOBE	*Hypotrachyna* sp.	(Vain.) Hale
GREEWART	CRUST	*Rinodina tephraspis*	(Tuck.) Herre
TANCUP	CRUST		
TEALCRST	CRUST		
CLAD	FRUIT	*Cladonia* sp.	P. Browne
PSYCHO	CRUST	*Lepraria neglecta*	(Nyl.) Erichsen
GREPAPER	POWDER	*Phlyctis petraea*	R.C. Harris, Musc. Ladd & Lendemer
BLAWHT	FOL_LOBE		
GREYBLDOT	CRUST	*Aspicilia cinerea*	(L.) Körb.
CLADBSTK	FRUIT	*Cladonia squamosa*	Hoffm.
GRYBRN	FOL_LOBE	*Parmotrema perlatum*	(Hudson) M. Choisy
SOILCR	CRUST	*Pycnothelia papillaria*	Dufour
RAMALI	FRUIT	*Ramalina* sp.	Ach.
GRYBR	CRUST	*Stereocaulon dactylophyllum*	Flörke
TANBUB	CRUST		
BLASM	FOL_LOBE		
WHITEFOL	FOL_LOBE		
BRNYELL	CRUST	*Acarospora fuscata*	(Nyl.) Arnold
CLADRC	FRUIT	*Cladonia* sp.	P. Browne
BRNGRFOL	FOL_LOBE	*Hypotrachyna imbricatula*	(Zahlbr.) Hale
TOADGR	FOL_UMB	*Lasallia pensylvanica*	(Hoffm.) Llano
BROPDR	POWDER	*Lepraria* sp.	Ach.

Table 3 (Continued)

Morpho Species	Functional Group	Species	Naming Authority
GRNCIL	FOL_LOBE	*Parmelia omphalodes*	(L.) Ach
SHIELD	FOL_LOBE	*Parmotrema crinitum*	(Ach.) Choisy
REDCRST	CRUST	*Phlyctis petraea*	R.C. Harris, Muscavitch, Ladd & Lendemer
BRNGRCRST	POWDER	*Rhizocarpon* sp.	Ramond ex DC.
PNKBLA	CRUST	*Trapelia glebulosa*	(Sm.) J. R. Laundon
BRNFOL	FOL_LOBE	*Tuckermanopsis ciliaris*	(Ach.) Gyelnick

Table 4. Indicator species analysis of all taxa by climbing effect. The individual component of each species is represented in two components, A is the sample estimate of the probability that the surveyed site belongs to the target site group given the fact that the species has been found. B is the sample estimate of the probability of finding the species in sites belonging to the site group. Fidelity (Fid) is the sensitivity of the species as indicator of the target site group. Taxa groups are lichens (L), bryophytes (B), and vascular plants (P). If species ID is not known, morphospecies is listed. For lichens, growth form (L Growth) is listed (powder, crust, lobed foliose, umbilicate foliose, or fruticose).

CLIMBED

Taxa	Species	L Growth	A	B	Fid	P
L	*Canoparmelia alabamensis*	FOL_LOBE	1	0.106	0.325	0.002
B	*Weissia controversa*		1	0.082	0.286	0.001
B	Moss #5		0.969	0.072	0.264	0.011
L	Lichen: GRNWDE	FOL_LOBE	0.894	0.077	0.262	0.017
L	*Rhizocarpon geographicum*	CRUST	1	0.063	0.250	0.012
L	*Lepraria* sp.	POWDER	1	0.058	0.240	0.014
L	*Lepraria neglecta*	CRUST	1	0.053	0.230	0.013
L	*Acarospora fuscata*	CRUST	1	0.048	0.219	0.024
B	Moss #10		1	0.038	0.196	0.045
L	*Xanthoparmelia conspersa*	FOL_LOBE	1	0.034	0.183	0.080
B	*Andreaea rothii*		1	0.034	0.183	0.073
B	*Bryum* sp.		1	0.034	0.183	0.061

UNCLIMBED

Taxa	Species	L Growth	A	B	Fid	P
B	Moss #6		0.074	0.278	0.453	0.001
L	*Acarospora fuscata*	CRUST	0.727	0.167	0.348	0.002
L	*Lepraria* sp.	POWDER	1	0.103	0.321	0.001
L	*Diploschistes actinostomus*	CRUST	0.761	0.103	0.280	0.012
L	*Rhizocarpon* sp.	CRUST	0	0.063	0.252	0.001
B	Moss #15		0.896	0.056	0.223	0.006
L	*Lepraria* spp.	POWDER	1	0.048	0.218	0.003
P	*Agrostis parennans*		1	0.040	0.199	0.009
L	*Lepraria neglecta*	POWDER	0	0.024	0.154	0.055

Table 5. Indicator species analysis of only lichen (Morphospecies code) by climbing effect. The individual component of each species is represented in two components, A is the sample estimate of the probability that the surveyed site belongs to the target site group given the fact that the species has been found. B is the sample estimate of the probability of finding the species in sites belonging to the site group. Fidelity (Fid) is the sensitivity of the species as indicator of the target site group. Growth form (L Growth) is listed (powder, crust, lobed foliose, umbilicate foliose, or fruticose).

CLIMBED

Species	L Growth	A	B	Fid	P
Canoparmelia alabamensis	FOL_LOBE	0.867	0.091	0.281	0.016
Lepraria sp. 1	POWDER	1	0.063	0.250	0.007
Rhizocarpon geographicum	CRUST	1	0.063	0.250	0.007
Lepraria sp. 2	POWDER	1	0.058	0.240	0.009
Acarospora fuscata	CRUST	1	0.048	0.219	0.010

UNCLIMBED

Species	L Growth	A	B	Fid	P
Cladonia pleurota	FRUIT	1	0.135	0.367	0.001
Cladonia chlorophaea	FRUIT	0.965	0.127	0.35	0.001
Fuscidea recensa	CRUST	1	0.111	0.333	0.001
Cladonia sp.	FRUIT	0.801	0.103	0.288	0.005
Cladonia arbuscula	FRUIT	1	0.079	0.282	0.001
Cladonia furcata	FRUIT	1	0.071	0.267	0.001
Diploschistes actinostomus	CRUST	0.762	0.087	0.258	0.063
Hypotrachyna imbricatula	FOL_LOBE	1	0.048	0.218	0.004

Table 6. Multiple linear regression of richness and diversity to large (slope, aspect) and fine (abiotic feature size and abundance) scale abiotic variation. Only the individual variables which explained at least 10% of the individual variation in hierarchal portioning model were selected. Taxa groups: all – all taxa, L – lichen, B – bryophyte, P – vascular plants, Div is Shannon Diversity Index. Adj. R^2 is adjusted R^2, Res. SE is residual standard error. Significance code: $P < 0.001$ ***, $P < 0.01$ **, $P < 0.05$ *.

Taxa	P	Adj. R^2	Res. SE	df	F	Ind. Var	Coef.	P	Sig
All Rich	< 0.001	0.15	2.31	4, 298	13.96	Eastness	0.508	0.0311	*
						Ledge area	0.003	0.0000	***
						Ledge count	0.198	0.0254	*
						Crack area	0.000	0.0004	***
All Div	< 0.001	0.12	0.3	4, 298	11.65	Eastness	0.071	0.0193	*
						Ledge area	0.000	0.0003	***
						Ledge count	0.025	0.0318	*
						Crack area	0.025	0.0016	**
L Rich	< 0.001	0.06	2.2	4, 298	5.36	Northness	0.529	0.0276	*
						Eastness	0.499	0.0554	
						Ledge area	0.002	0.0118	*
						Ledge count	0.175	0.0377	*
L Div	< 0.05	0.02	0.35	3, 299	3.06	Eastness	0.036	0.3220	
						Ledge area	0.000	0.1460	
						Ledge count	0.000	0.0910	
B Rich	< 0.001	0.13	0.90	4, 298	11.82	Northness	-0.190	0.0525	
						Eastness	0.239	0.0256	*
						Ledge area	0.000	0.0048	**
						Crack area	0.000	0.0011	**
B Div	< 0.001	0.11	0.30	3, 299	12.97	Eastness	0.065	0.0333	*
						Ledge area	0.000	0.0016	**
						Crack area	0.000	0.0000	***
P Rich	< 0.001	0.16	0.79	4, 289	10.50	Slope	0.005	0.0091	**
						Ledge area	0.000	0.0518	
						Crack area	-0.000	0.1082	
						Crack count	0.135	0.0747	
P Div	< 0.001	0.09	0.24	3, 290	10.57	Slope	0.002	0.0027	**
						Crack area	0.000	0.0004	***
						Crack count	0.034	0.1294	

Table 7. Burke County records of lichen species. I checked identified specimens with the records available through the Consortium of North American Lichen Herbaria (lichenportal.org) as of 20 April 2020. *Canoparmelia alabamensis* is the first report for this species in North Carolina.

Species	Naming Authority
Acarospora fuscata	(Nyl.) Arnold
Buellia spuria	(Schaer.) Anzi
Canoparmelia alabamensis	(Hale & McCull.) Elix
Cladonia caespiticia	(Pers.) Flörke
Cladonia submitis	A. Evans
Diploschistes actinostomus	(Ach.) Zalhbr.
Fuscidea recensa	(Stirton) Hertel, V. Wirth & Vězda
Hypotrachyna imbricatula	(Zahlbr.) Hale
Hypotrachyna rockii	(Zahlbr.) Hale
Lepraria neglecta	(Nyl.) Erichsen
Lepraria normandinoides	Lendemer & R.C. Harris
Parmelia omphalodes	(L.) Ach
Phlyctis petraea	R.C. Harris, Musc. Ladd & Lendemer
Porpidia subsimplex	(H. Magn.) Fryday
Rhizocarpon geographicum	(L.) DC.
Rinodina tephraspis	(Tuck.) Herre
Stereocaulon dactylophyllum	Flörke
Trapelia glebulosa	(Sm.) J. R. Laundon

Table 8. Comparison of vascular plant, bryophyte, and lichen species richness between this study and other cliff community surveys in the Southeastern US.

Study Location	[1]LGWA *(this study)*	[2]LGWA	[3]Obed River Gorge	[4]White Rocks	[5]Cumberland Gap	[6]Big South Fork	[7]New River Gorge National River
Vascular species	22	31	58	14	111	81	70
Bryophyte species	21		65	9	37	64	74
Lichen species	42	23	47	48	83	120	79
Total species count	85	54	170	71	231	265	223

[1] This study surveyed 39 transects with 382 1 m^2 survey plots at two sites (Table Rock: 19 climbed/12 unclimbed, Hawksbill 4 climbed/4 unclimbed).
[2] Smith (1998) sampled cliffs within the LGWA along 16 transect at the Gold Coast, Amphitheatre, and Chimney Areas. All plants (including bryophytes) were listed under “plants” in species count, but were broken up into seedless and seed plants for analysis.
[3] The Obed Wild and Scenic River (TN) was sampled at six extensively climbed, mainly south-facing cliff sites (Hill 2009).
[4] White Rocks is one large cliff system within Cumberland Gap (Ballinger 2011).
[5] Cumberland Gap National Historical Park (TN) was sampled at 11 cliff sites (Harkey 2013).
[6] Big South Fork (TN) was surveyed along 50 transects, 10 of which were climbed (Boggess et al. 2017).
[7] Clark & Hessl (2015) sampling 79 climbing routes and 32 unclimbed transects in the New River Gorge National River (WV).

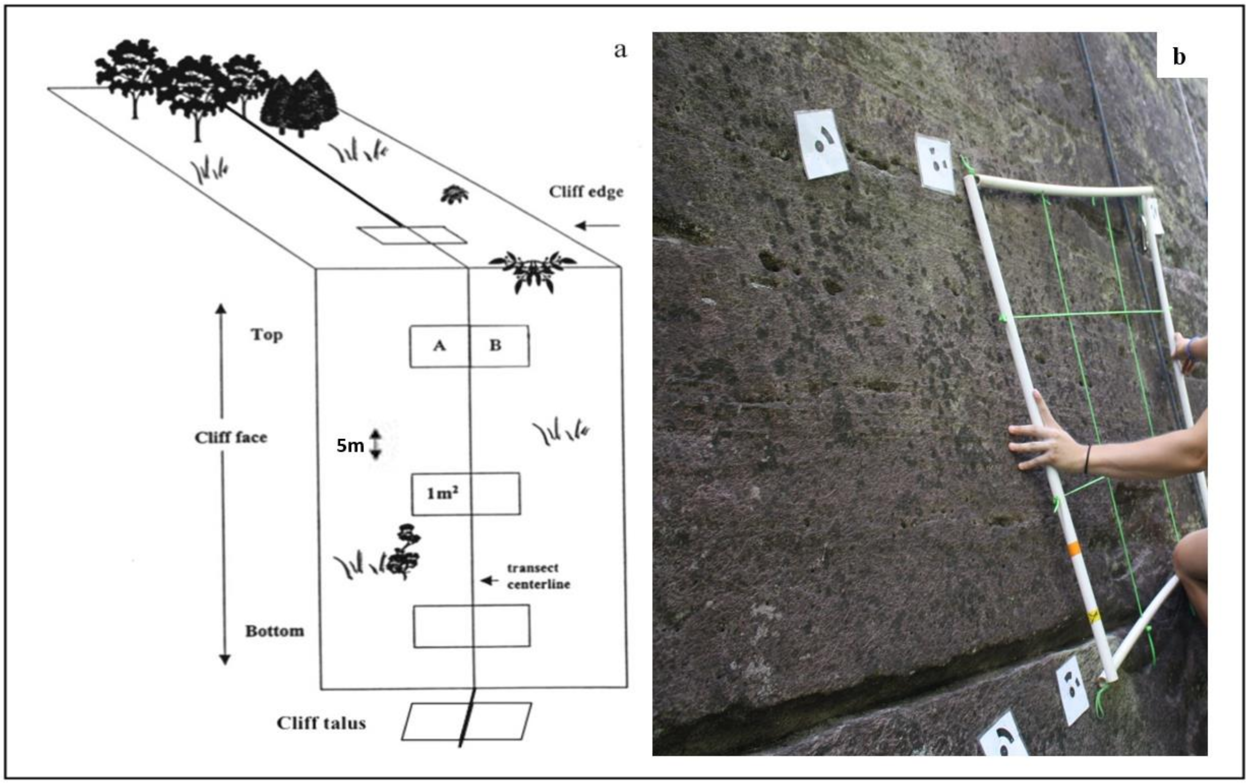

Figure 1. Diagram of a cliff face study system modified from Boggess et al. 2017. (a) 1 m^2 survey plots were placed on both sides of the transect centerline (rappel line). Plots were placed at the plateau and talus of each transect, as well as every 5 m down the cliff face. (b) Photograph of 1 m^2 survey plot used, including nine sub-plots.

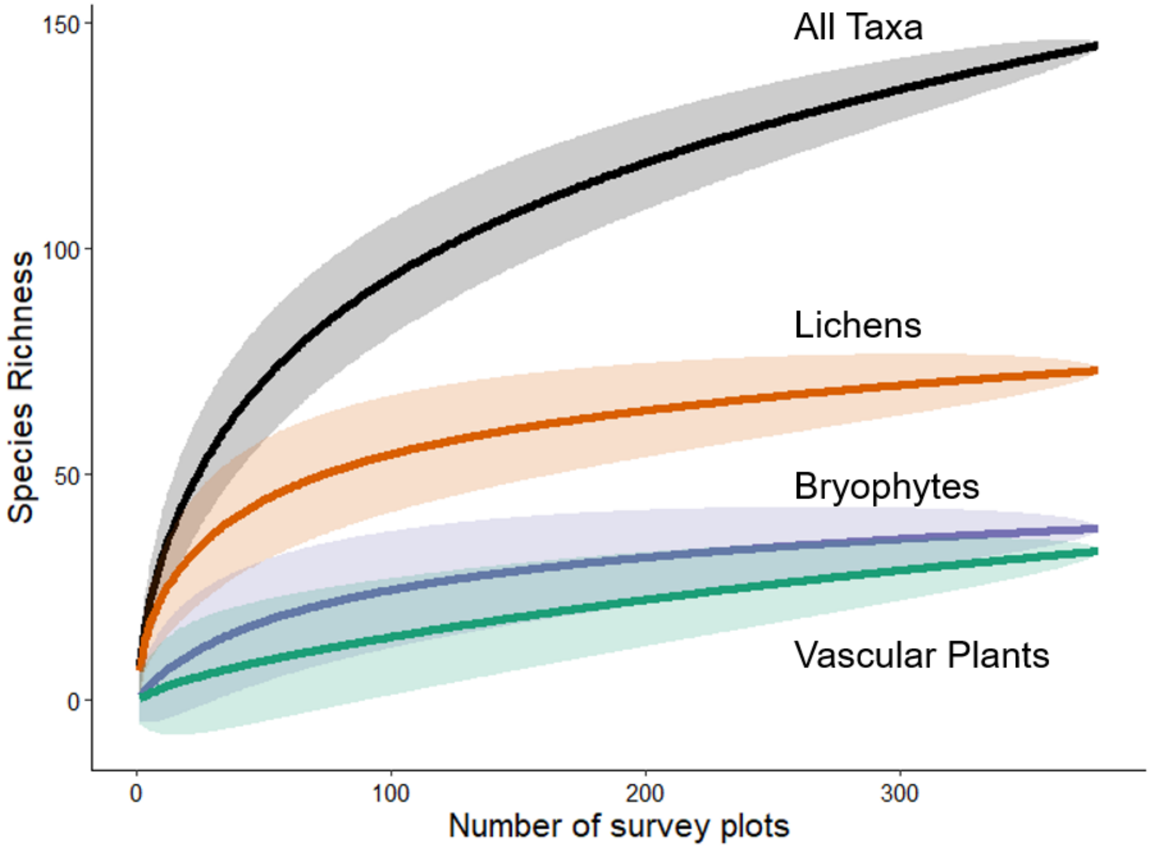

Figure 2. Species accumulation curves for all taxa as well as only lichens, bryophytes, and vascular plants, shown with shaded 95% confidence intervals. Species richness includes all cliff face, base, and top plots.

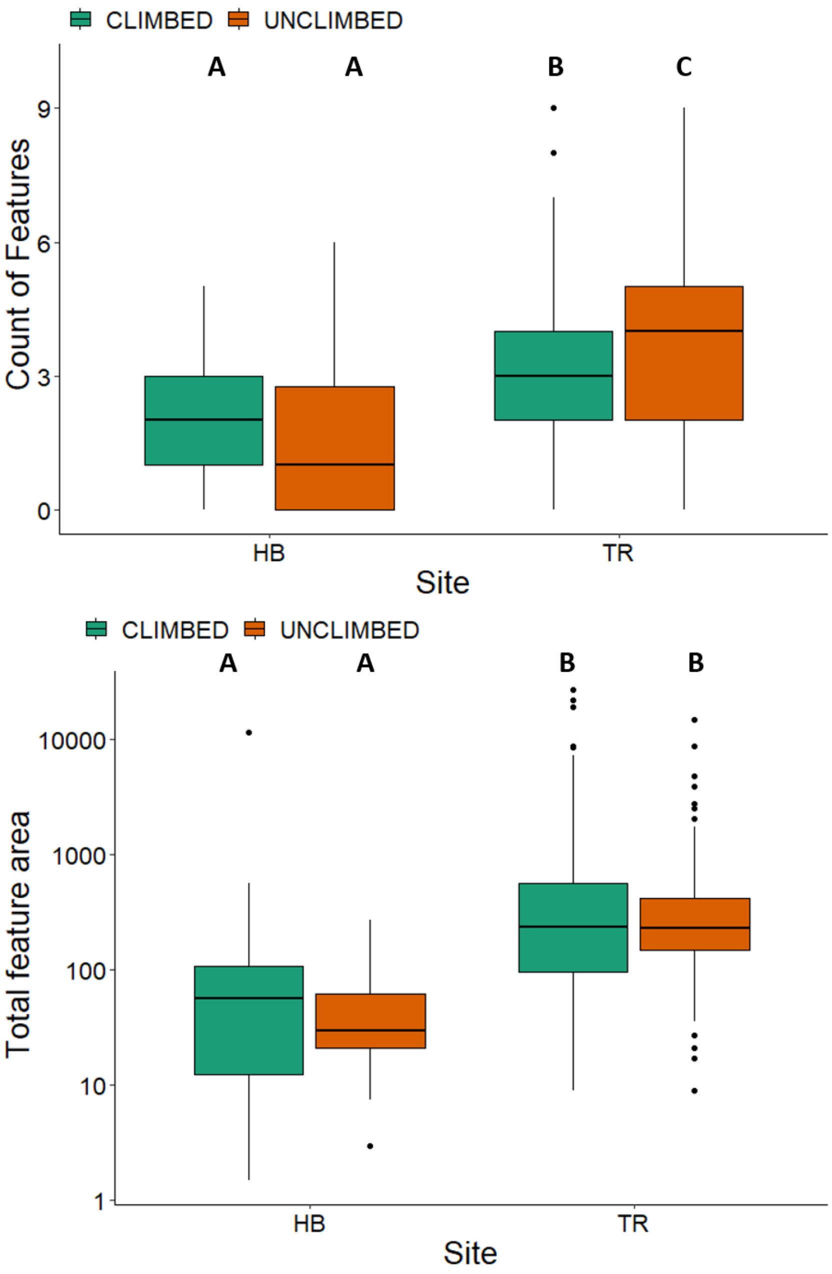

Figure 3. Total count of features (ledges, crevices, pockets) and total feature area (cm^2, displayed on a log scale) per plot by site and climbing presence with significance indicated by letters. Unclimbed plots at Table Rock had the most features, followed by climbed Table Rock plots, which were both higher than Hawksbill plots ($F_{1,330} = 4.928$, $P < 0.05$). Table Rock had higher feature surface area than Hawksbill ($F_{1,330} = 3028$, $P<0.1$).

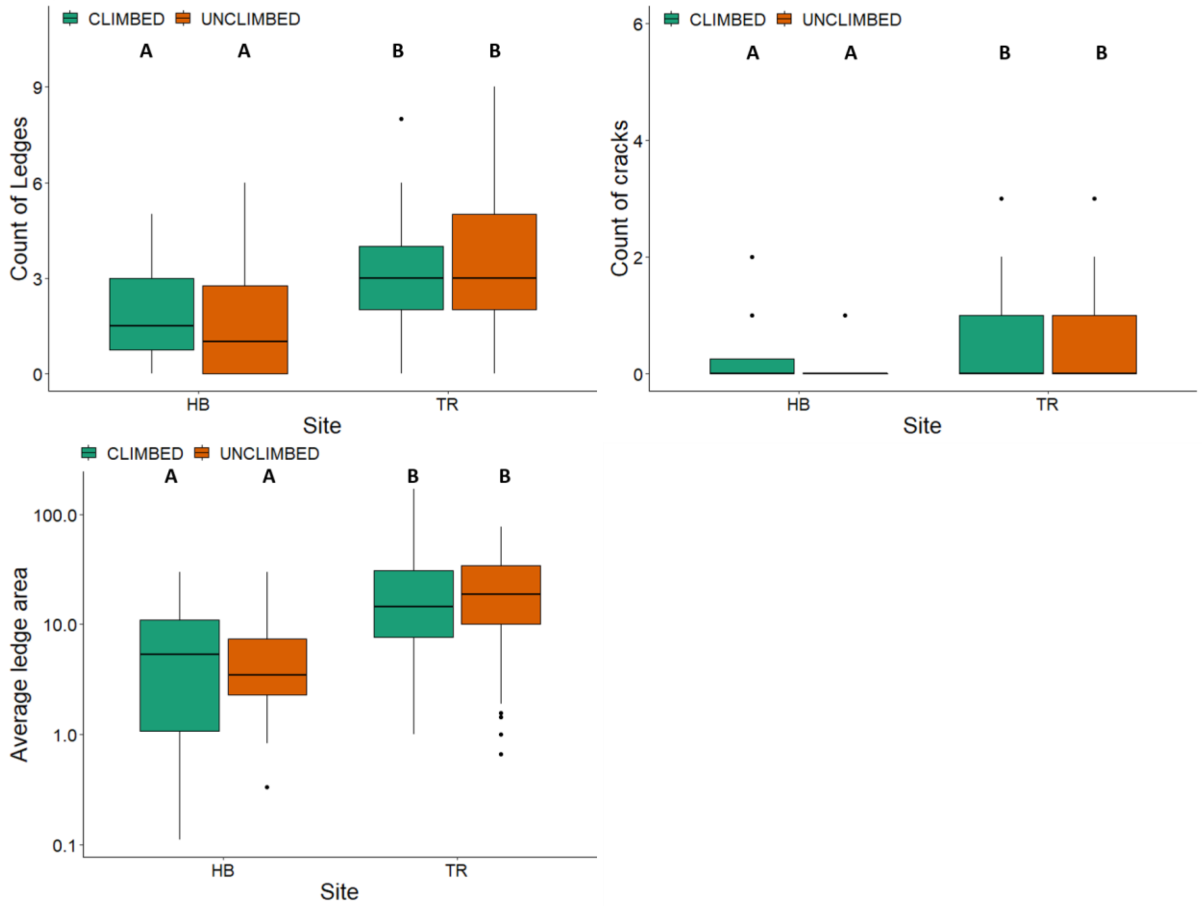

Figure 4. Total count of ledges and cracks and average ledge surface area (cm^2, displayed on a log scale) per plot by site and climbing presence with significance indicated by letters. Table Rock had more ledges ($F_{1,330} = 35.1$, $P < 0.001$) and higher average ledge surface area ($F_{1,330} = 28.6$, $P < 0.001$) than Hawksbill. Average ledge surface area was calculated by dividing total surface area by number of ledges in each plot. Table Rock also had more crevices per plot ($F_{1,330} = 7.9$, $P < 0.01$). There was no difference in abundance or area of pockets due to their rarity.

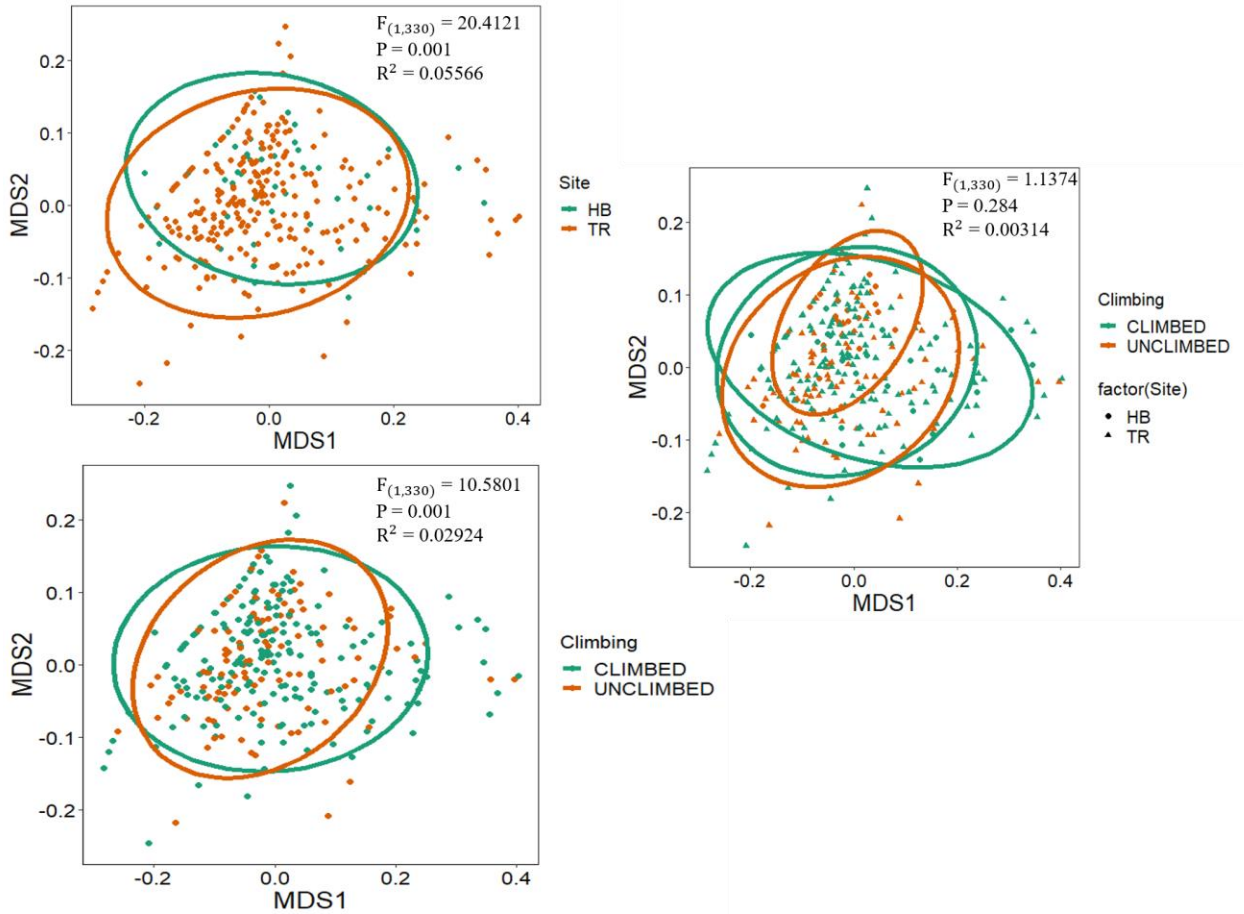

Figure 5. NMDS of abiotic features by climbing and site factors with PERMANOA tests for statistical significance. A PERMANOVA demonstrated no difference in abiotic feature community by climbing ($F_{1,299}$= 1.4, P = 0.15, R^2 = 0.005), site ($F_{1,299}$= 2.5, P = 0.01, R^2 = 0.008), or interaction between both factors ($F_{1,299}$= 1.96, P = 0.04, R^2 = 0.006).

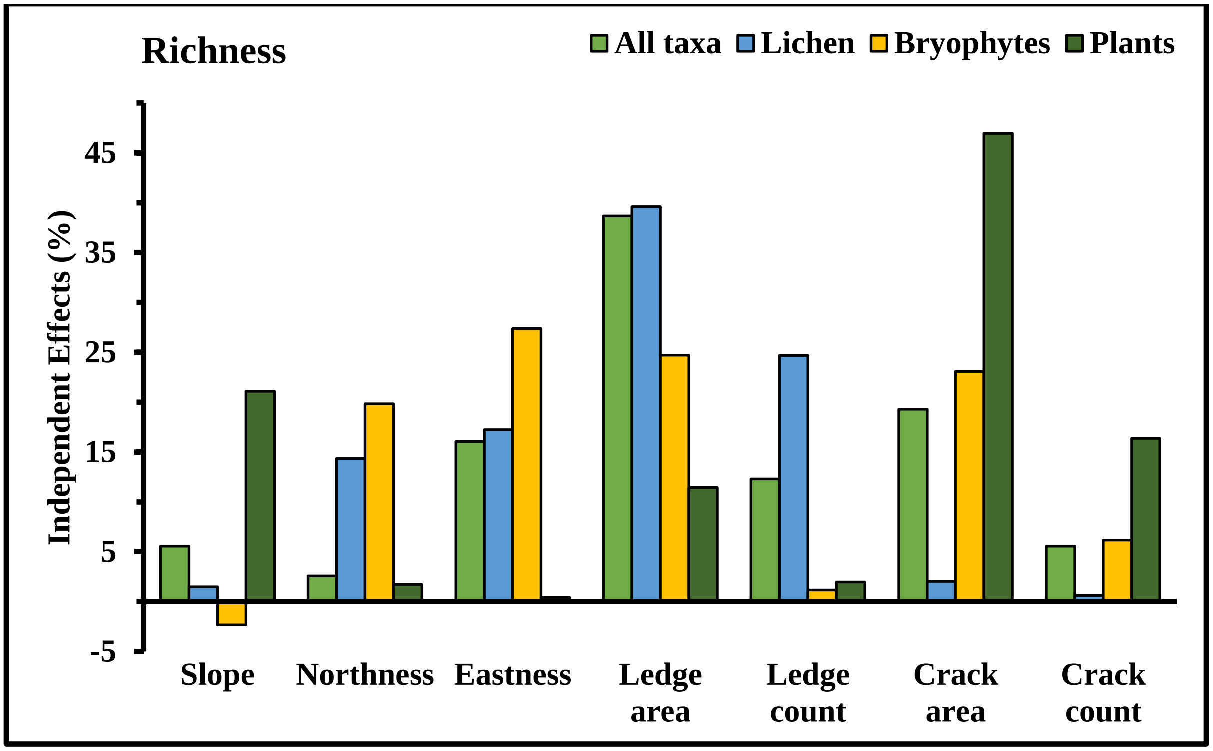

Figure 6. Hierarchical partitioning of variance independently explained by seven candidate predictor variables of plot species richness. Only variables which explained over 10% of independent effects for each taxa group were included in linear modeling. Negative percent values indicate suppressor variables. Transect aspect was transformed to two linear components: north-south (northness) and east-west (eastness) (Beers et al. 1966). Ledge and crack area were calculated by multiplying length x width and length x width x depth, respectively (Kuntz and Larson 2006). Only the area of each feature that was within the 1 m^2 survey plot was measured.

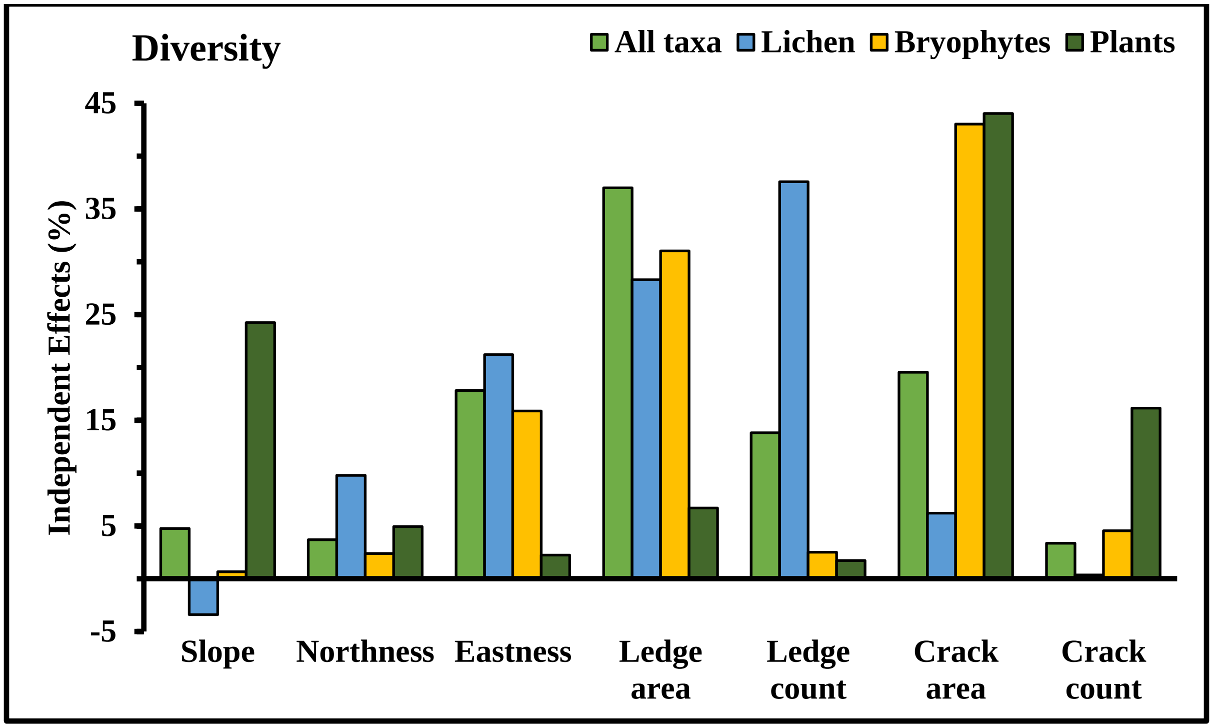

Figure 7. Hierarchical partitioning of variance independently explained by seven candidate predictor variables of plot Shannon Diversity Index. Only variables which explained over 10% of independent effects for each taxa group were included in linear modeling. Negative percent values indicate suppressor variables Transect aspect was transformed to two linear components: north-south (northness) and east-west (eastness) (Beers et al. 1966). Ledge and crack area were calculated by multiplying length x width and length x width x depth, respectively (Kuntz and Larson 2006). Only the area of each feature that was within the 1m^2 survey plot was measured.

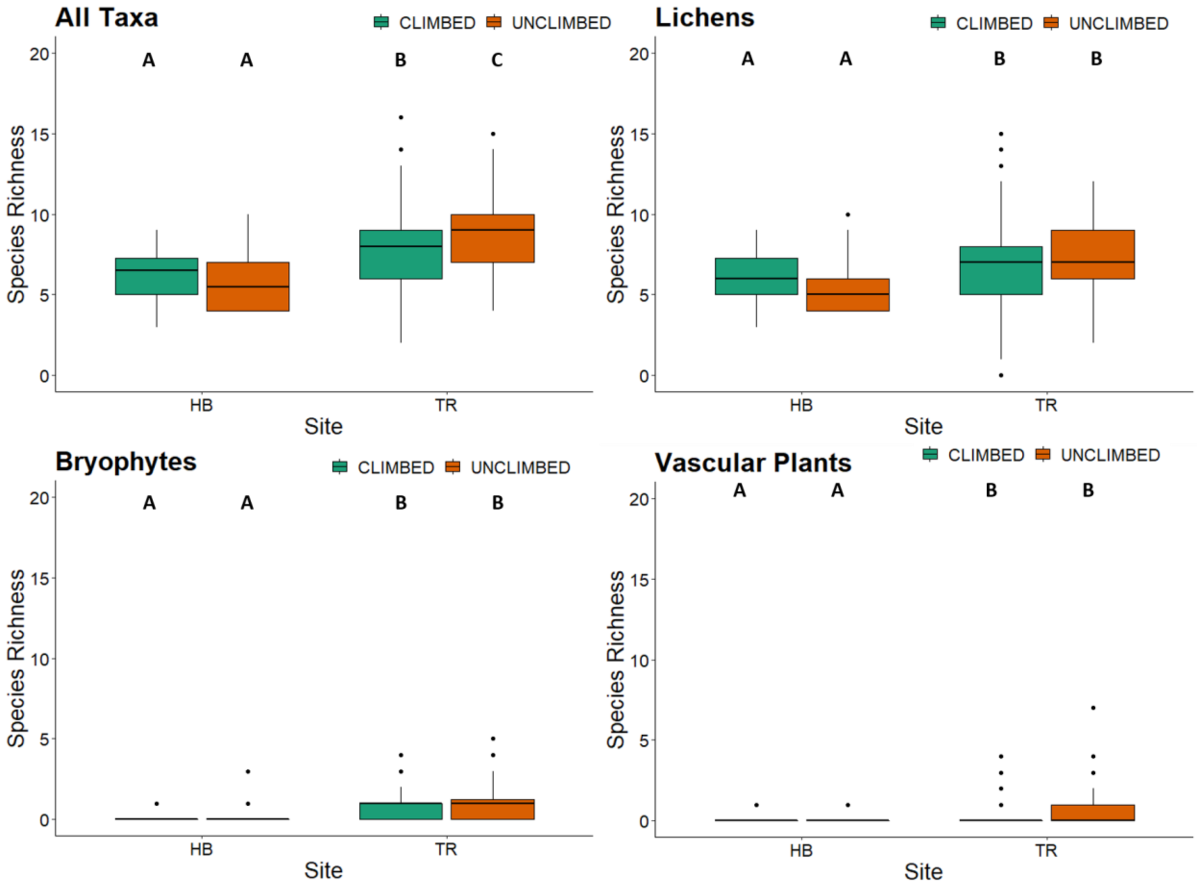

Figure 8. Species richness of all taxa and groups by climbing and site factors, statistically significant differences are indicated by letters. Unclimbed plots at Table Rock had the highest richness, followed by climbed plots at Table Rock, both of which were more rich than Hawksbill ($F_{1,330} = 4.4$, $P = 0.04$). Most of the species richness is due to lichens. Table Rock had higher lichen ($F_{1,330} = 16.08$, $P < 0.001$) and bryophyte richness ($F_{1,330} = 29.4$, $P < 0.001$). Vascular plant richness was highest in unclimbed, followed by climbed plots at Table Rock, both of which were higher than Hawksbill plots ($F_{1,330} = 8.9$, $P = 0.003$).

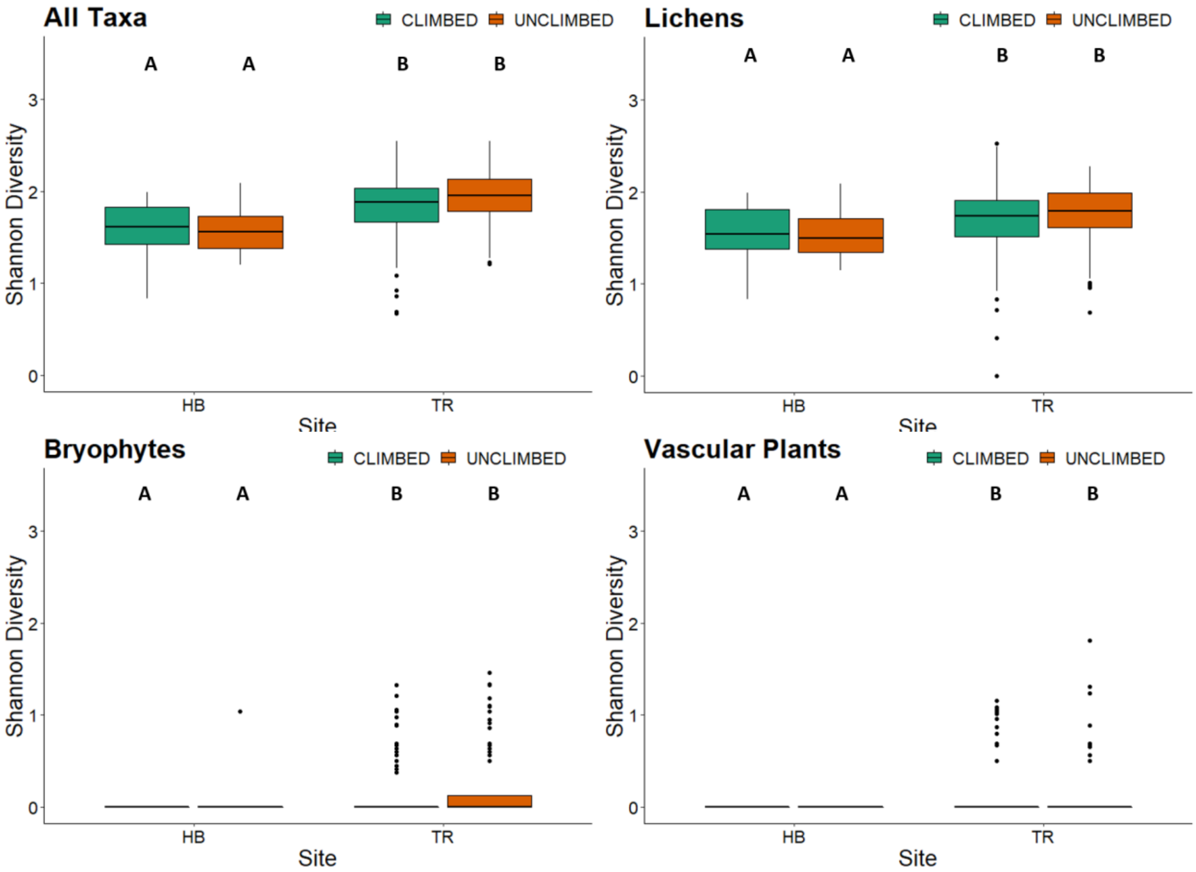

Figure 9. Shannon Diversity Index of all vegetation and taxa groups by climbing and site factors, statistically significant differences are indicated by letters. Overall, Table Rock had higher species diversity at than Hawksbill ($F_{1,330} = 49.6$, $P < 0.001$). Lichens accounted for most of the diversity due to their abundance. Both climbed and unclimbed plots at Table rock had higher lichen ($F_{1,330} = 11.8$, $P < 0.001$) and vascular plant ($F_{1,330} = 4.6$, $P < 0.05$) diversity than Hawksbill. Bryophyte diversity was highest on unclimbed plots at Table Rock ($F_{1,330} = 9.2$, $P < 0.01$).

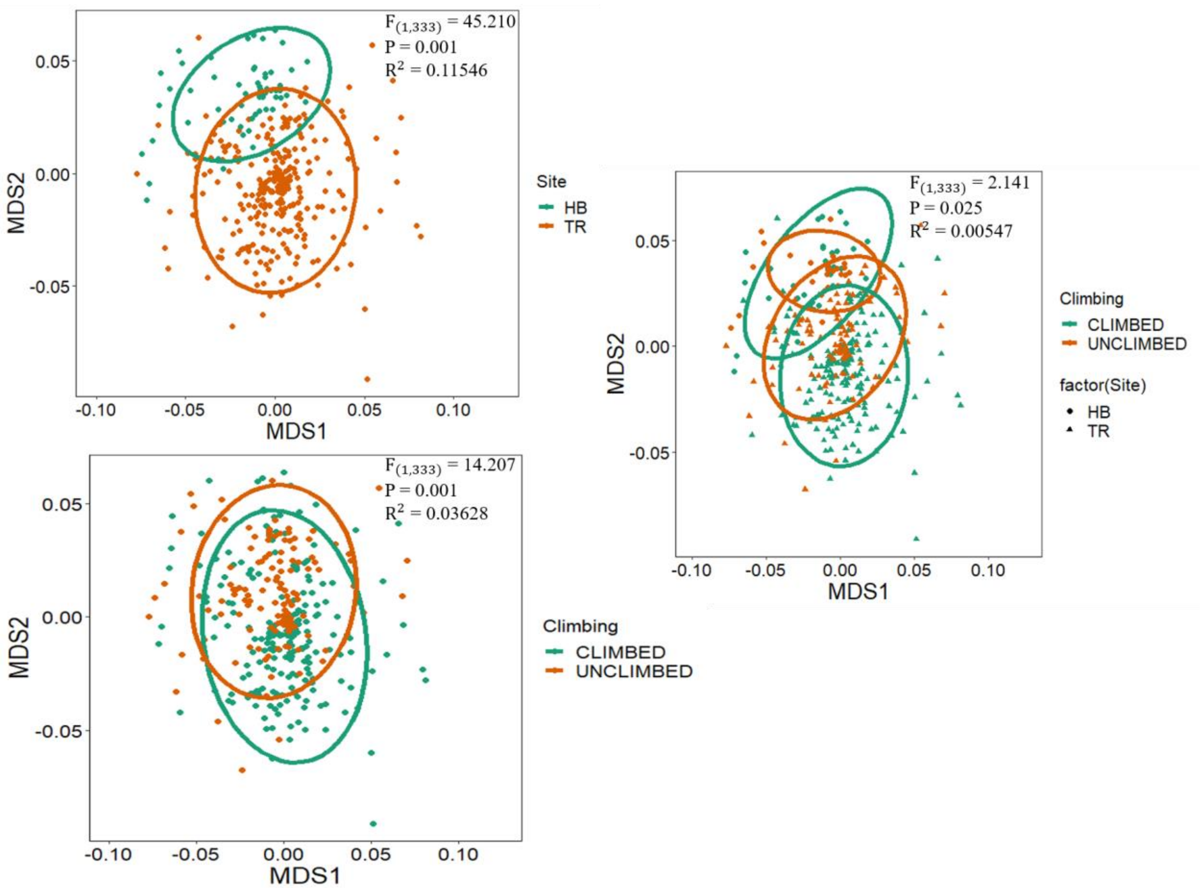

Figure 10. NMDS for all taxa with climbing and site factors with PERMANOA tests for statistical significance. Site ($F_{1,333}$= 45.2, P = 0.001, R^2 = 0.12) was more important in driving community variation than climbing impact ($F_{1,333}$= 17.2, P = 0.001, R^2 = 0.04). The interaction between climbing and site was statistically significant but with a low R^2 value ($F_{1,333}$= 2.1, P = 0.025, R^2 = 0.005). Clustering within the NMDS demonstrated that climbed plots at both sites were the most different from each other. Additionally, climbed plots were not clustered as a subset within unclimbed sites.

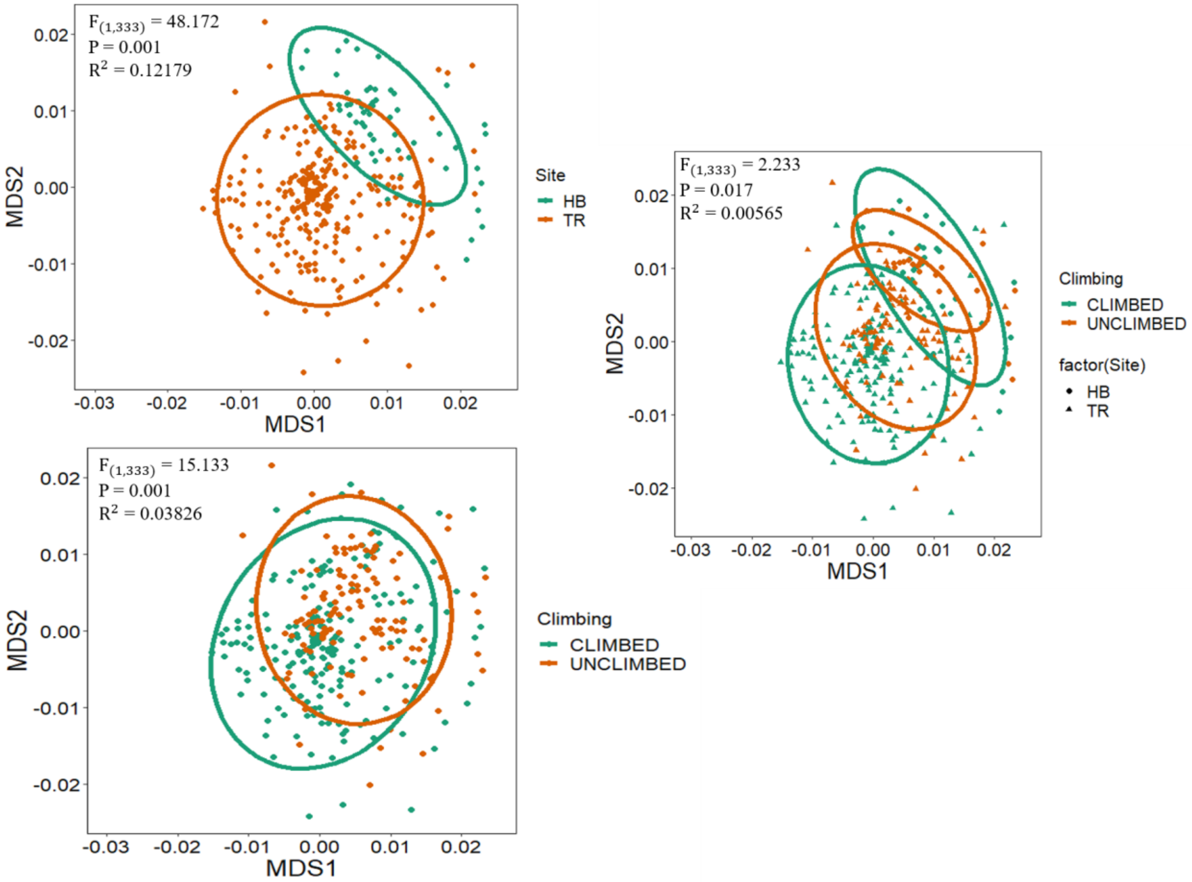

Figure 11. NMDS for only lichens with climbing and site factors with PERMANOA tests for statistical significance. An NMDS revealed similar patterns as observed with all taxa, but with weaker R^2 and significance. Differences were greater by site ($F_{1,333}$= 48.2, P = 0.001, R^2 = 0.0.12) than climbing impact ($F_{1,333}$= 15.1, P = 0.001, R^2 = 0.038) and climbed plots being the most different from each other when factors were combined ($F_{1,333}$= 2.2, P = 0.017, R^2 = 0.006).

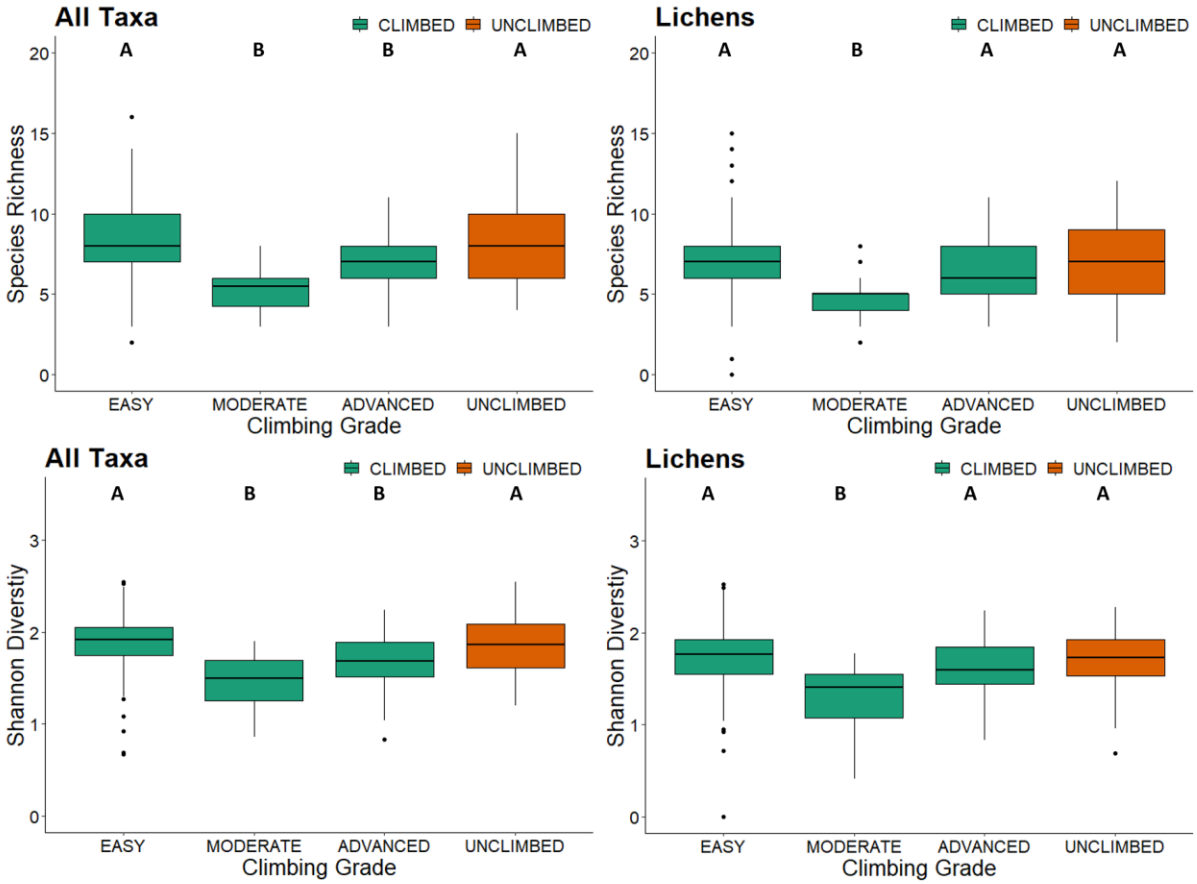

Figure 12. Shannon Diversity Index and species richness of all taxa and lichens only by climbing grade. Significance is shown by letters. Climbing routes were classified into three groups based on their YDS grade as reported by Lambert and Harrison (2002): ≤5.6 Beginner, 5.7–5.9 Moderate, 5.10-5.12 Advanced, ≥5.13: Professional. Climbing routes grouped into the "easy" grade, as well as unclimbed areas, had significantly higher species richness ($F_{3,330} = 11.4$, $P < 0.001$) and Shannon Diversity Index ($F_{3,330} = 14.2$, $P < 0.001$) than moderate and advanced climbing routes. Lichen species richness ($F_{3,330} = 5.9$, $P < 0.001$) and diversity ($F_{3,330} = 6.7$, $P < 0.001$) was significantly lower on moderate climbing routes than easy and advanced climbing routes, as well as unclimbed areas.

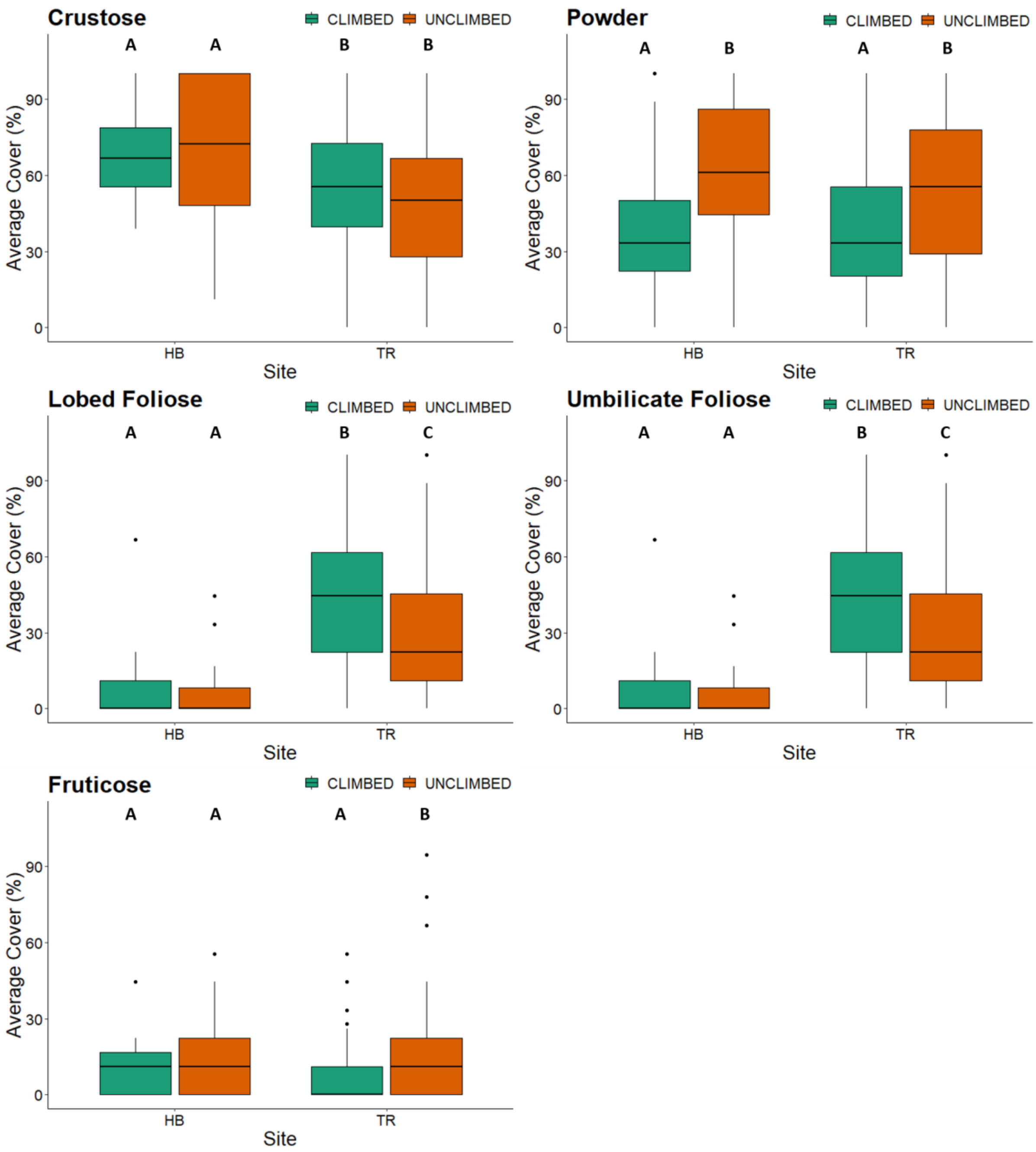

Figure 13. Average percent cover of lichen morphospecies (crust, powder, umbilicate foliose, lobed foliose, and fruticose), by site and climbing impact. Crustose lichens had higher coverage on Hawksbill Mountain than Table Rock ($F_{1, 330} = 18.2$, $P < 0.001$). Powder lichens had higher cover on unclimbed plots at both sites ($F_{1, 330} = 29.8$, $P < 0.001$). Both umbilicate ($F_{1, 330} = 7.05$, $P > 0.01$) and lobed foliose ($F_{1, 330} = 22.6$, $P > 0.001$) lichens has highest cover on climbed, followed by unclimbed plots at Table Rock, which were both higher than Hawksbill cover ($F_{1, 330} = 75.3$, $P > 0.001$). Unclimbed plots at Table Rock had the highest Fruticose lichen cover ($F_{1, 330} = 26.3$, $P > 0.001$).

Appendix A. Climbing routes surveyed. Location is either Hawksbill (HB) or Table Rock (TR) Mountain. For multipitch routes, all of the survey pitches which were surveyed are listed. Grade is on YDS, which is generally: ≤5.6 Beginner, 5.7–5.9 Moderate, 5.10-5.12 Advanced, ≥5.13 (Kuntz and Larson 2006). Stars is a scale of route quality and popularity, and is out of 5 with the highest stars being the most popular. Route name, pitch number, stars and grade were reported in Lambert and Harrison (2002) and supplemented by MountainProject.com. Sport climbing follows the path of preinstalled, permanent bolts, drilled into the rock face, whereas traditional ("Trad") climbing requires the placement of removable equipment into cliff features (Child 1998). Mixed is a combination of the two.

Climbing route name	Location	Survey pitch	Transect length (m)	Transect aspect (˚)	Total pitches	Grade	Stars	Route Type
Bongo Fury	HB	1	15	310	1	5.12-	2.5	Sport
If you Bolt it they will come	HB	1	20	310	1	5.10a	2.7	Sport
Psuedohardman	HB	1	14	310	1	5.11a	2.8	Sport
Tweakend	HB	1	13	310	1	5.12d	3	Sport
Block Route	TR	1	32	155	1	5.5	2.3	Trad
Cave Route	TR	1	23	120	2	5.5	2.3	Trad
		2	35	140	2	5.5	2.3	Trad
Fresh Garbage	TR	1 & 2	41	185	2	5.10a	1.7	Trad
Helmet Variation	TR	1 & 2	30	155	3	5.8	2.1	Trad
Jim Dandy	TR	1	25	155	3	5.4	2.6	Trad
		2	27	155	3	5.5	2.6	Trad
		3	22	135	3	5.5	2.6	Trad
My Route	TR	1	40	111	2	5.6	3.1	Trad
		2	35	111	2	5.6	3.1	Trad
North Ridge	TR	1	30	315	2	5.5	3.4	Trad
Slippin' into Darkness	TR	1 & 2	40	155	3	5.6	2.1	Trad
	TR	3	35	155	3	5.6	2.1	Trad
What's up Doc	TR	1	25	155	1	5.10d	3.2	Mixed
Wooly Aphid	TR	1 & 2	40	120	2	5.10a	2.5	Trad

CHAPTER 2:

A NOVEL APPROACH TO MODELING 3D FEFATURES OF CLIFF FACES USING STRUCUTRE-FROM-MOTION TECHNIQUES

ABSTRACT

Cliff ecosystems contain unique ecological communities that can harbor numerous rare and endemic flora, but are facing increased threats due to rock climbing. Surface heterogeneities such as crevices and ledges on the cliff face are critical in their ability to accumulate soil, water, and propagules for cliff-dwelling plants. Structure-from-Motion may provide an alternative field methods of quantifying surface heterogeneity by creating 3D models of the cliff face which can then be quantified, providing a more objective and reliable way of characterizing this parameter. Cliff face plots were surveyed for lichen, bryophyte, and vascular plant richness and diversity. Surface features (ledges, cracks, pockets) were measured and overlapping photos of each plot were taken. Point clouds, Digital Elevation Models (DEMs), and orthomosaic composite 3D images were created. Surface heterogeneity was calculated as the average, standard deviation, and coefficient of variation of four focal statistics for each plot at four different focal statistic neighborhood sizes. Roughness and average elevation at larger neighborhood cell sizes weakly correlated with surface area of all features as well as just crevices. Vascular plant richness and diversity was significantly correlated with a few measures of remotely modeled surface heterogeneity, which was consistent with predictions. Analyses may be more effective with larger neighborhood cell sizes or by combining with image classification. The methodology developed in this study will help lay the ground work for developing a novel structure-from-motion technique to

quantify spatial variability on cliff faces, which could lead to an increase in consistency among cliff ecology research methods.

INTRODUCTION

Cliff are unique ecosystems whose plant communities are not as well understood as those in terrestrial systems (Larson et al. 2000b). These communities typically lack the prevalent vascular flora found in terrestrial systems and have a prevalence of lichens and bryophytes (Larson et al. 2000b). Cliffs can support ancient forests and high levels of biodiversity, including large numbers of endangered, rare, and endemic species (Larson et al. 2000a, Kuntz and Larson 2006). Ecological succession appears to be arrested on cliff faces, in that the harsh environmental conditions prevent traditional successional processed and thus these communities maintain early successional stages all the time. Cliff-dwelling species are stress tolerant and dependent on low levels of disturbance.

Surface heterogeneity controls soil, water and propagule collection on cliff faces (Kuntz and Larson 2006). Bryophyte and vascular plant taxa are dependent on soil accumulation, and thus persist on cliff faces of low slope and high surface heterogeneity (Kuntz and Larson 2006; Clark and Hessl 2015). Saxicolous (rock-dwelling) lichen species are not dependent on soil accumulation and can persist on cliff faces with high aspect and low surface heterogeneity (Kuntz and Larson 2006).

Quantifying surface heterogeneity can prove challenging in practice and has not been consistently replicated among research groups (Kuntz and Larsen 2006; Clark and Hessl 2015, Spitale and Nascimbene, 2012; Carmo et al., 2016, Clark and Hessl 2015, Boggess et al. 2017). Farris (1998) first quantified microtopographic feature size, occurrence, and frequency on cliffs in Wisconsin and found that microtopographic features had unequal probabilities of supporting vegetation. The most extensive approach measured surface area and of each feature to calculated total abundance and total area or volume of features for each plot (Kuntz and Larson 2006). Methodologies are not consistent, which prevents comparing cliff communities among environmental and topographic variation (Holzschuh 2016).

Structure-from-motion (SfM) may provide an alternative and consistent method for quantifying spatial variability by creating 3D models of the cliff face (Westoby et al. 2012, Mertes et al. 2017). Traditional methods of 3D modeling require the 3D location of the camera and control points to be known (Westoby et al. 2012). In SfM, camera pose and scene geometry are reconstructed simultaneously through the automatic identification of matching features (tie points) in multiple images, allowing users an easy and efficient method to generate three-dimensional models from a series of overlapping, offset images. SfM is ideal for cost-effective projects in remote areas with difficult access (Westoby et al. 2012). In this study, I used SfM to create 3D models of survey plots and to calculate cliff surface heterogeneity. This novel technique has the opportunity to provide a straightforward and quantifiable measure of surface heterogeneity, which could be consistently replicated among other cliff systems.

MATERIALS & METHODS

Cliff-face field sampling

My study took place at Table Rock and Hawksbill Mountain in the Linville Gorge Wilderness Area (LGWA) of northwestern North Carolina (Burke County, 35.8910° N, 81.8829° W, elevation 4,101 feet). Plant community sampling followed a modified protocol as described in Chapter 1 (Figure 2). In brief, vascular plant, bryophyte, and lichen species were collected and ledge area (length, width) and pocket and crevice volume (length, width, depth) was measured within 1 m^2 survey plots which descended the cliff face. Slope of each plot and aspect and height of each transect were recorded.

I placed a unique, laminated Agisoft marker in the corner of each plot (Figure 2). Overlapping photographs from at least three angles of each pair of plots were taken using a DSLR camera. Care was taken to ensure that I captured sufficient overlapping of plot corners. Photos were visually inspected and removed if poor quality, out of focus, or had feet or legs of surveyors inside plots.

Modeling Surface Heterogeneity

Structure-from-motion was implemented using Agisoft PhotoScan Professional (V.1.3.4 64 bit; Agisoft LLC, St. Petersburg, Russia). Photos from each set of neighboring plots were uploaded and aligned using high quality and generic precision settings (Figure 3). I manually identified the eight markers per pair of plots (Figure 2, 3). In addition, if present, I created markers for any permanent and clear features, such as bolts. I manually corrected each marker's location in every photo. I then added a 1 m scale bar between two markers and an x, y, z location for each marker such that the z direction represents surface elevation and all plots were oriented in the same direction. The following x, y coordinates were added to each marker 1 (1, 1), 3 (2, 1), 5 (1, 2), 7 (2, 2), 9 (3, 1), 11 (4, 1), 13 (3, 2). 15 (4, 2). Z coordinates were all set to zero. I optimized camera angles using these new coordinates and scale bar. Next, I built a dense cloud using high quality settings and aggressive filtering. After visual inspection of each point cloud, I built the remaining data layers (mesh, texture, DEM, and orthomosaic) using batch processing (Figure 4). Final products (point cloud, DEM, and orthomosaic) were exported (Figure 5). Only area within survey plots was exported (using the local coordinate system for each marker), even though additional areas were modeled due to the overlapping nature of the initial photos.

Analysis of Models

All statistical analyses were conducted in R (v3.5.1). I partitioned plant community data into four groups: total taxa, vascular plants, bryophytes, and lichens and calculated species richness and Shannon's Diversity Index (H′) for each plot in package vegan (Chapter 1). DEMs were analyzed using packages ggmap, ggplot2, devtools, rgdal, sp, raster, and tmap. First, plot resolution and dimension were calculated. Due to high variability, plots were reclassified using aggregation to 0.25 cm cell size resolution. I performed standard focal statistics for each plot to measure heterogeneity: Terrain Roughness Index, Topographic Position Index, and roughness (Wilson et al. 2007). TRI (Terrain Ruggedness Index) is the mean of the absolute differences between the value of a cell and the value of its surrounding cells. TPI (Topographic Position Index) is the difference between the value of a cell and the mean value of its surrounding cells. Roughness is the difference between the maximum and the minimum value of a cell and its surrounding cells (Wilson et al. 2007). I also determined average elevation of surrounding cells. The size of surrounding cells were four different matrices: 3x3, 9x9, 21x21, 51x51. I calculated mean, standard deviation, and coefficient of variation for each roughness measure at each matrix size. In addition, I calculated a rumple index, which is a measure used in forestry applications to calculate forest canopy complexity by dividing ground by canopy surface area in lidar point clouds, using R package lidR.

I tested for correlation between all remotely modeled 3D measures (mean, standard deviation and coefficient of variation of TRI, TPI, roughness, elevation at four focal statistic sizes, and rumple index) to field measurements surface heterogeneity (count and total surface area per feature for all features, ledges, cracks, and pockets) in JMP Pro (13.0.0, 64 bit). I also explored 3D measures to plot species richness and diversity of all taxa, lichens, bryophytes, and vascular plants using linear regression. Only correlations with R greater than 0.40 were reported.

RESULTS

In total, 246 plots were photographed in the field and over 25,000 photos were processed, with 187 plots successfully modeled. Each pair of plots had on average ~100 photos, ranging from 75 to around 250 photos per plot, creating dense point clouds, DEMs, and orthomosaics. The original plot resolution was on average 0.06 (± 0.01) cm per point, with a range from 0.027 to 0.097. The original plot dimensions were 1712.5 (± 371.8) rows and columns, with a range from 1027 to 3635. Each plot had to be reclassified in groups of 4 (±1) cells, with a range from 3 to 9 cells to standardize resolution to 0.25 cm cell size. After reclassification, each plot had on average 397.9 (± 32.2) rows and columns, but ranged from 292 to 522.

Linear regression between field measurements of surface heterogeneity and 3D model surface heterogeneity revealed that total surface area of all features (ledge, crevice, and pockets) as well as only crevice surface area were weakly ($R = 0.42 – 0.56$) correlated with some remotely modeled measures of heterogeneity ($P < 0.05$, Table 1). At a 9x9 cell matrix size, only standard deviation of TRI was correlated with total feature surface area (Table 1). At the 21x21 cell matrix size, average TRI, standard deviation of Roughness, average elevation, and coefficient of variation were related to total feature surface area (Table 1). At the 51x51 cell matrix size, standard deviation of TPI, average and coefficient of variation of roughness, and average and standard deviation of elevation were related to total feature surface area (Table 1). Total crevice surface area relationships mirrored that of total feature surface area.

Vascular plant species and richness were correlated ($P < 0.0001$, $R > 0.40$) with average plot roughness at the 51x51 cell matrix size (Figure 6) and rumple index (Figure 7). Correlations between 3D models of surface heterogeneity were driven by two outlier points, so correlation lines are not displayed. None of the 3D modeling measures were significantly correlated with all taxa, lichen, and bryophyte richness or diversity.

DISCUSSION

Quantifying Surface Heterogeneity

Some of the remotely-modeled measures of surface heterogeneity were able to quantify variation in surface areas for all features and crevices. Roughness and elevation were the best methods for modeling surface heterogeneity, especially at larger cell matrix sizes. Of the methods explored for classifying model heterogeneity, roughness allowed for the widest range of values as it is a simple subtraction between the maximum and minimum value of a cell and its surrounding cells (Wilson et al. 2007). Simple measures of mean and standard deviation were best correlated to field measurements of surface heterogeneity. An additional approach that may be beneficial would be to select for cells which are the most rugged. The absolute value of elevation could be calculated, and cells which pass a certain threshold height could be deemed great enough to be a concave or convex feature. Total feature surface area would then be counted. This method of cell selection would only account for feature area and not necessarily magnitude. In addition, more complex spatial statistics, such as those used to interpretive airborne LIDAR point clouds, may better model cliff face surface heterogeneity (Doneus 2013). Openness highlights high and low (elevations) of each area (plot), and highlights features without degrading them in relation to topography. Positive openness account for large features, while negative openness is able to capture micro-topographic relief.

Ledges were the most abundant feature on cliff face plots, but ledge area was not significantly correlated with any of the 3D modeling measures. Ledges and crevices dimensions were measured differently in the field. Following Kuntz and Larson (2006), ledge length x width and crevice length x width x depth were measured to calculate area and volume, respectively. Measuring these dimensions may be effective in measuring the amount of surface area that could be colonized by cliff-dwelling plants. However, for the purposes of 3D modeling, a ledge is just a horizontal crevice, so both should be measured to the same extent (either area or volume). In future studies, features should not be broken up into feature classes, since differentiation can prove to be subjective in the field and may not vary in their ability to support cliff-dwelling vegetation.

Since cell size was standardized around 0.25 cm, the 21 and 51 cell matrices account for variation within 5.25 and 12.75 cm^2 areas, respectively. These 3D modeling measures will miss features and variability that occur outside that size range. For large features (i.e. 1 m wide ledges), indices only dectect the edges of variation (for instance, the corner of a ledge). Larger cell matrix sizes or implementing a buffer layer around selected cells may allow for more accurate modeling of these large features.

Remote measures of heterogeneity were significantly correlated with vascular plant richness and diversity. Vascular plants are the most dependent taxa on surface heterogeneities in the cliff face, as they rely on them to collect soil, water, and seeds (Kuntz and Larson 2006, Larson et al. 2000a, b). However, vascular plants were relatively rare on the cliff face in this study. Lichen richness and diversity was not correlated with remote measures of surface heterogeneity, since dominant growth forms on cliff faces are epilithic and do not require soil as a substrate and are thus less dependent on surface features (Kuntz and Larson 2006). Many bryophytes in my study were epipetric, meaning that they would not depend on surface features to accumulate soil and water (Kuntz and Larson 2006). Other important factors such as aspect, slope, and climbing presence have been shown to impact cliff community diversity and species richness and were not factored into this analysis (Kuntz and Larson 2006, Clark and Hessl 2015, Boggess et al. 2017).

Future Research Direction

Since 3D models were visible color, it may be possible to perform image classification to model biological species abundance, cover, and diversity. Some image analysis has been used in cliff ecology, but only to identify vascular plant species (Lortie et al. 2017). Cliff faces are dominated by non-vascular plants and lichens which are often cryptic and challenging to identify, even with thorough sampling. Image classification could be a mechanism to identity functional groups or morphospecies and estimate species richness. Nonetheless, remotely sensing richness and cover would still require field collections for ground-truthing, including creating a potential species list for a study site. Image classification could be optimized by combination with terrain analysis. For example, programs such as ENVI allow the user to select for topographic features, including peaks, ridges, passes, planes, channels, and pits. Other topographic measures, such as minimum and maximum curvature, and convexity may also be informative.

Since a majority of the plots surveyed were not blank rock faces, the surface of lichens and other cliff-dwelling species are being modeled, meaning that the DEMs created using structure-from-motion are actually Digital Surface Models (DSMs, Figure 6). In particular, many areas at Table Rock are characterized by large and abundant *Umbilicaria mammulata*, (Rock tripe, a foliose lichen) and tufts of *Selaginella tortilla* (a seedless vascular plant) and *Cladonia rangiferina* (Reindeer lichen, a fruticose lichen, Figure 8). These tufts are interesting and important biologically, but complicate modeling by covering the rock face (Figure 8). DSMs model the surface of both biotic and abiotic features, not just the bare rock.

There was high variability in the number of raw photos per plot, ranging from around 75 to over 250 photos per plot, which leads to varied point densities among plots. Plots with fewer photos contained more frequent gaps and holes. In addition, some plots were unsuccessfully modeled when there were insufficient photos from multiple angles. Photos were most useful for modeling when they included multiple markers in one photo so they can be references in space to other images. Photos needs to be taken at the same zoom level, with as much of the plot in focus as possible, but clear focus on the markers should be the priority. Taking sufficient quantity of photos, especially zoomed out and from different angles is challenging in the field since surveyors are rappelling very close to the cliff face.

This study sought to model a subset of the cliff face to correspond with vegetation survey plots. However, surveying the entire cliff face may allow us a better model of both micro and macro topographic feature influence on cliff plant communities. Pre-placed markers make modeling significantly more accurate, so surveying an entire cliff face would involve using multiple rappel lines to place markers all over the cliff, especially on topographically complex areas, and taking photos. Plot locations, especially on climbed routes, could be determined by measured distance to known markers or permanent features, such as bolts or prominent rock features. In addition, structure-from-motion photos are frequently captured using Unmanned Aircraft Systems (UAS, Westoby et al. 2012). However, UAS flight would be challenging to control near cliffs, especially near the base where cliff base canopy cover is often very close to the cliff face. Depending on the size of the cliff, a camera could also be mounted on a telescoping platform, such as those used in terrestrial lidar collection (Westoby et al. 2012).

The methodology developed in this study suggests that structure-from-motion is a valid methodology for quantifying cliff-face surface heterogeneity, though analysis of 3D models still needs to be explored. Creating 3D models will hopefully result in a corresponding increase in consistency among cliff ecology research methods. With more consistent methods, cliffs across broad climactic and geologic distributions could be compared and understood. Ultimately, improvements in survey methodologies could lead to more accurate management of threats, including rock climbing, to these unique ecosystems.

LITERATURE CITED

Boggess, L. M., G. L. Walker, and M. D. Madritch. 2017. Cliff flora of the Big South Fork National River and Recreation Area. Natural Areas Journal 37:200–211.

Clark, P., and A. Hessl. 2015. The effects of rock climbing on cliff-face vegetation. Applied Vegetation Science 18:705–715.

Doneus, M. 2013. Openness as Visualization Technique for Interpretative Mapping of Airborne Lidar Derived Digital Terrain Models. Remote Sensing 5: 6427-6442.

Farris, M. A. 1998. The effects of rock climbing on the vegetation of three Minnesota cliff systems. Canadian Journal of Botany 76:1981–1990.

Holzschuh, A. 2016. Does rock climbing threaten cliff biodiversity? - A critical review. Biological Conservation 204:153–162.

Kuntz, K. L., and D. W. Larson. 2006. Microtopographic control of vascular plant, bryophyte and lichen communities on cliff faces. Plant Ecology 185:239–253.

Larson, D. W., U. Matthes, J. A. Gerrath, N. W. K. Larson, J. M. Gerrath, J. C. Nekola, G. L. Walker, S. Porembski, and A. Charlton. 2000a. Evidence for the Widespread Occurrence of Ancient Forests on Cliffs. Journal of Biogeography 27:319–331.

Larson, D. W., U. Matthes, and P. E. Kelly. 2000b. Cliff ecology: pattern and process in cliff ecosystems. Cambridge University Press, Cambridge, UK ; New York.

Lortie, J., F. Serrano, A. Lorenzo, E. M. Canadas, M. Ballesteros, J. Penas. 2017. Rock climbing alters plant species composition, cover, and richness in Mediterranean limestone cliffs. PLOS One.

Mertes, J. R., J. D. Gulley, D. I. Benn, S. S. Thompson, and L. I. Nicholson. 2017. Using structure-from-motion to create glacier DEMs and orthoimagery from historical terrestrial and oblique aerial imagery. Earth Surface Processes and Landforms 42:2350–2364.

Wilson, M.F.J., O'Connell, B., Brown, C., Guinan, J.C., Grehan, A.J., 2007. Multiscale terrain analysis of multibeam bathymetry data for habitat mapping on the continental slope. Marine Geodesy 30: 3-35

Westoby, M.J., Braisington, J., Glasser, N.F., Hambrey, M.J., Reynolds, J.M. (2012). ‘Structure-from-Motion’ photogrammetry: A low-cost, effective tool for geoscience applications, Geomorphology 179: 300-314.

Table 1. Output of exploratory linear regression of field measurements of plot surface area for all features (ledge, crevice, and pockets) and only crevices, with R values only reported if above 0.4. All were statistically significant at p of 0.05. Feature counts and ledges and pockets were poorly correlated. Measures of roughness area Terrain Roughness Index (TRI), Topographic Position Index (TRI), Roughness, and average elevation (Elevation). Summary statistics are average (Avg), standard deviation (SD), and CV (coefficient of variation). Matrix size refers to the cell block in which focal statistics were performed.

Field measurement	3D model method	R
Total feature surface area		
	SD of TRI at 9x9 cell matrix size	0.4285
	Avg of TRI at 21x21 cell matrix size	0.4374
	SD of TPI at 51x51 cell matrix size	0.5031
	SD of Roughness at 21x21 cell matrix size	0.4742
	Avg of Roughness at 51x51 cell matrix size	0.5219
	CV of Roughness at 51x51 cell matrix size	0.4322
	Avg of Elevation at 21x21 cell matrix size	0.4489
	CV of Elevation at 21x21 cell matrix size	0.5633
	Avg of Elevation at 51x51 cell matrix size	0.5435
	SD of Elevation at 51x51 cell matrix size	0.5665
Total crevice surface area		
	SD of TRI at 9x9 cell matrix size	0.4198
	Avg of TRI at 21x21 cell matrix size	0.4254
	Avg of TRI at 51x51 cell matrix size	0.5108
	SD of TRI at 51x51 cell matrix size	0.428
	SD of TPI at 51x51 cell matrix size	0.4889
	SD of Roughness at 21x21 cell matrix size	0.4638
	Avg of Roughness at 51x51 cell matrix size	0.5081
	SD of Roughness at 51x51 cell matrix size	0.4186
	Avg of Elevation at 21x21 cell matrix size	0.4476
	SD of Elevation at 21x21 cell matrix size	0.5512
	Avg of Elevation at 51x51 cell matrix size	0.5399
	SD of Elevation at 51x51 cell matrix size	0.5564

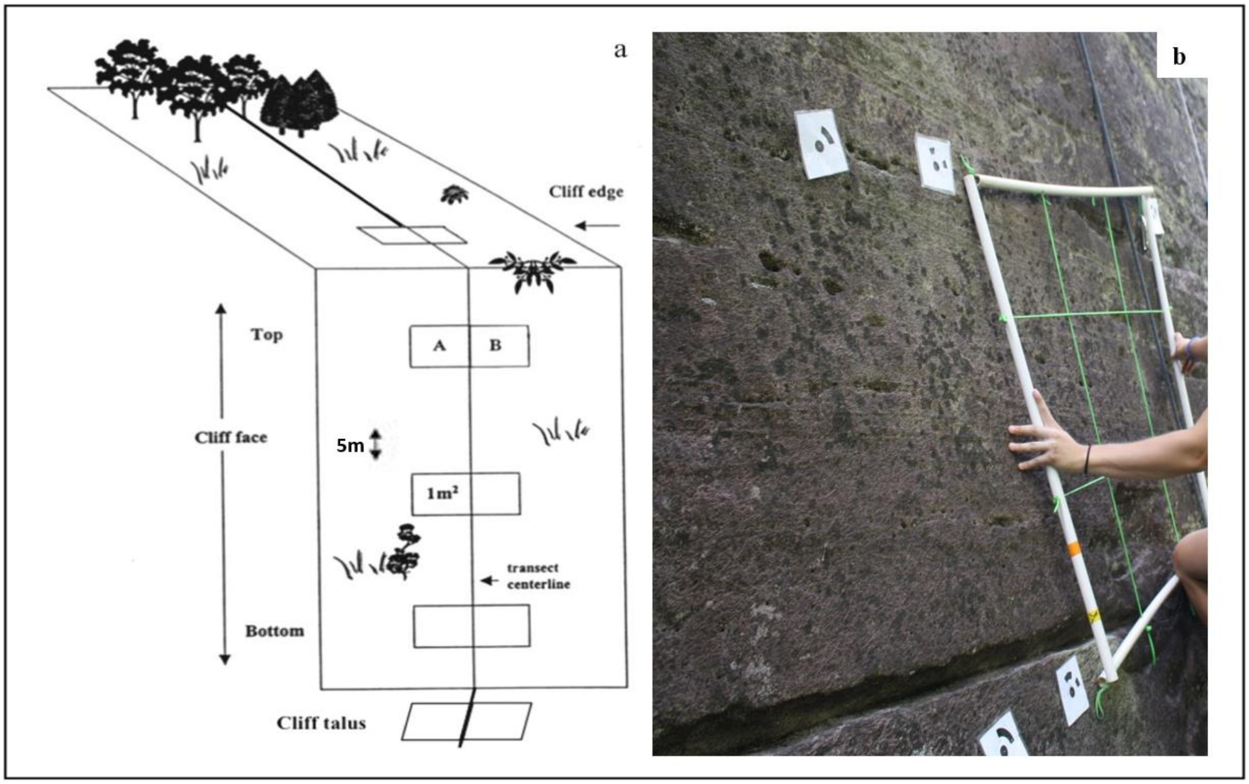

Figure 1. Diagram of a cliff face study system modified from Boggess et al. 2017. (a) 1 m^2 survey plots will be placed on both sides of the transect centerline (rappel line). Plots were placed at the plateau and talus of each transect, as well as every 5 m down the cliff face. (b) Photograph of 1 m^2 survey plot used, including nine sub-plots.

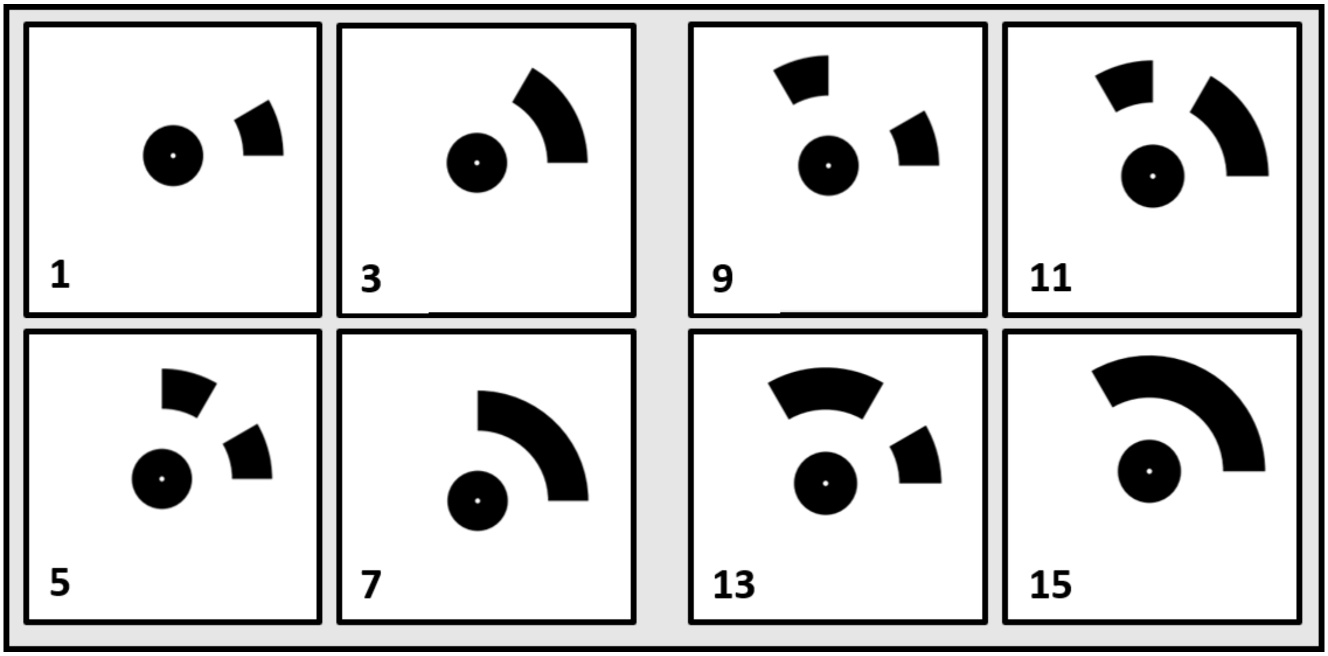

Figure 2. Markers placed at the corner of each 1x1 m quadrat. Photos were taken of neighboring quadrats (for a total of 1x2 m) from three angles. Each marker was laminated and attached to cliff faces with poster putty. In Agisoft, markers were identified in each photo that they were present. The following x, y coordinates were added to each marker 1 (1, 1), 3 (2, 1), 5 (1, 2), 7 (2, 2), 9 (3, 1), 11 (4, 1), 13 (3, 2). 15 (4, 2). Z coordinates for each marker was set to 0.

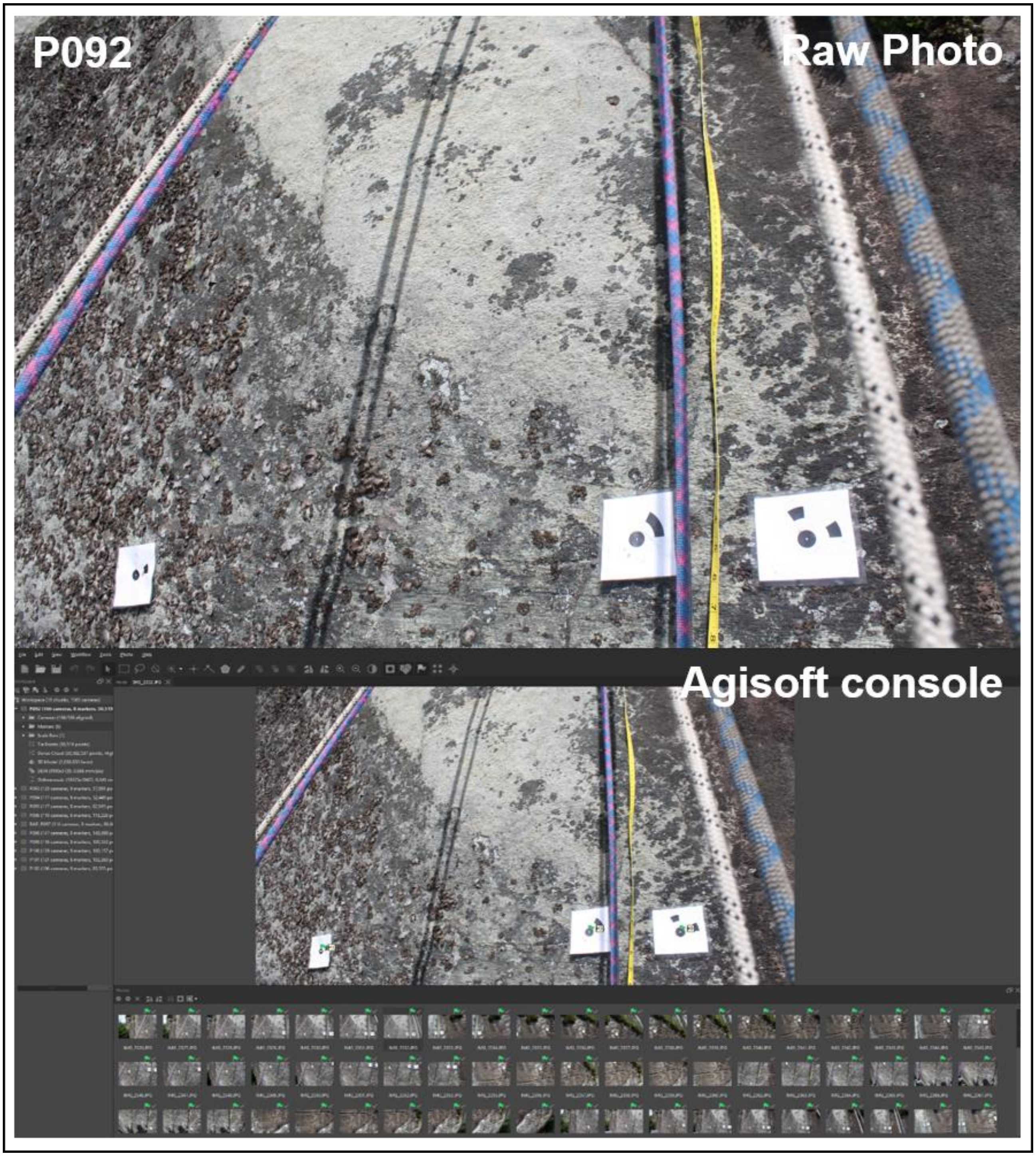

Figure 3. Processing photos collected in the field in Agisoft console. For each photo, markers (GPUs) were placed. Additional GPUs were added if other permanent and easily identifiable features were present, such as bolts used for rock climbing. After adding markers for all of the photos in one chunk, a scale bar and x,y locations for each marker was added. The example pictured here has 266 photos with the eight original markers.

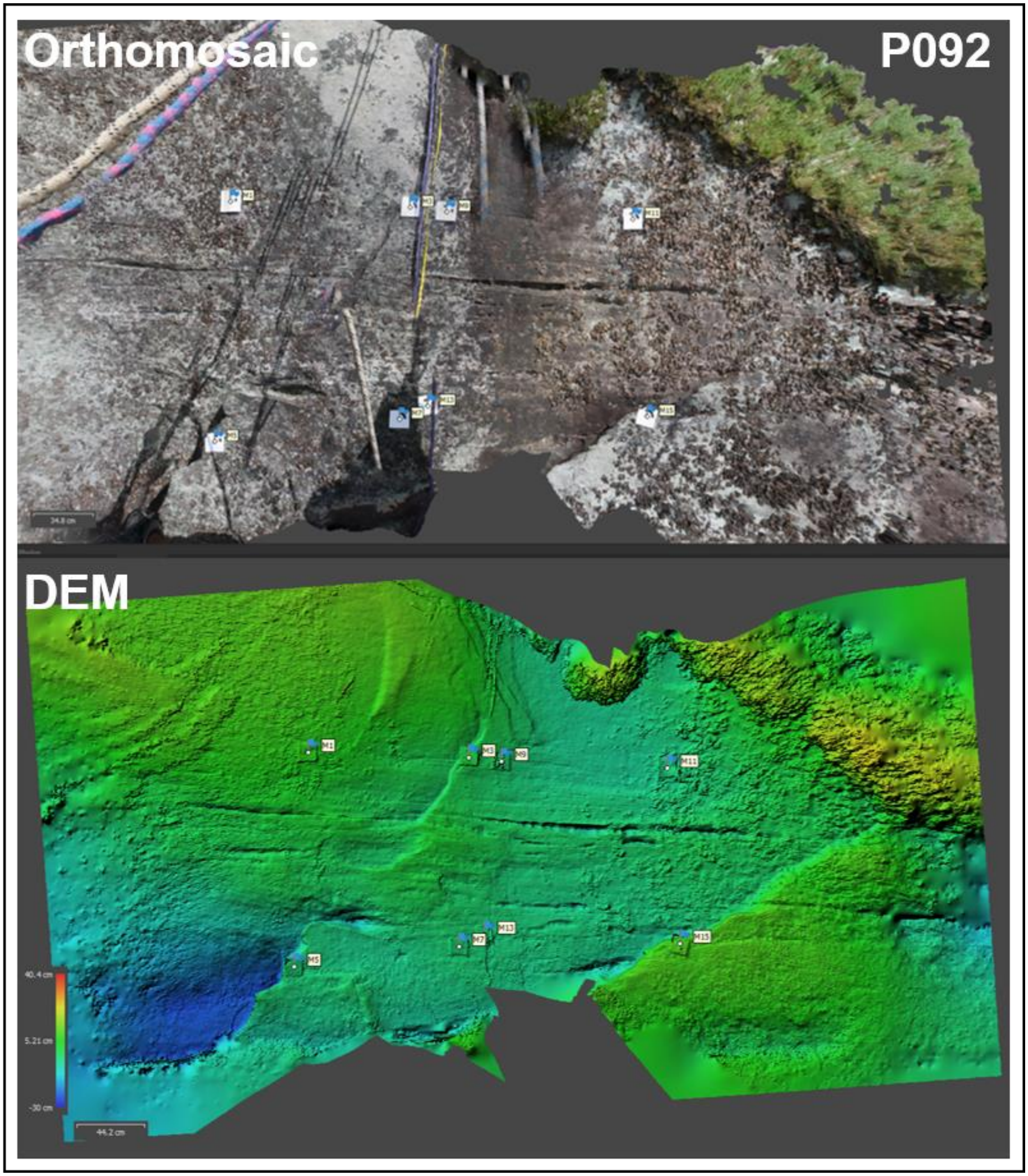

Figure 4. Orthomosaic and DEM as viewed in Agisoft, including scale bars in lower left corner. After this, 3D files need to be timed to each survey plot's boundaries, as indicated by markers. For the example pictured here, the high precision dense cloud created contained 30,580,537 points, 3D model contained 2,038,830 faces, DEM point spacing was 0.686 mm/pix and orthomosaic point spacing was 0.343 mm/pix.

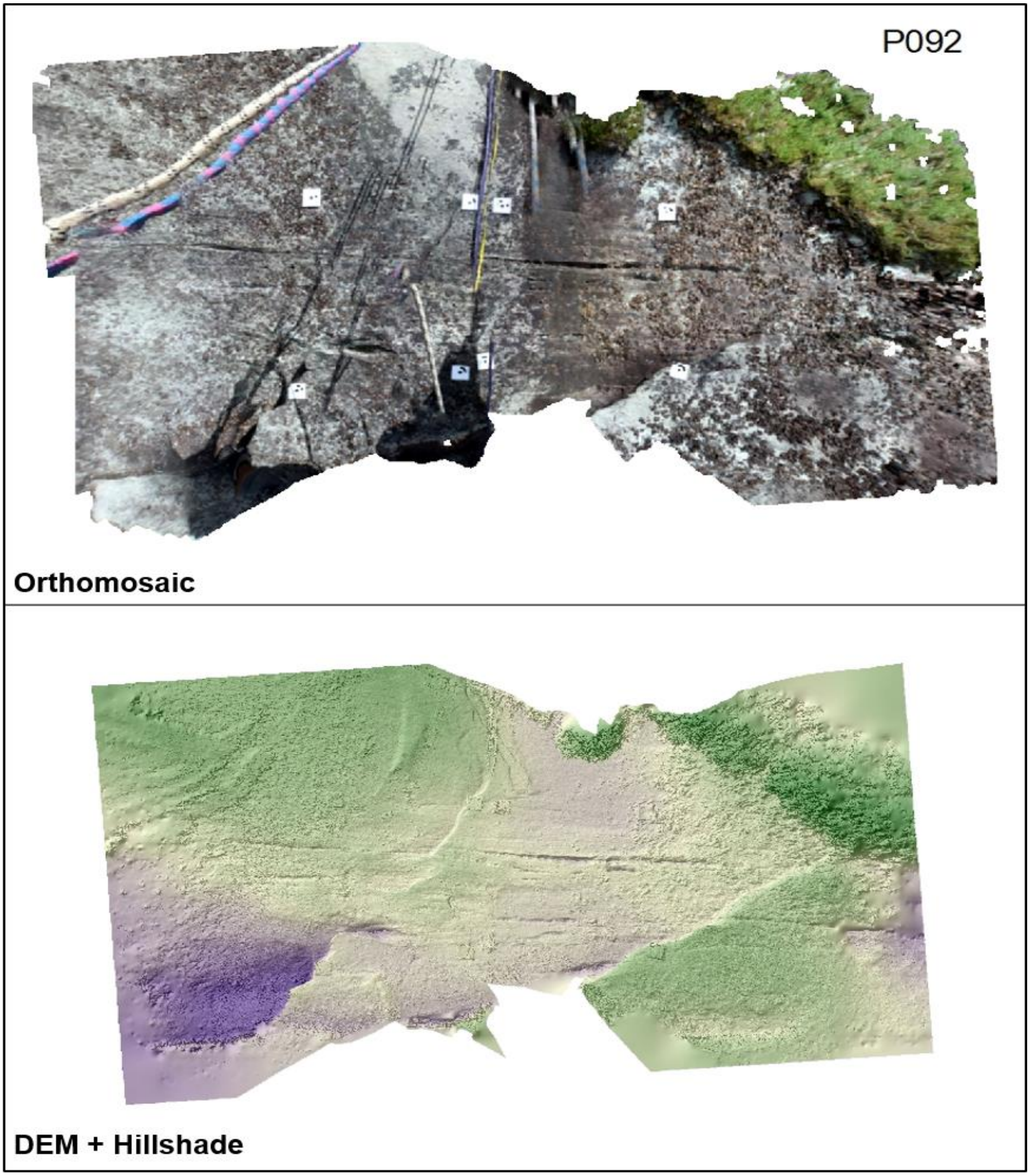

Figure 5. Orthomosaic and DEM as viewed in ArcMap. Models are not georeferenced and thus do not have scale bars. This plot occurred near the top of a climbing route at Hawksbill Mountain.

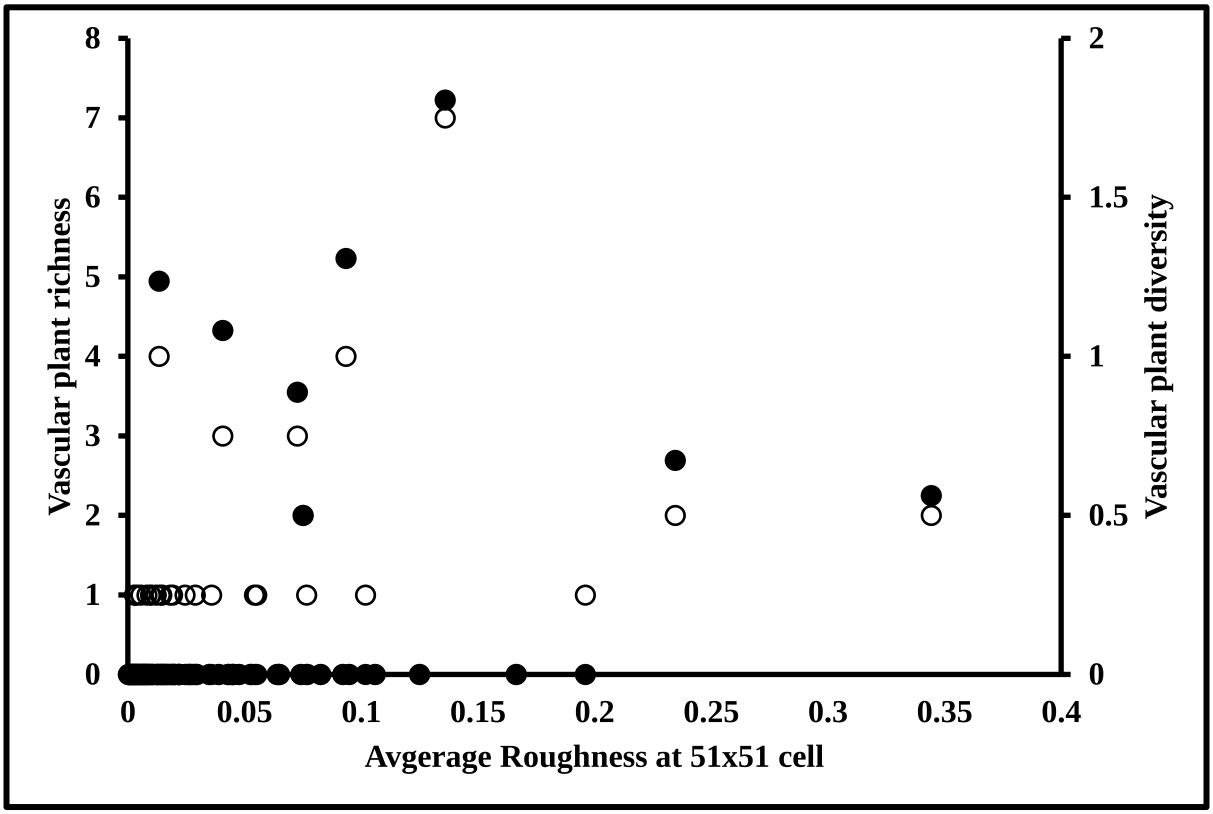

Figure 6. Average plot roughness within a 51x51 cell matrix size with vascular plant richness (empty circles) and diversity (filled circles, Shannon Diversity Index). Roughness is the difference between the maximum and the minimum value of a cell and its surrounding cells (Wilson et al. 2007). Plot resolution was reclassified (aggregated) to 0.25 cm cell size resolution.

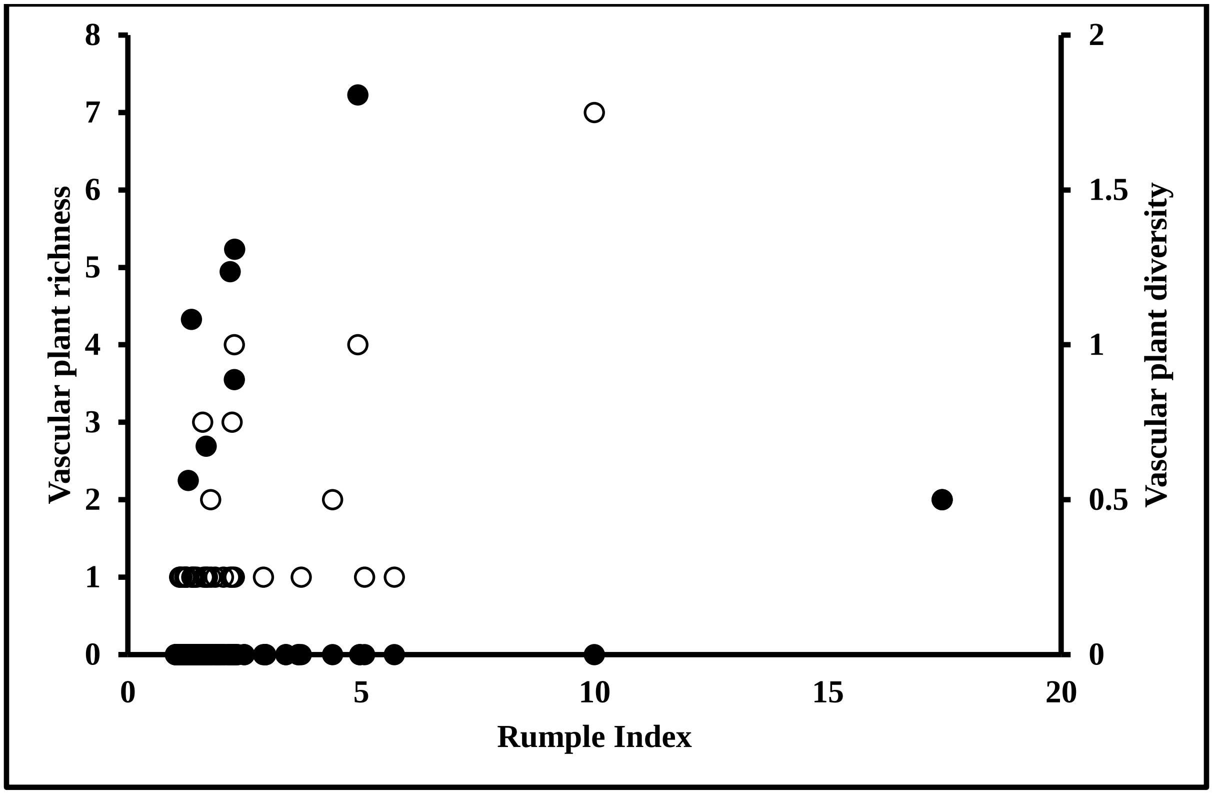

Figure 7. Linear regression of plot rumple index with vascular plant richness (open circles) and diversity (filled circles, Shannon Diversity Index). Rumple index is a measure of a complexity of a forest's canopy by dividing ground surface area by canopy surface area in lidar point clouds, using R package lidR.

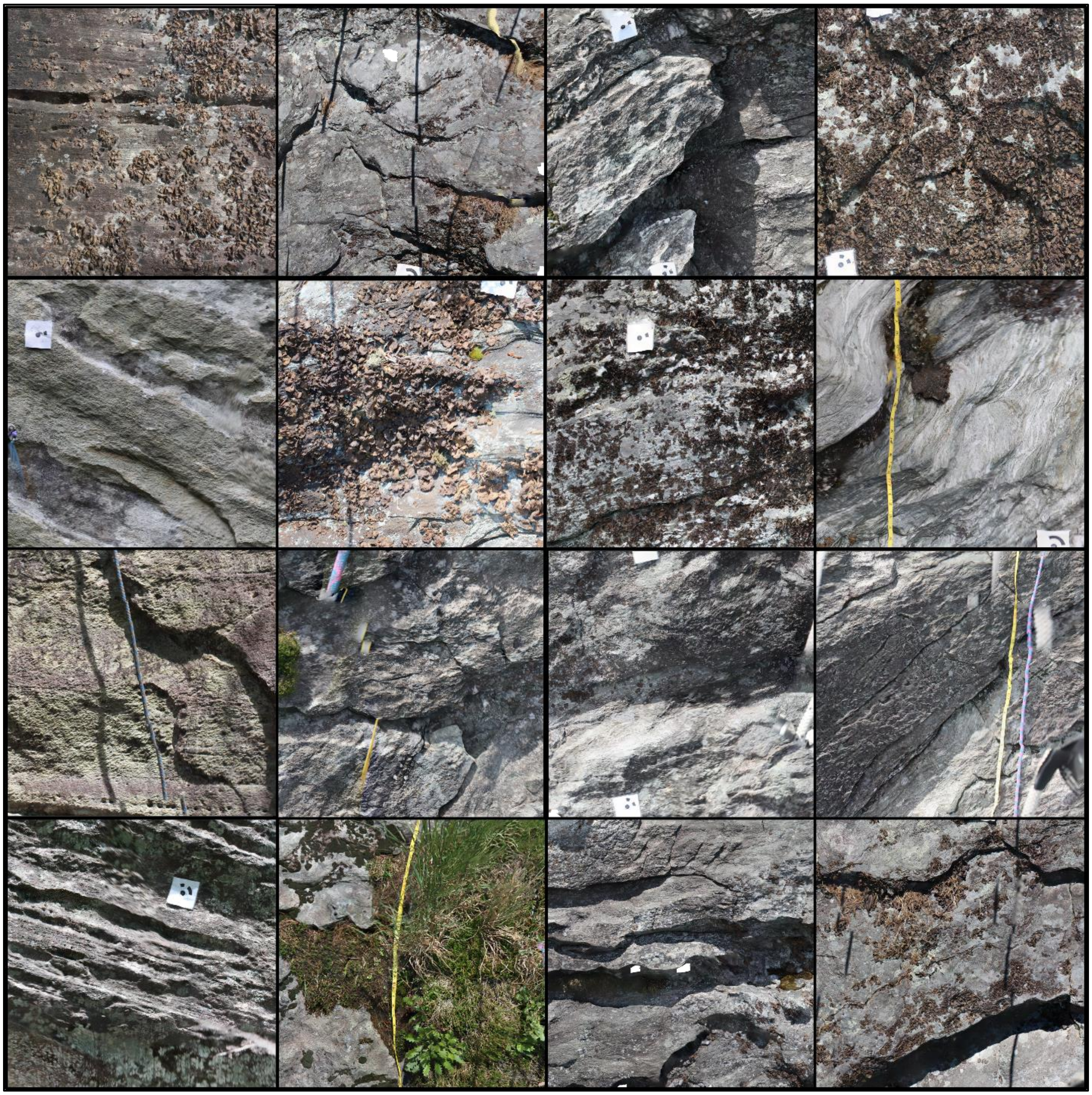

Figure 8. Photos of 16 orthomosaic (3d composite images) of cliff face plots at Table Rock and Hawksbill Mountain. Measuring tapes and climbing ropes are present in many of the photos and are unavoidable as a safety necessity during cliff field surveys. Orthomosaics were generated using structure-from-motion techniques.

Vita

Georgia Rae Harrison was raised on her family's sesquicentennial farm in Hopkins, Michigan. She worked at the Kalamazoo Nature Center as an environmental educator for five years and developed a love for teaching others about the natural world. Georgia moved to Michigan's Upper Peninsula in 2015 to attend Northern Michigan University. While at Northern, she studied biology and environmental sustainability, traveled to Zambia, Guatemala, and India and worked in community engagement and education. She researched cliff-dwelling lichens on the South Shore of Lake Superior and continued learning about life in the vertical realm during her Masters at Appalachian State University. Georgia is seeking wide open spaces and thus heading west to continue her education as a Ph.D. student in Plant Sciences at University of Idaho.