

SPECIES-AREA RELATIONSHIPS OF CLIFF SYSTEM VEGETATIONAL
COMMUNITIES IN CUMBERLAND GAP NATIONAL HISTORICAL PARK

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by
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Abstract

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Within the last three decades, cliff ecosystems have received increasing attention from ecologists. They are composed of distinct plant and lichen communities due to their unique physical conditions and reduced anthropogenic disturbance. Recent developments in cliff-face ecology focus mainly on the patterns and processes that determine plant community structure on cliffs. As recreational activities continue to pose a threat, understanding this ecosystem for preservation and management purposes has become a priority.

A vegetational survey of vascular plants, bryophytes, and lichens was conducted on eleven discrete cliff systems in Cumberland Gap National Historical Park (CUGA) during the summer of 2011 and 2012. Slope, aspect, and percent cover was measured along 25 individual transects among the cliff systems. A systematic protocol was used to sample each site, recording data from a 1 m² plot, at three meter increments. Species-area curves were constructed using PC-ORD and JMP. Multiresponse Permutation Procedures (MRPP) and Non-metric Multidimensional Scaling (NMS) were used to determine differences in community and diversity aspects.

A total of 231 species were collected and identified, including 111 vascular plants, 37 bryophytes, and 83 lichens. Non-nested and nested species-area curves indicate that the

sampling protocol was efficient at capturing diversity, and that larger cliff systems had higher levels of diversity. The steep slope of a generated log-transformed species-area curve, and the relatively low diversity compared to southern Appalachian forests, supports the hypothesis that cliff systems are similar to insular habitats. Multivariate analyses revealed that vascular plant, bryophyte, and lichen communities varied extensively across transects and cliff systems, largely unrelated to slope, aspect, or area. Based on these observations, it is imperative that each cliff site, and possibly each transect, be carefully surveyed before permitting recreational climbing. Several listed species were found during this survey, and all were established on smaller cliff systems. If the Park were most concerned with the protection of threatened, endangered, or disjunct species, it would be wise to preserve several small cliff systems, as opposed to a larger, more speciose cliff system.

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Table of Contents

Abstract.....	iv
Acknowledgments.....	vi
List of Tables.....	viii
List of Figures.....	ix
Introduction.....	1
Materials and Methods.....	9
Results.....	14
Discussion.....	33
Literature Cited.....	44
Appendix A – Species List.....	47
Appendix B – Enlarged Map.....	51
Biographical Sketch.....	52

List of Tables

Table 1. Comparison of the vascular plant, bryophyte, and lichen diversity between the current CUGA survey, White Rocks, and the Obed Wild and Scenic River cliff systems.....	14
Table 2. State and global conservation status for species of interest on cliff systems sampled in CUGA	17
Table 3. Site characteristics for each of the cliff systems sampled in CUGA. Cliff systems are listed by increasing area	18
Table 4. Expected species numbers using the first-order jackknife estimator.....	20
Table 5. MRPP results testing for differences between the cliff edge and the cliff face, among each of the eleven cliff systems, and among each of the 25 transects	22
Table 6. Canonical Correspondence Analysis (CCA) explaining how well environmental variables explain community structure.....	24

List of Figures

Figure 1. Attributes of a cliff system (Larson et al. 2000).....	1
Figure 2. Location of transects sampled in the current study (red triangles) and on White Rocks (blue circles)	9
Figure 3. Diagram of the sampling quadrat	10
Figure 4. Diagram of the sampling design (Smith 1998)	11
Figure 5. Species of interest on cliff systems sampled in CUGA.....	17
Figure 6. Non-nested species-area curve for cliff systems sampled in CUGA.....	19
Figure 7. Nested species-accumulation curves for cliff systems sampled in CUGA	20
Figure 8. NMS ordination comparing the edge plot with the face plots for the total species sampled on all eleven cliff systems in CUGA	26
Figure 9. NMS ordination comparing total species sampled across each of the eleven cliff systems in CUGA.....	27
Figure 10. NMS ordination comparing total species sampled across each of the 25 transects in CUGA.....	28
Figure 11. NMS ordination comparing total species sampled on transects with open and closed cliff-edge forest canopies in CUGA and White Rocks (Ballinger 2007).....	29

Introduction

Cliff systems can be found in nearly every ecosystem throughout the world. While there is no concrete definition that distinguishes a cliff from a steep, sloping bank, three distinct physical components are usually present. Larson et al. (2000) describe a cliff system as being a vertical rock outcrop with an edge, face, and talus. The cliff edge is the area at the top of a cliff, separating the upper ecosystem from the cliff face. The cliff face is the vertical element of the cliff. The talus is located at the base of the cliff and is usually containing rock fragments (Figure 1).

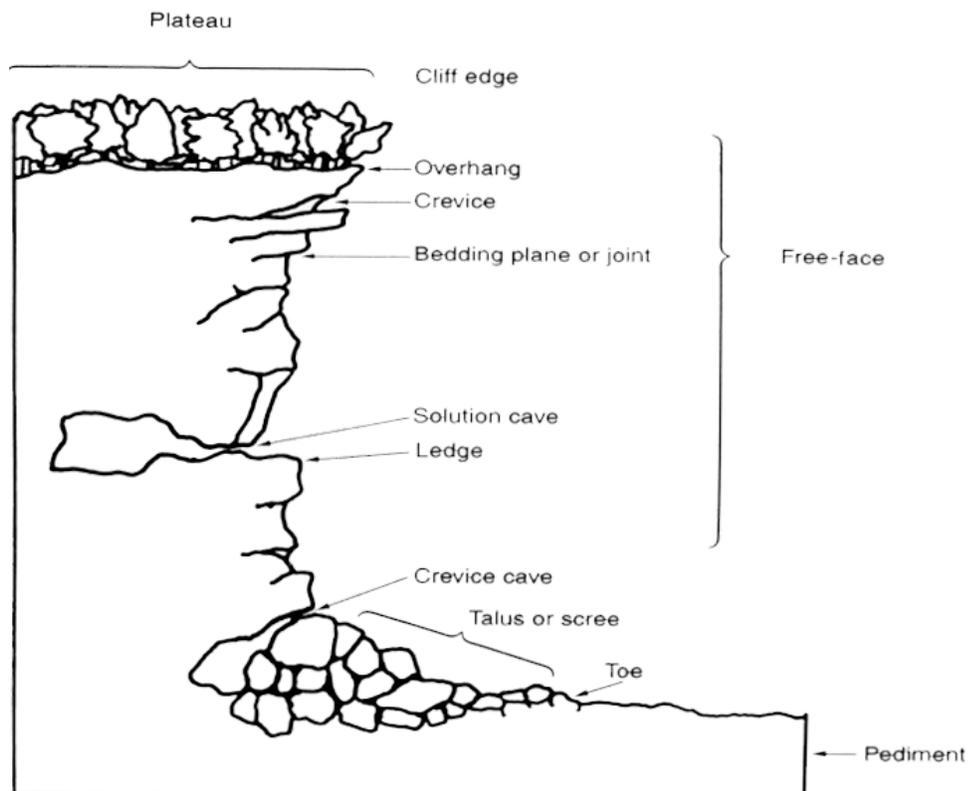


Figure 1. Attributes of a cliff system (Larson et al. 2000).

To the public, cliffs are sites of beauty and inspiration. They have become a focus for various activities; including photography, advertising, and recreational sports. In response, the establishment of national and state parks have preserved cliffs in their natural state (Larson et al. 2000). This, and their inaccessibility, provides researchers with cliff system study areas of relatively low human impact. Cliff faces along the Niagara Escarpment in Ontario, Canada for example, harbor some of the least disturbed and oldest growth forests in eastern North America (Booth and Larson 1998).

Cliff-Face Ecology

Prior to the 1980's, ecological research focused mainly on forests, deserts, oceans, tundra, wetlands, and grasslands (Larson et al. 2000). The lack of studies involving cliff systems is due, in part, to the idea that they were once considered an ecotone, or geological feature (Ursic et al. 1997). However today they are regarded as distinct and important ecosystems in their own right (Larson et al. 2000). Recent developments in climbing technology are partly responsible for the advancement of cliff-face ecology, making cliff faces safe for both recreation and biological investigations.

The Cliff-Face Ecology Research Group (CERG) from the University of Guelph in Canada has done some of the earliest work on cliff systems. The group was established by Dr. Doug Larson who led his team in various research areas investigating both physical and biological attributes, as well as plant community structure on cliff systems of the Niagara Escarpment in Southern Ontario, Canada. Larson et al. (1989) give the analogy that the physical and biological differences occurring between a cliff face and the surrounding ecosystem can be greater than the differences occurring between a forest and tundra ecosystem. This quick transition can be useful for studying how adjacent communities are assembled, whether initially through seed rain, or over time via competition and adaptation (Booth and Larson 1998). Specifically, Booth

and Larson (1998) were able to compare community assemblages of three distinct habitats over a horizontal distance of only a few meters, an opportunity available in only a few other habitats (i.e., rock outcrops).

Recent studies have revealed that the vertical orientation of a cliff face results in a challenging environment, characterized by varying temperatures, low nutrient availability and water flux, and almost non-existent soils (Bartlett and Larson 1990). This environment likely impacts species diversity and indirectly provides an important refuge from competitive exclusion for stress-tolerant species (Larson et al. 1989). *Thuja occidentalis* L., with a main range in boreal forests, is a classic example that utilizes cliff faces as a retreat from more competitively dominant species, especially in its southern, disjunct range (Walker 1987, Bartlett and Larson 1990). Cliff communities are known to harbor other disjunct species and relict plants of the Pleistocene glacial period occurring twenty thousand years ago, along with many rare and endemic species that may be absent from the surrounding landscape (Clebsch and Walker 1988). Several archetypal characteristics are prevalent of plants found on cliff faces. Slow growth and long-life spans provide a semi-closed system that likely excludes the immigration and establishment of new species (Booth and Larson 1998). An ecosystem with these characteristics is usually intolerant to high levels of disturbance and would likely be slow to recover from such events.

Climbing Impacts

As rock climbing and rappelling become more prevalent, it is important to understand how they will affect cliff-face plant communities. Farris (1998) demonstrated such disturbances to a cliff system and how it led to deterioration of particular aspects of the community. Abrasion of the rope along the face negatively impacted sensitive lichen communities and structures placed within the rock crevices removed important (scarce) soil and vegetation (Farris 1998). It

is also common for climbers and hikers to trample sensitive taxa in the talus area when they hike in and prepare for climbs, and on the cliff edge when they top off. The fruticose and foliose lichens were among the groups most impacted by climbing (Farris 1998). Other studies reveal an increase in abundance and diversity of crustose lichen in climbing routes (Smith 1998, Hill 2009). Many lichen populations serve as pioneer species on bare rock that contribute to the entire cliff community through rock weathering, fine, particulate organic matter production, and alterations in water chemistry. If keystone species such as these are disturbed, then the whole cliff community can be affected. McMillan and Larson (2002) revealed a similar effect of climbing on the vascular plant and bryophyte communities. As climbing increased, there was an overall decrease in percent cover of vegetation observed. Most climbing-related studies reveal that disturbed cliffs don't demonstrate complete species turnover in the presence of climbing, but instead only contain a subset of the original community found in similar, undisturbed cliffs (Kuntz and Larson 2006). This decrease in native species sometimes results in a proportional increase of invasive plants in the community (McMillan and Larson 2002). These climbing studies signify the great need for management plans in order to maintain the integrity of cliff ecosystems.

Species-Area Relationships

The majority of biological studies today employ models that interpolate data for entire communities based on a subset of data (Krishnamani 2004, Chung and Jang 2011). Cliff systems usually require more time and effort to sample than an equally-sized horizontal landscape, comparatively. Increased time and effort make it essential for researchers to utilize models to accurately and efficiently describe a cliff system. Arrhenius (1921) developed a well-known quantitative model that explains the correlation between species diversity and the area of their habitat. This relationship presented a practical way of understanding a system in terms of its

species richness and diversity based on its size. Under normal circumstances, the relationship demonstrates an increase in species with an increase in area, to a certain extent (MacArthur and Wilson 1963, Neigel 2003). The species-area curve is explained by the formula: $S = cA^z$, where S is the number of species, A is the area, c is a constant representing the y-intercept of the log-transformed plot, and z is a constant representing the slope of the log-transformed plot. The slope is most important for interpretive purposes and, depending on the habitat, usually falls within a set range of values. Species-area curves for insular habitats, such as mountaintops and islands, have slopes ranging from 0.20–0.40, whereas non-isolated habitats have a species-area curve with slopes ranging from 0.12–0.19 (MacArthur and Wilson 1967). The asymptote and slope of the curve suggest how diverse a system is and how quickly that diversity is achieved. Slope values also vary based on scale: local, regional, or continental. Local and continental habitats have a relatively steep slope, whereas regional habitats have a more gradual slope (Connor and McCoy 1979, Rosenzweig 1995).

Three main hypotheses have been proposed to explain the species-area relationship. The most parsimonious explanation proposed by MacArthur and Wilson (1963) states that an increase in area results in an increase in species. This is termed the *passive-sampling* hypothesis (Neigel 2003). The *habitat-diversity* hypothesis states that with an increase in area, not only is there an increase in habitat, but also in heterogeneity and niche diversification within the habitat (Williams 1943, Neigel 2003). The third hypothesis is the *equilibrium theory of island biogeography*, which incorporates the size and degree of isolation of an island (MacArthur and Wilson 1963). The number of species present on an island is influenced by the immigration and extinction rates of species. Islands that are closer to source populations would have a predictably higher immigration rate than those further away. Also, islands that are smaller in size have a higher risk of extinction of species by natural disasters, such as tsunamis or diseases. Most of MacArthur and Wilson's work was derived from their studies of island

biogeography and the processes that drive species abundance and distributions on oceanic islands. The term island can be used interchangeably to characterize any insular habitat surrounded by a sea of unsuitable habitat.

Prior to the present study, there have been no species-area statistics presented on cliff ecosystems. Observations from a preliminary study on a cliff system in Todd, NC conducted by a colleague and I, predicts that species-area curves of cliff systems in CUGA will behave similarly to species-area curves of oceanic islands (MacArthur and Wilson 1963, Marui et al. 2004, Triantis et al. 2008). Results from this preliminary study revealed a steep slope and rapid rise in species diversity along the curve. The data also demonstrated low species repetitiveness and the *relaxation effect* as described by Connor and McCoy (1979). This effect states that non-continuous habitats decrease in species diversity over time due to fragmentation and isolation. As one moves to a larger scale, previously documented species are found repeatedly due to an increase in recurring habitat types. This produces a curve that is much shallower. On an even larger continental scale, the slope becomes steep again as exotic and rare species, as well as differing biomes, are incorporated. These trends are not universal, but provide a good null hypothesis for comparative purposes. I hypothesize that since habitat heterogeneity and immigration and emigration rates are likely low on cliffs, the species-area relationship is most likely a product of the passive sampling hypothesis (Neigel 2003).

As climbing becomes more popular, the efficiency of sampling cliff systems is crucial for developing management plans for land managers to minimize recreational impacts. Species-area curves can be useful in developing climbing management plans by determining the appropriate habitat size for conservation prioritization. The SLOSS (**S**ingle **L**arge **O**r **S**everal **S**mall) debate represents the idea of preserving a habitat based on its area (Diamond, 1975). Both sides of the debate are important and usually emphasize the requirements of their focal species. A single large habitat is continuous, whereas several small habitats may offer a greater

diversity of niches. With several small habitats, more endemic species that require specialized niches may be protected (Losos and Ricklefs 2010). However, the non-continuous nature of the small fragments disregards the range requirements of larger animals, and may be inappropriate for extinction prone species (Neigel 2003, Losos and Ricklefs 2010). Creating web-like corridors between patches can alleviate some of the problems caused by fragmentation. By understanding the composition of a cliff community, researchers may be better able to determine the appropriate habitat necessary to preserve it. In general, simply preserving a habitat with the appropriate diversity and proportions of species seems to be more important than actual patch sizes (Losos and Ricklefs 2010).

Nested vs. Non-Nested Design

A nested design is an experimental design in which the first subplot builds upon itself until the entire study area is captured, accounting for total species accumulated by plot and not necessarily by area. A non-nested design uses subplots that are independent from one another, allowing more efficient surveys of larger study sites. It also relieves any non-independence issues with least square values of the slope (Leitner and Rosenzweig 1997).

There are several benefits to each type of design when conducting vascular plant surveys. Nested designs tend to be simpler and yield more consistent data collection than non-nested designs. Nested designs also allow for better comparisons of community richness, but in turn, restrict the size of the sampling area to subplots dependent on one another (Stohlgren et. al 1995). This can under-represent the heterogeneity of the landscape as spatial autocorrelation decreases, biasing the data around the first subplot (Stohlgren et. al 1995). Nested designs can sometimes give curves that over-represent the steepness of the slope and exhibit a more prominent asymptote (Rosenzweig 1995). For example, if a new habitat is breached as the study area expands then there will be a spike in species number based on habitat requirements.

The largest difference between the two designs is the amount of data that can be captured within the study area. Nested designs do not utilize the entire landscape pattern because it focuses on a central localized area, whereas non-nested designs cover a larger spatial extent while sacrificing the detail of the local site (Barnett and Stohlgren 2003).

The goal of this study was to collect species-area data from small, fragmented cliffs and larger, more continuous cliffs within the Park. Several questions will be addressed in this study.

1) Are the sub-sampling techniques presented in this study effective at capturing the diversity of a cliff system? 2) Can a useful species-area curve be applied to a cliff ecosystem? 3) Is area the most important driver of species diversity on a cliff? 4) Can the SLOSS debate be applied to a cliff ecosystem? 5) What biotic factors drive communities on a cliff? 6) What physical factors drive communities on a cliff? 7) What physical factors drive diversity on a cliff? 8) Is there a difference between the community composition of the cliff edge and the cliff face, among each transect, among each cliff system, or between open and closed cliff-edge forest canopies.

Materials and Methods

Study Site

Cumberland Gap National Historical Park (CUGA) is located on the escarpment of the Cumberland Plateau on the edge of the Ridge and Valley physiographic region, and at the state borders of Tennessee, Kentucky, and Virginia. The cliff systems within the Park are part of the Lee Formation, composed mainly of a sandstone conglomerate (Hinkle 1975, Rice 1984). The area receives an average of 127 cm of rain per year, with a humid climate that is typically five to ten degrees cooler than the surrounding lower elevations (Hinkle 1975).

Field Collections

The data from CUGA was collected in the summer of 2011 and 2012 by a team of cliff-face researchers from Appalachian State University (ASU) Department of Biology. Transects were placed along each cliff system depending on accessibility. Overhanging faces were not sampled because it was too difficult to collect complete samples from such approaches. A photograph and GPS coordinates were recorded at each transect location where the rappelling anchors were established (Figure 2). Area of the cliff face was then determined by measuring the height and width of the cliff face.

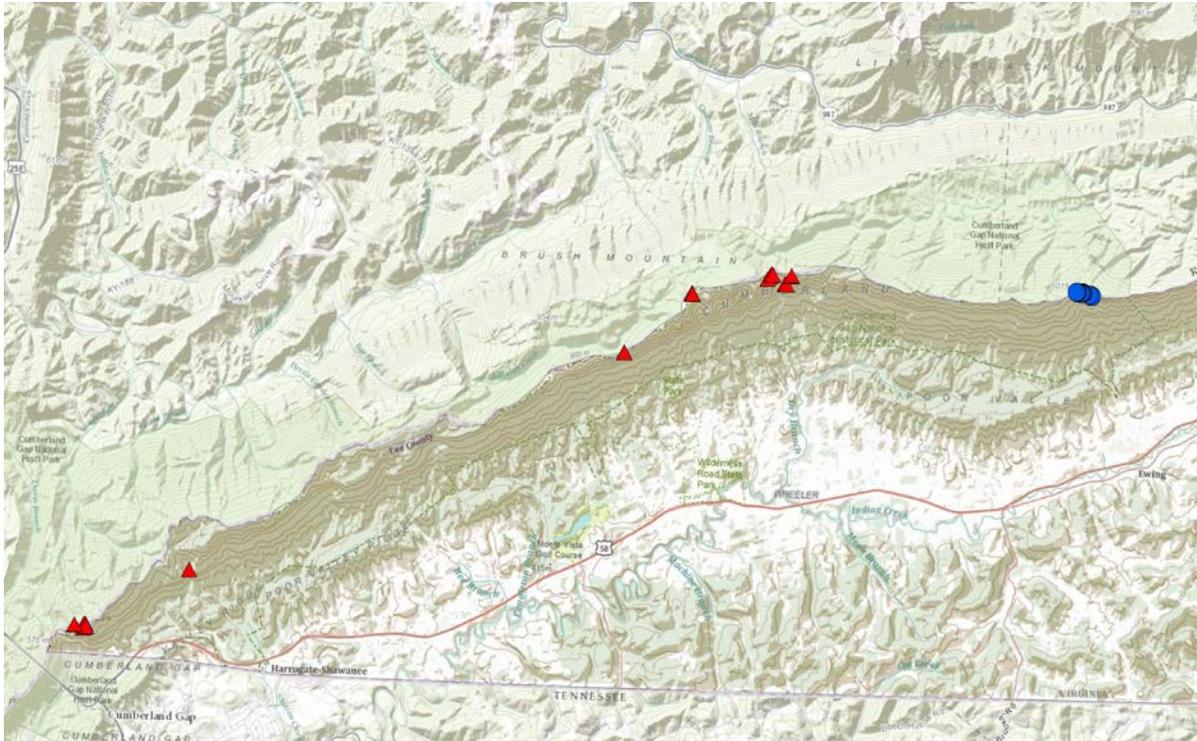


Figure 2. Location of transects sampled in the current study (red triangles) and on White Rocks (blue circles). An enlarged map can be found in Appendix B.

Samples of vascular plants, lichens, and bryophytes were collected along each transect beginning with one plot on the cliff edge, and every three meters along the cliff face thereafter, including one plot in the talus. Sample locations were delineated by a 1 m² plot constructed of PVC pipe (Figure 3). Each location had a Plot A and a Plot B, separated by the rappel line, left and right (Figure 4). Aspect and slope of the cliff face, and percent cover of each species were recorded in all plots. Percent cover was visually estimated, assuming that a hand-width is approximately three percent of the quadrat. Aspect and slope were measured with a compass and inclinometer respectively.

Aspects were converted to Northness and Eastness values for statistical analysis. Northness was calculated by taking the cosine of the aspect. North-facing cliffs received a value of 1 and south-facing cliffs received a value of -1. East-facing and west-facing cliffs both received

a value of 0. Eastness was calculated similarly by taking the sine of the aspect, except in this case, east-facing cliffs received a value of 1 (Roberts 1986).



Figure 3. Diagram of the sampling quadrat.

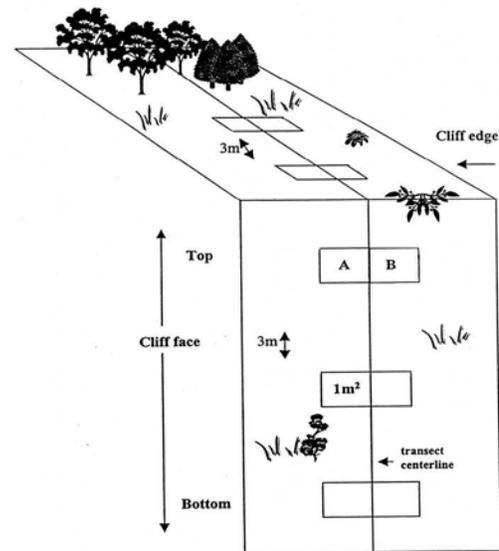


Figure 4. Diagram of the sampling design (Smith 1998).

Samples of vascular plants, bryophytes, and lichens were collected by hand, when possible, and put into plastic bags. Some species, especially crustose lichens, were collected with a hammer and rock chisel. Each bag was labeled describing a distinctive morphotype, transect number, and plot number. Corresponding descriptive data was recorded in a Rite-In-The-Rain field notebook. Each sample was chosen based on sexual maturity and then carefully removed to maintain its integrity. Repeated species were only collected once per transect. Vascular plants were pressed and dried, and the bryophytes and lichens placed into herbarium envelopes within 24 hours. The collected specimens were taken back to ASU for identification. Derrick Poindexter of Appalachian State University herbarium identified the vascular plants using Weakley (2006). Dr. Keith Bowman, bryologist, identified the mosses and liverworts using Stotler and Crandall-Stotler (1977). Dr. Coleman McCleneghan, a mycological consultant, identified the lichens using Brodo (2003).

Area of each cliff face was calculated from the height and width. Horizontal extent of the face was measured with a metric tape, and determined by cracks forming distinct vertical breaks that isolated the face. Vertical height was measured along each transect sampled by dropping a weight attached to a spool of 550-paracord down the cliff face. The paracord was then measured with a metric tape, and average vertical height was calculated.

Statistical Analyses

Non-nested species-area curves were constructed using JMP (10, SAS, Cary, NC) and nested species-accumulation curves were constructed using PC-ORD (6, MjM Software, Gleneden Beach, Oregon). Non-nested species-area curves were created with occurrence data and nested species-area curves created with percent cover data. Log-transformed species-area curves and their corresponding line equations and R^2 values were constructed in JMP.

Multiresponse Permutation Procedures (MRPP, PC-ORD) were used to describe variation in vegetational communities. This procedure is useful for testing differences among groups of entities in non-normal community data, either categorically or quantitatively (McCune and Grace 2002). Significant differences among groups within a dataset are measured by calculating the distances between each entity within the groups. It then analyzes intergroup differences among all possible variable combinations. If the variance of the intragroup distances is smaller than the variance of intergroup distances chosen at random, then the procedure will yield a significant MRPP. This analysis determined if plant communities on a cliff edge differed from those on a cliff face (cliff edge effect), differed by transect (transect effect), and differed by cliff system (cliff system effect). Differences between open and closed forest canopies along the cliff edge were also considered.

McCune and Grace (2002) explain the function of each variable reported in Table 5. The T statistic explains the separation between the groups being tested, with more negative values

having a greater separation. The A statistic explains the effect size. If all entities within a group are identical, then there is a large effect size ($A = 1$). If heterogeneity exists within the groups due to chance, then there is a small effect size ($A < 0$). Ecological data typically have an A value less than 0.1 (McCune and Grace 2002). MRPP p -values explain the likelihood that the observed difference is due to chance or statistical error ($p < 0.05$).

Significantly different groups determined by the MRPP's were further analyzed using the multivariate analyses Canonical Correspondence Analysis (CCA) and Nonmetric Multidimensional Scaling (NMS). CCA ordination reveals how well the environmental variables measured explain plant community structure. It assumes that the most important environmental variables have been considered, and that the data is unimodal (McCune and Grace 2002). Most CCA eigenvalues are misinterpreted, leading to faulty conclusions. The *percent of variance explained* tells how much of the community structure is explained by the environmental variables measured.

Non-metric Multidimensional Scaling (NMS) is most appropriate for community data that may be highly skewed, sparse, and non-normal (McCune and Grace 2002). It is a superior ordination compared to CCA and DCA and is ideal for interpreting community data, even when the important environmental variables possibly driving the data are unknown. NMS ordinations were used to visually represent the significant MRPPs and highlight comparative differences among groups. The Euclidian Distance Measure was used for each of the aforementioned tests. It calculates distance among entities using the Pythagorean theorem across multiple dimensions (Peck 2010). This distance measure is useful for sparse datasets containing many zeros.

Results

Species Richness

During the summer months of 2011 and 2012, a total of 215 different species of bryophytes, lichens, and vascular plants were collected from eleven discrete cliff systems in CUGA (Table 3). From these samples, 111 vascular plants, 37 bryophyte species, and 83 lichen species were identified (Appendix A). Mosses and liverworts were grouped together as bryophytes for all statistical analyses. Four species of special interest, one lichen and three vascular plants, were found on the cliff systems sampled in the Park (Table 2, Figure 5). Each cliff system is named in correspondence to the Park's trail guide (Table 3).

Table 1. Comparison of the vascular plant, bryophyte, and lichen diversity among the current CUGA survey, White Rocks, and the Obed Wild and Scenic River Cliff systems.

	Obed River Gorge (six cliff systems)	White Rocks (one cliff system)	CUGA (eleven cliff systems)
Total Vascular Plant Richness	58	14	111
Total Bryophyte Richness	65	9	37
Total Lichen Richness	47	48	83

Species of Interest

Ballinger (2007) revealed several previously undocumented, threatened, endangered, and arctic and boreal disjunct species on the White Rocks cliff system on the Cumberland Plateau Escarpment. The current study found four species of interest, one of which was reported by Ballinger (2007) occurring on the White Rocks cliff face.

Melampyrum lineare var. latifolium, narrowleaf cowwheat, is a member of the Scrophulariaceae listed as threatened in the State of Kentucky with a global rank of G5T5 (widespread and common) and a state rank of S2 (imperiled). It has an eastern distribution

from the mountains of North Georgia northward to Quebec and Ontario in Canada. It is an annual, herbaceous species listed as a facultative wetlands species. It is associated with dry, open, sandstone ridges, often with dry to dry-mesic second growth forests, along road edges and rock outcrops. It flowers from early June to late August. The populations of *Melampyrum lineare* var. *latifolium* were found along the cliff edge of two cliff systems. The population of this species at Upper Chadwell was estimated between 600 and 1000 individuals along the cliff edge. The Teaberry population was less abundant, with only around 50 individuals observed along the cliff edge. No individuals were seen on the cliff face or in the talus.

Dicchanthelium aciculare, needleleaf rosette grass, is a member of the Poaceae family listed as (E) endangered in the state of Tennessee under the common name of needleleaf witchgrass. It has a southeastern distribution from coastal Texas then northward to New York. This species is a county record, first documented, for the State of Virginia and represents a biogeographical disjunction, as the species range in that state is largely coastal plain and piedmont. It is also listed as a facultative wetlands species. Its habitat is usually sandy, xeric, open old fields and upland oak woodlands. It has graygreen foliage and green flowers with a rapid growth rate reaching a height of 0.3 meters. It blooms during the summer and is somewhat tolerant of shade but intolerant of fire. *Dicchanthelium aciculare* was collected at the Pinnacle; along the cliff edge of transects 17-19. There were approximately 20 individuals in clusters of 15 cm². A ledge about six meters down transect 17 had a colony of six individuals within a 1 m² area. Only one cluster was found directly on the cliff face and none in the talus.

Rhododendron carolinianum, Carolina azalea or Carolina rhododendron, is a perennial, mound-shaped evergreen shrub in the Ericaceae family growing from 1-2 m in height. It has a distribution that ranges from Tennessee, to North and South Carolina and with a northern disjunction in the State of Connecticut with regard to native populations but is in cultivation in many states. This is a state record for Virginia and the location in this study is very close (a few

meters) from the Kentucky state line where it would also constitute a state record. It is often found in full to partial shade, rooted in moist-well drained acidic soils, often on cliff faces and rock outcrops. It blooms in spring, bearing white to rose or lilac-rose colored funnel-shaped flowers in terminal clusters. It has dark green leaves that are aromatic when crushed and that have a purplish tinge in winter. Only one individual of *Rhododendron carolinianum* was noted on the cliff face at Ridge Trail 2. The extent was likely greater than this, but was difficult to identify since the rhododendron wasn't in bloom.

Cladonia pocillum, cup lichen, is found at the Teaberry cliff site in multiple transects there. It is a southern disjunct from a more boreal range and was part of a species group of boreal and arctic disjuncts found at White Rocks in the Ballinger (2007) study. *Cladonia pocillum* distribution is not tracked by the USDA. Arctic habitats are circumpolar and boreal habitats are high latitude or high elevation habitats. The extent of individuals of *Cladonia pocillum* wasn't measured, but they were only recorded on the cliff face at Teaberry along transects 7-9.



Figure 5. Species of interest on cliff systems sampled in CUGA. Clockwise from top left: *Melampyrum lineare* var. *latifolium* (Elaine Haug @ USDA-NRCS PLANTS Database), *Dicchanthelium aciculare* (James H. Miller @ USDA-NRCS PLANTS Database), *Rhododendron carolinianum* (Smithsonian Institution @ USDA-NRCS PLANTS Database), *Cladonia pocillum* (Sheri Hagwood @ USDA-NRCS PLANTS Database).

Table 2. State and global conservation status for species of interest on cliff systems sampled in CUGA. Rankings are derived from NatureServe (2012).

Species	KY State Rank	TN State Rank	VA State Rank	Global Rank
<i>Melampyrum lineare</i> var. <i>latifolium</i>	S2	SNR	S5	G5T5
<i>Dicchanthelium aciculare</i>	S3	S1	SNR	G5
<i>Rhododendron carolinianum</i>	-	SNR	-	G4
<i>Cladonia pocillum</i>	-	-	-	G4

Site Characteristics of Cliffs

The cliff systems surveyed in this study demonstrated substantial between-site variability with regards to slope, aspect, and area that may affect overall species diversity. Sampled cliff-face areas ranged from 683 m² (Ridge Trail 2) to 27,400 m² (Teaberry), across most aspects except due north (Table 3). The majority of the names assigned to each cliff system are based on the CUGA trail guide to assist the Park in management and conservation of particular species of interest.

Table 3. Site characteristics for each of the cliff system sampled in CUGA. Cliff systems are listed by increasing area.

Number	Cliff Site	Area (m²)	Northness	Eastness	Slope	Number of Species
1	Ridge Trail 2	683	-0.0497	-0.8248	51	19
2	Ridge Trail 1	1116	0.2467	-0.0545	68	12
3	Upper Chadwell	1195	0.4471	-0.1615	82	30
4	Lewis Hollow	2087	-0.2145	0.0237	55	24
5	Indian Rocks	2637	-0.1970	0.2318	65	41
6	Pinnacle Overlook	3641	0.0080	-0.1159	67	67
7	West Chadwell	9564	-0.1585	-0.3558	69	70
8	Skylight Cave	9639	-0.3637	-0.3323	68	30
9	Lower Chadwell	18064	-0.1487	-0.1876	71	57
10	Cumberland Trail	19685	-0.0131	-0.1757	76	48
11	Teaberry	27400	-0.1830	0.0843	72	69

Non-Nested Species-Area Curve

The non-nested species-area curve represents species occurrence on the y-axis and area in meters-squared on the x-axis (Figure 6). The curves for all groups approached asymptotes, indicating that our sampling process was sufficient at capturing the plant diversity on cliff systems sampled in the Park.

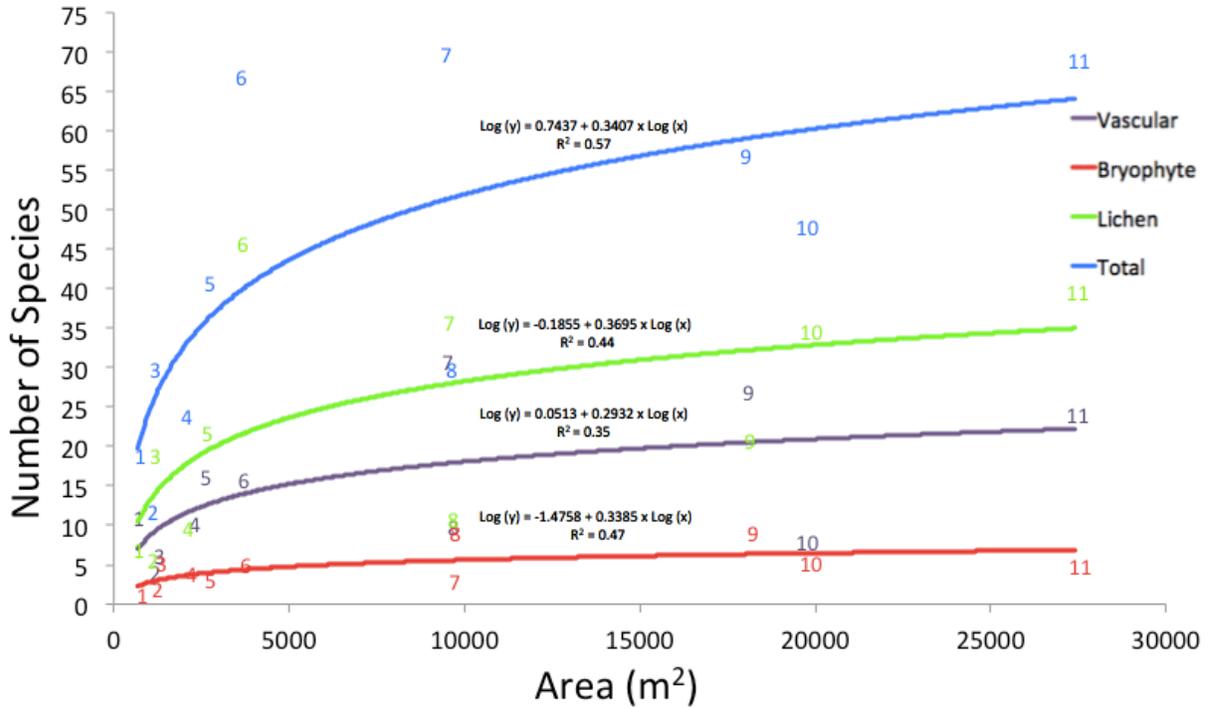


Figure 6. Non-nested species-area curves for cliff systems sampled in CUGA. Each number denotes an individual cliff system (Table 3) and each trend line corresponds to vascular, bryophyte, lichen, or total species.

Nested Species-Accumulation Curve

A nested species-area curve represents species accumulation per sampling effort (Figure 7). This type of design describes an area with non-independent subplots as opposed to disjunct subplots. This main purpose for this analysis was to obtain estimated species richness (Table 4). Estimated species richness was calculated using the first-order jackknife estimator in

PC-ORD (Table 4; Palmer 1990, Smith and Pontius 2006). This tool gives a calculated prediction of actual species richness that sub-sampling underestimates. The largest overestimate is seen in the lichen group, as observed species richness was only 57% of that estimated by the first-order jackknife. Expected species richness of vascular plants and bryophytes was much closer to the observed species richness.

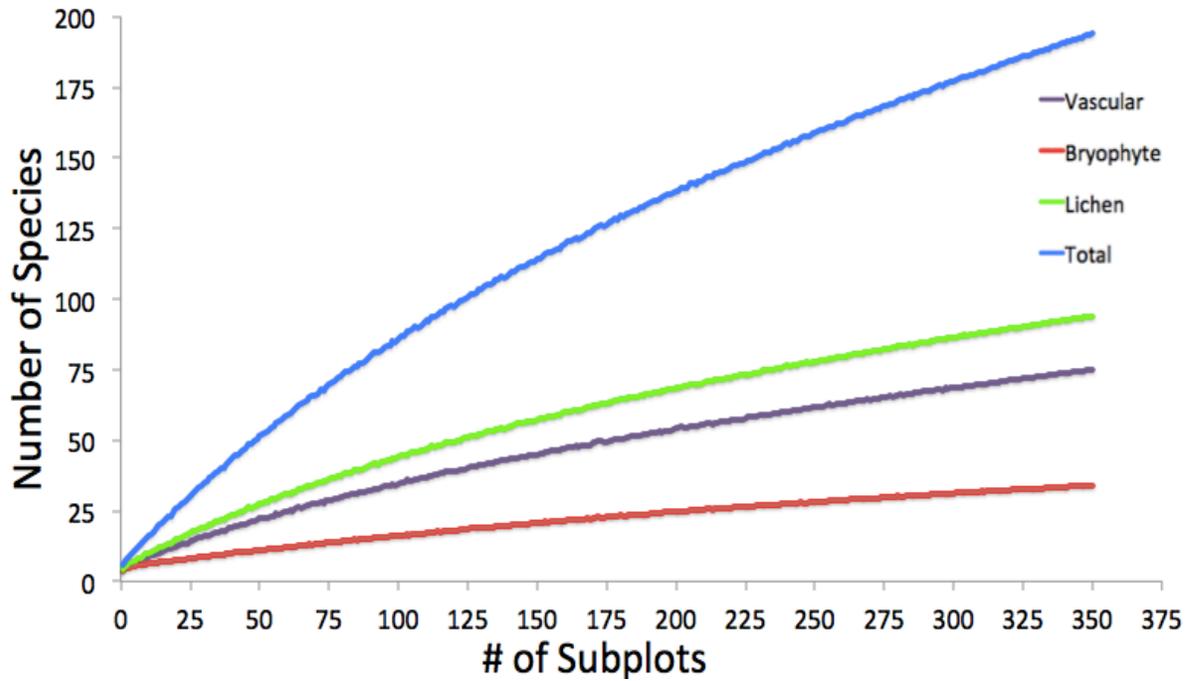


Figure 7. Nested species-accumulation curves for cliff systems sampled in CUGA. The four lines correspond to vascular plants, bryophytes, lichens, and total species.

Table 4. Expected species numbers using the first-order jackknife estimator.

Group	Observed Species Richness	Estimated Species Richness
Vascular	111	118
Bryophyte	37	52
Lichen	83	145
Total	231	315

General Linear Models

General Linear Models (GLM) were employed to model diversity with the environmental variables measured. Bivariate fit modeled a linear regression between any relationships that were significant. Eastness and bryophyte diversity were the only significantly correlated variables, and therefore no results were reported.

MRPP Analyses

Multiresponse Permutation Procedures (MRPP) were calculated in PC-ORD. These analyses were used to determine if plant communities on a cliff edge differed from those on a cliff face (cliff edge effect) and if communities differed by transect (transect effect). In addition, because several transects were used to survey contiguous cliffs, adjacent transects that covered continuous cliff systems were grouped, and MRPP was employed to determine if plant communities differed by cliff system (cliff system effect). Significant differences were detected for each of the four groups in all three treatments, except for differences in bryophytes found in the cliff edge and cliff face community.

Table 5. MRPP results testing for differences between the cliff edge and the cliff face, among each of the eleven cliff systems, and among each of the 25 transects.

Cliff Edge

Class	T	A	P
Vascular	-28.2	0.025	* $p < 0.001$
Bryophyte	-0.7	0.001	0.179
Lichen	-23.9	0.015	* $p < 0.001$
Total	-9.9	0.004	* $p < 0.001$

Transect

Vascular	-7.9	0.041	* $p < 0.001$
Bryophyte	-25.9	0.150	* $p < 0.001$
Lichen	-54.6	0.187	* $p < 0.001$
Total	-61.3	0.161	* $p < 0.001$

Cliff System

Vascular	-5.6	0.019	* $p < 0.001$
Bryophyte	-14.1	0.052	* $p < 0.001$
Lichen	-37.4	0.081	* $p < 0.001$
Total	-40.6	0.068	* $p < 0.001$

Canopy

Total	-13.1	0.092	* $p < 0.001$
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* Significant

CCA Ordination

Canonical Correspondence Analysis (CCA) was calculated for vascular plant, bryophyte, lichen, and total species datasets (Table 6). The *percent of variance explained* tells how much of the community structure is explained by the environmental variables measured. No figures are presented, since less than 5% of variance is explained for each of the three axes in all four datasets tested (Table 6). From these results, it is evident that only a small fraction of the community structure is driven by the physical factors reported.

Detrended Correspondence Analysis (DCA) was also considered and yielded results similar to CCA. It is not a recommended tool for community data analysis because the accuracy of the calculation varies, depending on the number of segments used for the analysis. According to McCune and Grace (2002), this ordination removes the arch effect that is apparent in some data sets by dividing Axis 1 into segments and then revolving the center data points of that segment around the 0 value of Axis 2. This essentially plots the data in a more linear fashion, making Axis 2 an artifact of the process and making it difficult to interpret distances between points (Hill and Gauch 1980, McCune and Grace 2002). For this reason, I chose to use NMS ordinations to explain the community structure differences.

Table 6. Canonical Correspondence Analysis (CCA) explaining how well environmental variables explain community structure.

		Axis 1	Axis 2	Axis 3
Vascular	<i>Eigenvalue</i>	0.604	0.277	0.214
	<i>% Variance Explained</i>	1.6	0.7	0.6
	<i>Cumulative % Explained</i>	1.6	2.3	2.9
Bryophyte	<i>Eigenvalue</i>	0.483	0.306	0.127
	<i>% Variance Explained</i>	2.1	1.3	0.5
	<i>Cumulative % Explained</i>	2.1	3.4	3.9
Lichen	<i>Eigenvalue</i>	0.22	0.112	0.075
	<i>% Variance Explained</i>	0.7	0.3	0.2
	<i>Cumulative % Explained</i>	0.7	1.0	1.2
Total	<i>Eigenvalue</i>	0.552	0.147	0.089
	<i>% Variance Explained</i>	1.1	0.3	0.2
	<i>Cumulative % Explained</i>	1.1	1.3	1.5

NMS Ordination

Non-Metric Multidimensional Scaling (NMS) was calculated for all sites yielding significant MRPP results (Table 5). Multiresponse Permutation Procedures only state that a significant difference is present, and NMS is useful for visually representing these differences. The figures that follow (Figures 7, 8, and 9) are representative of all eleven NMS ordinations calculated. Each of the four groups were tested for differences between the edge plots and the face plots (Figure 8), differences among cliff systems (Figure 9), and differences among transects (Figure 10).

The NMS ordination between the cliff edge and cliff face demonstrates that the communities are different from one another. The cliff-face community only comprises a small subset of the cliff-edge community (Figure 8), and the data supports the observation that cliff-edge ecosystems are different than cliff-face ecosystems. Since this study focused mainly on the cliff-face plant communities, all other statistical tests were analyzed using cliff-face plots only.

Useful NMS ordinations were also determined for cliff systems (Figure 9) and transects (Figure 10). Ellipses in both graphs overly crowd in the figure, but the size and distribution of the ellipses can allude to some differences detected by the MRPP analyses. For example, cliff systems 4, 10, and 11 supports vastly different plant communities, regardless of the overlapping nature of the ellipsoids (Figure 9). Some overlap may be an artifact of the figure being a two dimensional representation.

The NMS ordination showing differences among open and closed cliff-edge forest canopies is perhaps the most visually useful (Figure 11). There is distinct clustering and separation among the sites with open and closed canopies that represents significant differences between the two entities. There is minimal overlap within the dataset, and the Pinnacle site represents one of the distinctive outliers.

Biplot vectors were insignificant on all of the NMS ordinations since the environmental variables that we measured did not drive variation in the communities. None of the environmental variables met the standard R^2 cutoff threshold ($R^2 < 0.10$) for the ordinations testing for transect differences and cliff-system differences. Cumulative variation explained by Axis 1 and Axis 2 was 82 percent for all eleven NMS ordinations.

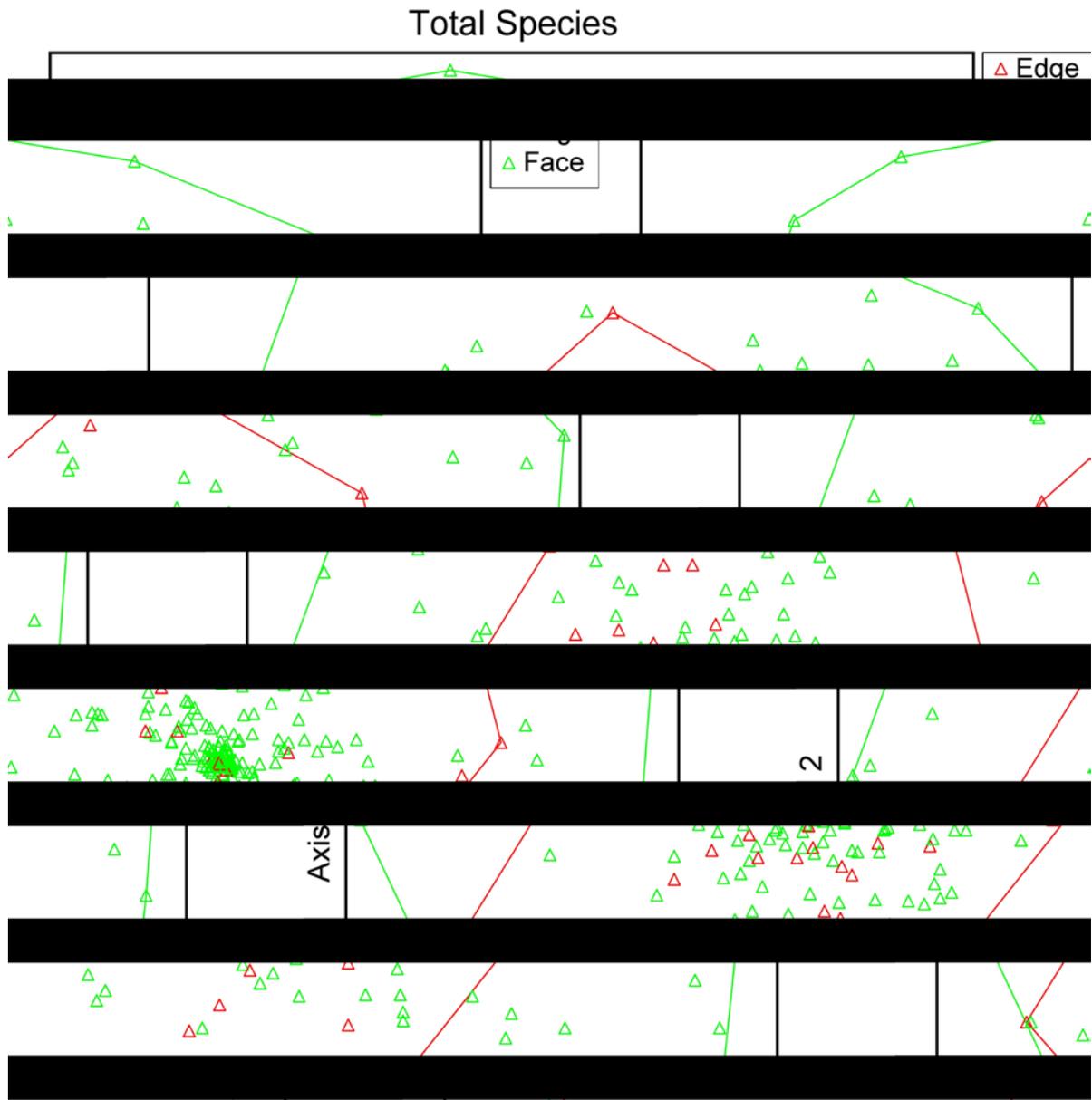


Figure 8. NMS ordination comparing the edge plots with the face plots for the total species sampled on the eleven cliff systems in CUGA. Edge plots are denoted by the red triangles and face plots are denoted by the green triangles.

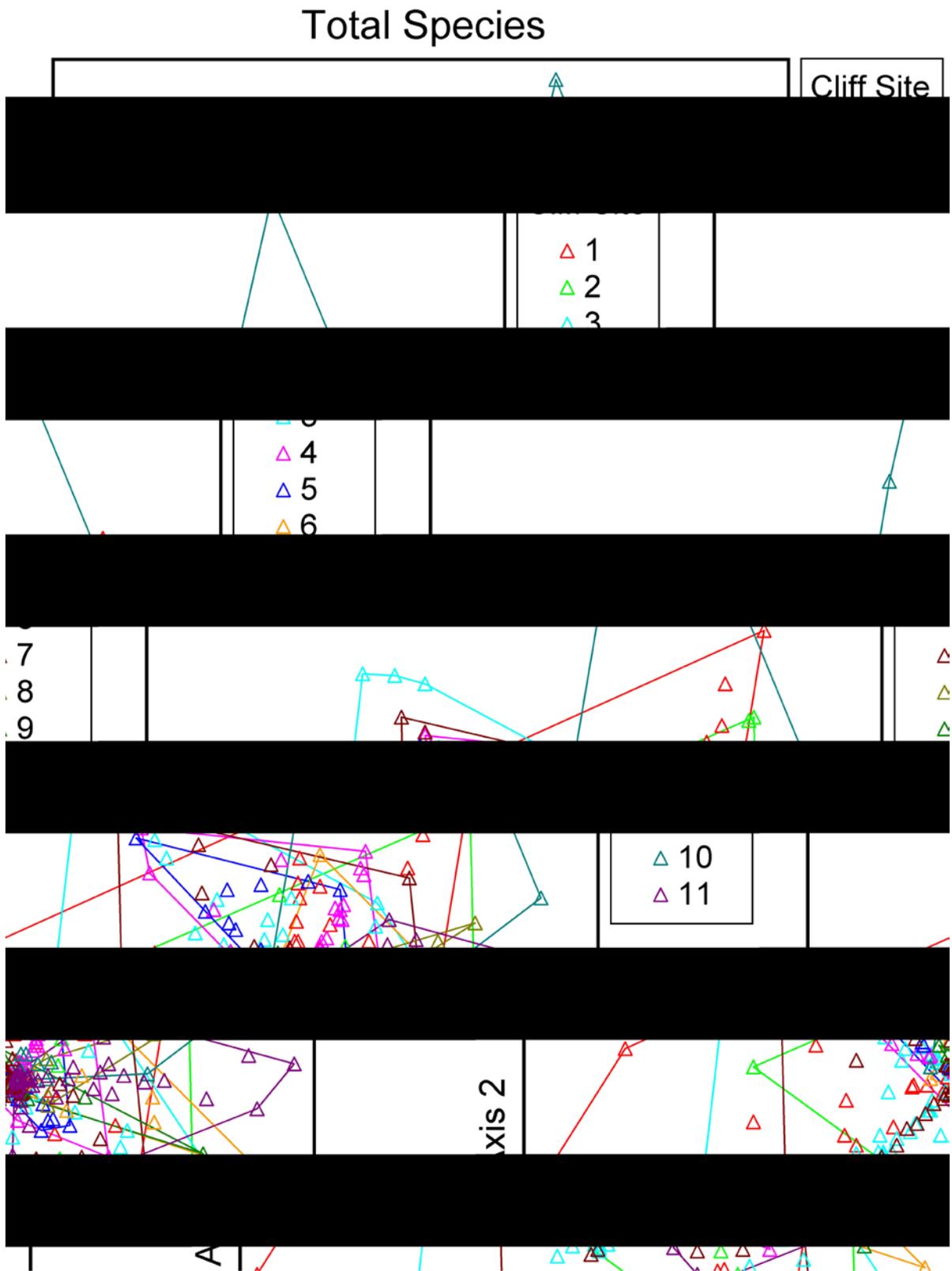


Figure 9. NMS ordination comparing total species sampled across each of the eleven cliff systems in CUGA.

Total Species

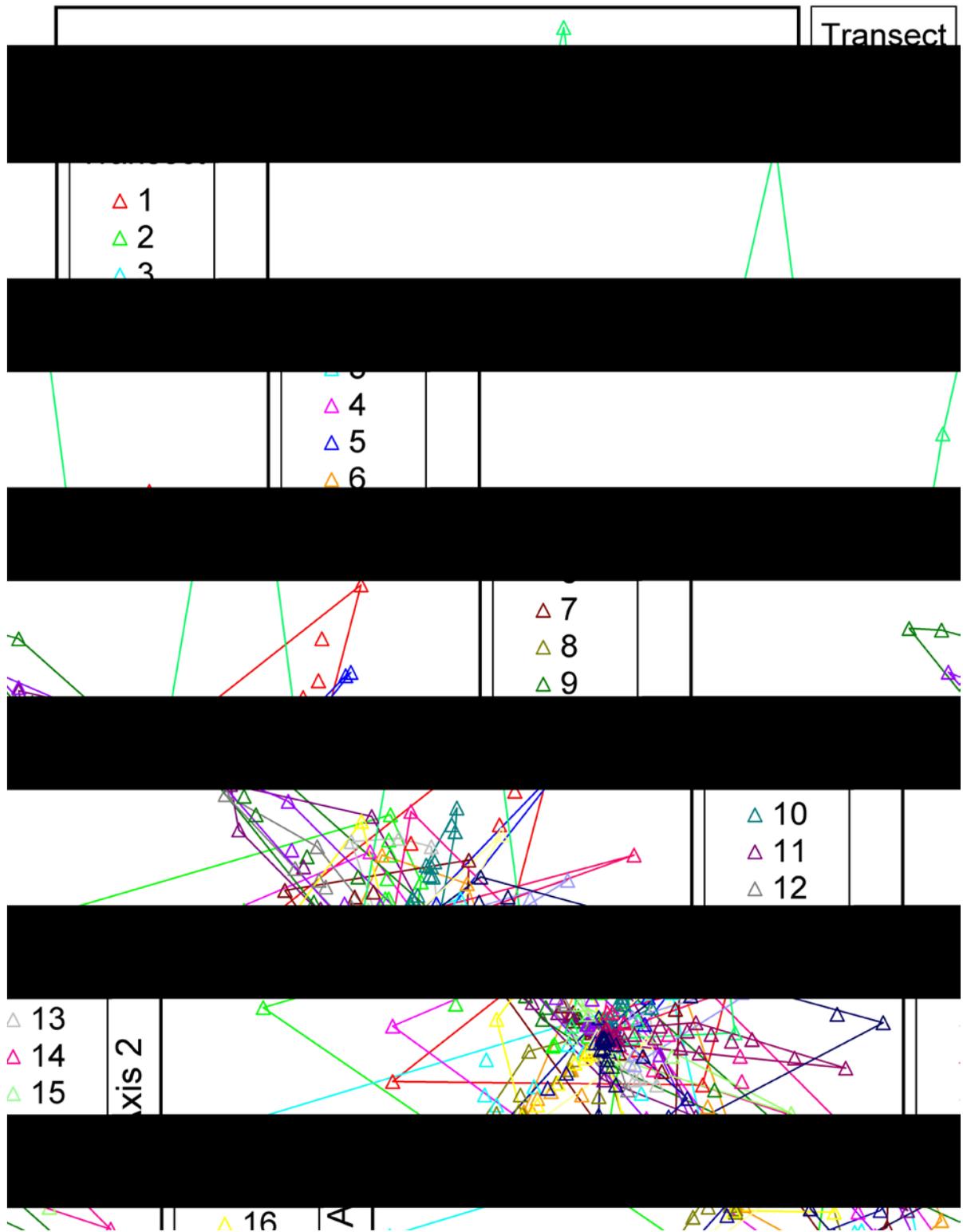


Figure 10. NMS ordination comparing total species sampled across each of the 25 transects in CUGA.

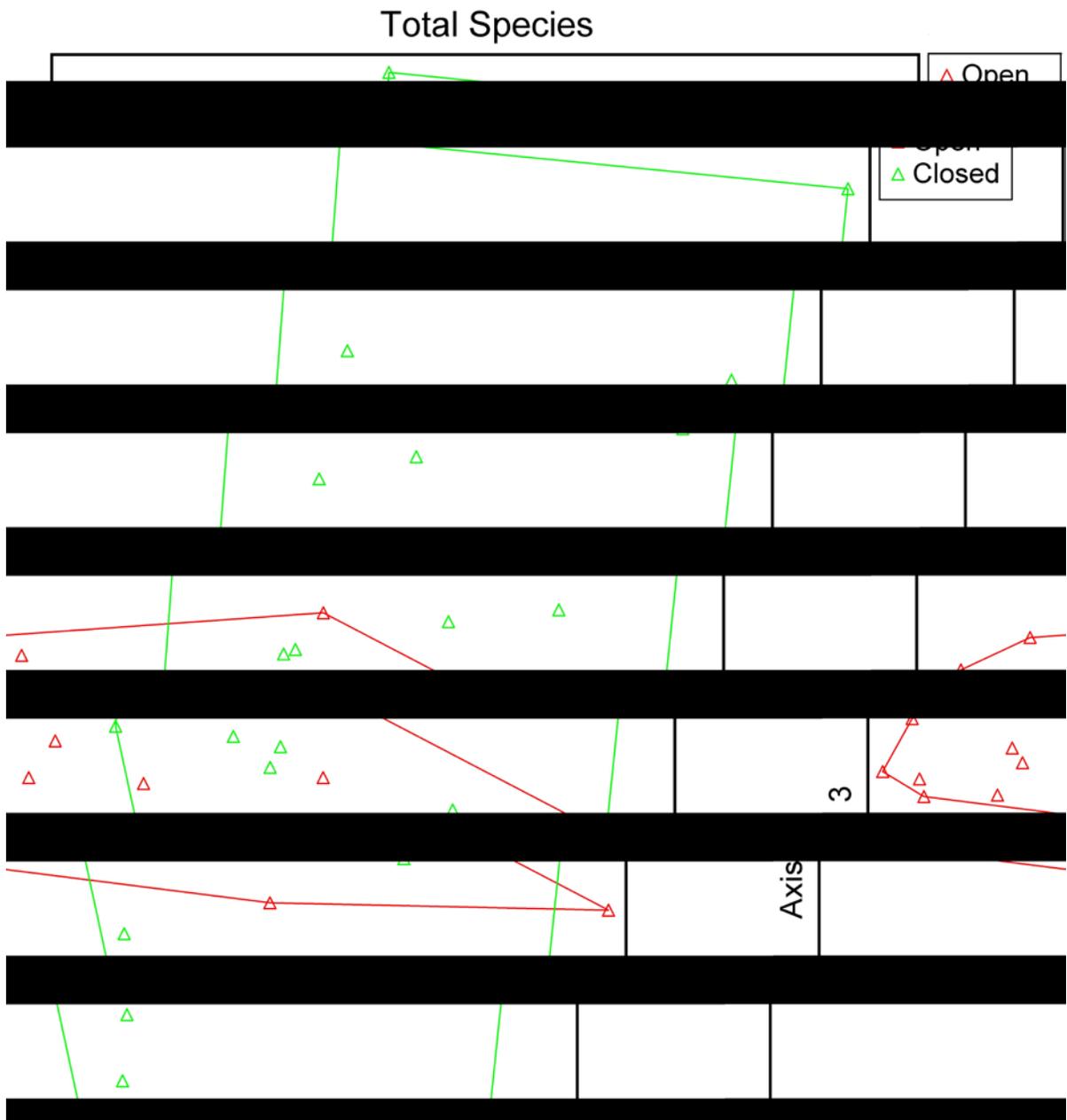


Figure 11. NMS ordination comparing total species sampled on transects with open and closed cliff-edge forest canopies in CUGA and White Rocks (Ballinger 2007).

Site Descriptions

Ridge Trail 2 and 1 (#1 and #2)

Ridge Trail 1 and 2 cliff systems were the smallest and least diverse of the cliff systems sampled. Despite their low diversity, *Rhododendron carolinianum* was established on the cliff face, a state record for Virginia. The cliff sites were adjacent to one another, located only a few meters apart. Likely due to their close proximity, both sites represented similar levels of diversity. These cliff sites were located along a paved trail running through the Park and were among the most heavily-trafficked areas that were sampled. There was nearly half the number of vascular plant species present on Ridge Trail 1 compared to Ridge Trail 2, which was heavily vegetated above the cliff face. Both cliff sites faced one another and were moderate to heavily shaded. Bryophyte and lichen numbers were relatively similar on both cliffs.

Upper Chadwell (#3)

This cliff site had a closed canopy, located in the middle of a densely wooded area within the Park. There was a seep present along one transect, and trees in the talus provided shade on the cliff face. Despite the low diversity observed, this cliff site contained *Melampyrum lineare* var. *latifolium* individuals on the cliff edge, a threatened species in the state of Kentucky.

Lewis Hollow (#4)

This cliff site consisted of two adjacent transects with differing aspects. One of the transects was mostly shaded and moist. Both transects were somewhat exposed with a closed canopy, but not nearly as much as other faces sampled. Lichen numbers were fairly low.

Indian Rocks (#5)

The Indian Rocks cliff site revealed a higher than expected number of vascular plant species. The face was only partially shaded, with a significant amount of shorter vegetation on the cliff edge, resulting in an open canopy.

Pinnacle Overlook (#6)

This location had several unusual features compared to others sampled in this study. The entire cliff edge was developed into a visitor's overlook and was almost completely devoid of vegetation. However, several individuals of *Dicchanthelium aciculare* were collected here, a species endangered in the state of Tennessee. This species is a county record for Virginia and biogeographically disjunct within its range for that state. This area also represented a continuous cliff with three different aspects. The cliff face was exposed on all sides.

West Chadwell (#7)

West Chadwell and Skylight Cave are two sites with approximately the same area, yet very different species diversities. Vascular plant and lichen diversity are above what is expected by the species-area curve, with bryophyte diversity being below expected. This particular cliff site was observed to have an open cliff edge, likely resulting in a relatively high level of direct exposure.

Skylight Cave (#8)

At the Skylight Cave cliff site, very different conditions existed compared to those observed at nearby West Chadwell. The forest canopy was closed at this site. The species-area curve under-estimated actual bryophyte diversity observed.

Lower Chadwell (#9)

Lower Chadwell revealed a higher level of vascular plant and bryophyte diversity than expected. This cliff system was surrounded by closed forest canopy, with minimal exposure and direct sunlight on the cliff face.

Cumberland Trail (#10)

The Cumberland Trail cliff site was one of the largest cliff systems sampled. It was fully exposed with only a partial forest canopy, with an exceptionally diverse lichen community. Vascular plant diversity was less than expected, with the majority of the taxa occurring on a fairly large cliff ledge a few meters from the cliff edge. Overall, with respect to size, Cumberland Trail was one of the least-diverse cliff systems sampled.

Teaberry (#11)

Teaberry was the largest cliff site sampled in the Park. The cliff edge was mainly rock and the forest canopy was set back several meters and was open. Bryophytes were slightly below the expected levels of diversity.

Discussion

Cliffs are among the most unique ecosystems in the world for both biological investigations and recreational sports. They provide unexplored habitat, as well as activities that fulfill a person's desire for adventure. Prior to the advent of rock climbing, rappelling, and BASE-jumping, cliff ecosystems were immune to direct anthropogenic disturbance. They serve as natural fire barriers and were protected from logging and development. As recreational activities continue to increase, it is important that such effects are monitored and regulated for the benefit of cliff-face communities. Cliff ecosystems are important to the plant communities they harbor by providing a refuge from competition, as well as a suitable environment for disjunct species, along with rare and endemic species that may be absent from the surrounding landscape (Walker 1987, Clebsch and Walker 1988, Larson et al. 1989, Bartlett and Larson 1990). Walker (1987) demonstrated the dependence of *Thuja occidentalis* L. on cliff faces for refuge from more competitively dominant species in the horizontal landscape, especially in its southern disjunct range. Some southern disjunct cliff populations of *T. occidentalis* L. may actually hold more genetic diversity than populations in its northern main range. (Walker 1987).

Cliff-face ecology is a continually developing field, with limited information on biotic and abiotic factors that drive its community vegetational structure. Results from ordinations of the environmental variables measured in CUGA reveal that slope, aspect, or area alone is not the sole driver of plant community structure or diversity on cliffs. Many factors not measured in this study may better describe diversity and community structure. Some observed differences seen among the eleven cliff systems sampled in the Park were differences in amount of

insolation, moisture levels, and microhabitats, which may explain some variation. Based on general observations of site characteristics, a cliff's degree of insolation may be a large contributor to differences seen in vascular, bryophyte, and lichen diversities. Varying levels of exposure was used to describe an estimated amount of insolation occurring on the cliff face. It represented whether the observed cliff was thought to receive light, moderate, or heavy levels of sunlight.

The current cliff survey was initiated from a similar study done by Ballinger (2007) on the White Rocks cliff system in CUGA. Ballinger's study revealed several rare vascular plants and arctic and boreal disjunct lichen species that were previously unknown in the Southern Appalachian Mountains. The current study revealed similar results, noting several state and county records, some threatened and endangered species, as well as an arctic and boreal disjunct lichen species also found in the White Rocks survey (Ballinger 2007). Compared to the White Rocks survey, which is also part of the Cumberland Plateau escarpment, a greater diversity of vascular plant, bryophyte, and lichen diversity was found in the current study (Table 1). These results support the concept of conservation of several smaller cliff systems to protect maximum species diversity, rather than a large continuous cliff system.

The differences between the White Rocks and CUGA studies are likely an effect of sampling eleven discrete cliff systems in the current study, as opposed to the single, continuous cliff system at White Rocks. This follows the same trend observed in the Niagara escarpment in Southern Ontario, Canada. Cliffs were sampled along a horizontal gradient with no new species accumulated after a certain extent for hundreds of miles (Larson et al. 2000). The White Rocks cliff system also exhibited signs of illegal climbing that was determined by the presence of fixed anchors at one location, as well as a mostly denuded cliff edge due to hiking and horseback riding (Ballinger 2007). The cliff sites in the current study are more pristine and unimpacted by climbing and less impacted by hiking. Varying aspects and other differing physical conditions

observed at the different site locations of the current study may have also increased overall diversity. Of the eleven cliff sites, each varied in amount of insolation, aspect, and slope, as well as the amount of vegetation on the cliff edge, leading to variable shading and the possibility for greater vascular plant seed rain. White Rocks cliff sites were heavily impacted at the cliff edge, with the forest canopy set back several meters from the edge of the face (Ballinger 2007). This wasn't observed for sites in the current study, with most of these cliff sites having an intact forest canopy up to the cliff edge. One of the exceptions was the Pinnacle cliff site. There was a paved visitor's overlook at the cliff edge that removed all vegetational cover. This likely resulted in a substantial increase in lichen diversity, and a decrease in vascular plant diversity, similar to that observed with Ballinger's data (Figure 11).

As predicted by the species-area relationship, the general trends observed demonstrated an increase in overall species diversity with area, but only to an extent (Figure 6). Since cliffs are vertical systems, their aspect and slope likely affects community composition. Some of the cliff sites were exposed with minimal shading suggesting why total lichen diversity was highest overall in this study compared to vascular plants. In others that were shaded, diversity increased for moisture and shade-dependent bryophytes. The R^2 -values for the species-area curves represent how well species are predicted by area (Table 4). Although the R^2 appears highest for the bryophytes, it can be easily misinterpreted since there was a large number of total species collected overall, the vascular plant and bryophyte groups with lower diversity may be affected by scale. Overall bryophyte diversity was lower, with some cliff systems having only one or two species present. As expected, total species represents the best-fit line on the species-area curve (Figure 6) as species numbers should increase with area. The bryophyte, lichen, and vascular curves all have a somewhat lower statistical fit perhaps due to environmental variables, such as shading, moisture levels, or heterogeneity independently driving each of the different taxa on different cliff faces. It appears that as one group increases

in diversity, another group decreases in diversity at most sites. This interaction may be driven by either competition or environmental variables, and the abundance of one group may directly affect the abundance of another group.

Both species-area curves demonstrate that the sampling method employed in this study is effective at capturing the plant diversity present on the cliff sites sampled. The asymptote of each curve denotes that a continued rate of increase in diversity doesn't occur with an increase in area beyond a certain point. Collected species are found repetitively and therefore continued sampling effort likely would not result in additional substantial diversity increases.

The species-area curves representative of the cliff systems in CUGA are typical of what would be predicted for insular habitats. Although no species-area statistics for cliffs have been published, several papers dealing with species richness on oceanic islands and in insular mainland habitats reveal a similarly steep slope (Marui et al. 2004, Triantis et al. 2008). A steep slope denotes a rapid rise in diversity, followed by a gradual asymptote. The slope of the log-transformed plot was likely steep due to cliffs being representative of local sites, which typically have steep slopes due to low species repetitiveness and the relaxation effect (Connor and McCoy 1979). The relaxation effect occurs when landscapes are fragmented and isolated. There is usually a decrease in species diversity due to limited number of habitats and therefore, lower species diversity. This study demonstrates that comparative species-area curves can be applied to cliff ecosystems that resemble other insular habitats and that diversity was sufficiently estimated using the sampling technique employed.

Outliers present in the species-area curve may support the idea that cliff systems have some factors that drive diversity and community structure that aren't accounted for in present sampling strategies (Table 3, Figure 6, # 6 and #7). The causes of these outliers aren't explained by slope or aspect, and are probably best explained by other abiotic factors occurring on the cliff face. This would also lend credence to the idea that area may not be the only important

driver of diversity among cliffs, but is instead a combination of many attributes, such as, sunlight, moisture, competition, and habitat heterogeneity. These attributes are difficult to measure on vertical systems and would require a more complex sampling protocol.

Site Specific Community Patterns

Ridge Trail 1 and 2 cliff systems were the smallest and least-diverse of the cliff systems sampled, with areas of 683 m² and 1116 m² respectively (Table 3). These cliff sites were located along a paved trail running through the Park and were among the most heavily-trafficked areas that were sampled. This may have especially influenced Ridge Trail 1, which had a cliff edge composed mostly of bare rock and lichen communities.

The low diversity of vascular plants observed at Upper Chadwell may have been due to lack of vegetation at the cliff edge, and therefore reduced vascular plant seed rain, which may have released the lichen species from competition, allowing them to increase in abundance and diversity. The unusually high bryophyte diversity observed at this site is most likely driven by a seep present along one transect, and because of shading of the face by trees in the talus.

The cliff site at Lewis Hollow had a high diversity of bryophytes along one of two transects. Both transects were only somewhat exposed, with an intact forest canopy at the cliff edge. Vascular plants were more abundant than lichen species. Therefore, lichen species may have been outcompeted by vascular plants for light and space.

At Indian Rocks cliff site, the cliff edge was forested with a closed canopy. Vascular plants may have been able to establish themselves from a source population at the cliff edge and outcompete the lichen species via shading.

High levels of exposure on the cliff faces at Pinnacle likely explain the comparatively high levels of lichen species observed at this site. The preferences of many lichen species for high levels of sunlight and tolerance of wind and desiccation may give lichens a competitive

advantage in extreme conditions such as those observed at this site. With no vegetation on the cliff edge and with a fully exposed cliff edge, there was a decreased possibility of vascular plant seed rain. This might explain the lower representation of vascular plant and bryophyte competitors for lichens on the cliff face, with exposed conditions on this face. Vascular plant and bryophyte diversity was more accurately predicted by the species-area curve at this site likely because of an east-facing transect that was partially shaded by an adjacent cliff. The adjacent cliff was only a few meters away and was densely vegetated at the cliff edge, providing the possibility for vascular plant seed rain onto the Pinnacle cliff-face.

West Chadwell and Skylight cave have approximately the same area of 9500 m² (Table 3), yet very different plant community structure. This lends credence to the idea that area isn't the only factor driving diversity among the cliff sites sampled. High levels of exposure with minimal shading likely resulted in a decrease in moisture levels and decreased bryophyte diversity. High levels of vascular plant and lichen diversity likely lowered the bryophyte diversity due to competition.

Relatively high levels of bryophyte diversity may have resulted from almost no direct sunlight hitting the cliff face at Skylight Cave, possibly providing a more mesic environment for this group. A thick, closed canopy cover likely over-shaded the vascular plant understory on the cliff face, which may have resulted in lower levels of vascular plants observed at this site.

Only a few lichen taxa, such as *Lepraria* spp. flourish in shaded sites. Many lichen species require more open environments and are usually low in abundance at sites such as Lower Chadwell.

Cumberland Trail had an area of 19,685 m² (Table 3), and was the second largest, fully exposed cliff site sampled. Bryophyte diversity was low, perhaps due to minimal shading. Vascular plant diversity was very low, again possibly due to high exposure levels and low amounts of vascular seed rain.

A large amount of cracks, crevices, and ledges along the Teaberry cliff face likely allowed for an increase in microhabitats that may have resulted in relatively high levels of diversity in vascular plants and lichens, and barely below the diversity prediction from the species-area curve for the bryophytes. This extensive cliff system had the largest areal extent of 27,400 m² (Table 3) and suggests that in some cases, a single large system may be the best conservation option for retaining high species diversity.

First-Order Jackknife Estimates

The main purpose for the nested species-accumulation analysis was to obtain first-order jackknife estimates of species richness (Table 4). This tool gives a calculated prediction of actual species richness that sub-sampling underestimates. There are several estimators commonly used for predicting actual species numbers in a study area. The jackknife estimator is a nonparametric technique that estimates species diversity based on occurrence data rather than percent cover. This offers a less-biased estimate (Smith and Pontius 2006). The second-order jackknife estimator is useful when measuring less than 25% of the species diversity (Hellmann and Fowler 1999). It is assumed that more than 25% of the diversity was measured in this study, and therefore the first-order jackknife estimator was considered. The largest overestimate is seen in the lichen group, as observed species richness was only 57% of that estimated by this analysis. This could be attributed to the high diversity of lichen species reported at a couple of sites, like the Pinnacle. High levels of lichen diversity at the Pinnacle and West Chadwell cliff sites may lead to the underestimation of the lower lichen diversity at more heavily-shaded cliff sites, with an intact vegetational community at the cliff edge. The large difference seen in the total species richness estimation is likely an artifact of the lichen group estimations being usually high.

For conservation purposes, choosing between preserving a single large cliff or several small cliffs for land managers would be difficult to do considering just area, slope, or aspect alone. Sampling of each cliff system, and possibly each transect, would be appropriate to identify and manage the conservation of maximum species diversity when faced with rock-climbing related disturbances. Several small cliffs would likely incorporate a greater variety of physical features, and as observed in the current study, harbor the majority of rare, endangered, and disjunct species, compared to extensive cliff systems. In this study, larger cliffs were more diverse overall, but lacked threatened and disjunct species. Comparing the amount of diversity and areal extent of the current study to the study done by Ballinger (2007) at White Rocks, it seems that the species accumulation on a substantially larger cliff may become repetitive after only a few transects, and that smaller cliffs would likely have more vegetation diversity in a smaller area. The study at White Rocks did not observe a horizontal shift in vegetation across transects (Ballinger 2007). Larson et al. (2000) observed a similar trend in the Niagara escarpment in Southern Ontario, Canada. By conserving enough of the smaller cliff systems, the Park would likely be able to obtain both diversity, as well as rare, endangered, and arctic and boreal disjunct species.

In the southern Appalachian region, the Cumberland Plateau physiographic province represents an area of high biodiversity (Shaw and Wofford 2003). It provides refuge for arctic and boreal disjunct species as reflected in the studies done along the Cumberland Plateau escarpment. These disjunct species were likely remnants of main-range populations dating back to the most recent glacial period. The Ridge and Valley physiographic region likely acted as a central corridor vital to the migration of many species (Delcourt and Delcourt 1987). For this reason the Cumberland Plateau escarpment may have served as a natural barrier and a refuge, preventing further westward migration, but providing habitat for migrating, post-glacial species with more northerly ranges today. Hill (2009) conducted a climbing study in the Obed River

Gorge. The Obed River Gorge cliff system is located on the western part of the Plateau and vascular plant and lichen species diversity identified in that study were nearly half of that observed in the current study, perhaps suggesting that the interior of the plateau harbors fewer glacial relicts such as the lichen community observed on White Rocks (Ballinger 2007).

Summary

Surveys were conducted along a total of 25 transects among eleven discrete cliff systems in Cumberland Gap National Historical Park. A total of 215 species were identified, representing 111 vascular plants, 33 mosses, 4 liverworts, and 83 lichens. Four species of interest were acknowledged as threatened, endangered, or disjunct.

The main purpose of this study was to determine if species-area curves could be applied to cliff ecosystems and that the sub-sampling technique employed in this study was effective at capturing the diversity of a cliff system. The species-area curves reveal that there is a general increase in diversity with area, but only to a certain extent. There are however other factors that may impact each cliff system in terms of their plant community structure. Species diversity numbers differ among cliff sites and the community composition may be completely different among equal-sized cliffs (Table 3, #7 and #8). Several small cliffs may incorporate a greater number of differences in physical conditions, and harbor a greater number of rare, endangered, and arctic and boreal disjunct species. Larger cliffs were more diverse, but lacked the threatened and disjunct species observed in this study.

Supplementary ordinations revealed that slope, aspect, and area alone don't necessarily drive differences observed in vascular plant, bryophyte, and lichen diversity on cliffs in CUGA. Each face differed drastically in heterogeneity, shading, and seep presence, which may help to explain differences observed in species diversity among cliff ecosystems. It was also shown that the cliff face plant community is only a subset of the cliff edge plant community. This lends

credence to the notion that cliff faces are an important ecosystem in their own right and may act as a refuge from competition and climate change, and possibly a required habitat for endemic species.

Management Implications

Climbing and rappelling is becoming an increasingly popular activity on cliff faces. Their direct effects on cliff ecosystems have been studied several times, but long-term effects such as nutrient cycling, are still unknown (Farris 1998, Smith 1998, McMillan and Larson 2002, Kuntz and Larson 2006, Hill 2009). The regulation of hiking and development along the cliff edge are important in preservation of this pristine habitat. Consistent disturbance can lead to serious degradation of the cliff edge community. Climbing exposes a new area to disturbance on the cliff face that traditional activities haven't directly impacted in the past.

There is currently no climbing permitted on cliff faces at CUGA. It is likely that rock climbers would respect the pristine plant communities of cliff systems. However, it is important that climbing be managed and restricted to particular climbing routes. This can only be done effectively by understanding the cliff-face vegetational community. Climbing should be allowed in areas where disturbance could be minimalized. Species-area curves can be useful in providing information that may help to develop climbing-management plans.

Based on this study and others, it is important that parks specifically and carefully sample proposed climbing routes before making them available, as well as installing maintained trails into the talus area and away from the cliff edge in order to reduce disturbance to the horizontal landscape associated with cliff communities. Multivariate analyses show that transects can be different from one another, and that it may be pertinent to open up distinct climbing routes instead of entire cliff faces. It may be effective to even install a no topping-out policy on climbing routes since several of the endangered or threatened species on cliff systems

sampled in the Park were located on the cliff edge in this study, and the study done by Ballinger (2007).

Future Considerations

There remain unknown parameters that would possibly shape vegetational community structure in cliff systems. Many ecologists lack the time and expertise to effectively investigate cliff ecosystems in their entirety. Advances in Geographic Information Systems (GIS) and spectrophotometry may make it possible to predict and capture some of this data virtually. Inventions such as quadcopters may allow researchers to remotely collect light readings and digital elevation models (DEM's) without even rappelling down the face. Continual development of GIS databases will be useful in exploring and predicting more features of this important and unique ecosystem.

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Appendix A - Species List

Vascular Plants

Acer rubrum var. *rubrum*
Acer saccharum
Agrimonia rostellata
Agrostis perennans
Amelanchier arborea
Anemone acutiloba
Arisema triphyllum
Asclepias quadrifolia
Asplenium montanum
Asplenium ruta-muraria
Betula alleghaniensis
Betula lenta
Bromus pubescens
Campanula divaricata
Campanula divaricata
Carex 1
Carex 2
Carex 3
Carex 4
Carex aff. *Communis*
Carex cf. *pennsylvanica*
Carex swanii
Carya cf. *glabra*
 cf. *Croton/Elaeagnus*
 cf. *Danthonia*

Bryophytes

Mosses

Andreaea rothii
Brotherella recurvans
Campylium chrysophyllum
Campylopus tallulensis
Cephalozia sp.
Ceratodon cf. *purpureus*
 cf. *Anomodon rostratus*
 cf. *Dicranum flagellare*
 cf. *Pylaisella* sp.
Dicranodontium denudatum
Dicranum condensatum
Dicranum fuscescens
Dicranum montanum
Ephebe lanata
Fissidens taxifolius
Hedwigia ciliata
Hypnum imponens
Hypnum pallescens
Isopterygium elegans
Lepraria membranacea
Leucobryum albidum
Leucobryum glaucum
Platygyrium repens
Polytrichum juniperinum

Lichens

Amandinea punctata
Bryoria nadvornikiana
Buellia spuria
Buellia stillingiana
Caloplaca citrina
Campylopus tallulensis
Canoparmelia crozalsiana
Chroococcus
Chrysothrix
Cladonia caespitica
Cladonia cenotea
Cladonia parasitica
Cladonia petrophila
*Cladonia pocillum*⁴
Cladonia rangiferina
Cladonia squamosa
Cladonia strepsilis
Cladonia subtenuis
Cladonia symphycarpia
Dicranodontium denudatum
Dimelaena oreina
Diploschistes scruposus
Ephebe lanata
Flavoparmelia baltimorensis
Heterodermia speciosa

<i>cf. Eupatorium pubescens</i>	<i>Polytrichum ohioense</i>	<i>Imshaugia aleurites</i>
<i>cf. eurybia divaricta</i>	<i>Pylaisiadelphina tenuirostris</i>	<i>Lasallia papulosa</i>
<i>cf. Helianthus microcephalus</i>	<i>Racomitrium cf. heterostichum</i>	<i>Lasallia pensylvanica</i>
<i>cf. Symphyotrichum patens</i>	<i>Schistidium cf. apocarpum</i>	<i>Lecanora oreinoides</i>
<i>Chimiphila maculata</i>	<i>Schistidium rivulare</i>	<i>Lecanora thysanophora</i>
<i>Clematis virginiana</i>	<i>Sematophyllum demissum</i>	<i>Lepraria elobata</i>
<i>Clethra acuminata</i>	<i>Sphagnum sp.</i>	<i>Lepraria lobificans</i>
<i>Danthonia cf. sericea</i>	<i>Taxiphyllum deplanatum</i>	<i>Lepraria membranacea</i>
<i>Danthonia compressa</i>	<i>Tortella humilis</i>	<i>Lepraria neglecta</i>
<i>Denstaedtia punctilobula</i>		<i>Lepraria rigidula</i>
<i>Dicchanthelium 1</i>	Liverworts	<i>Lepraria membranacea</i>
<i>Dicchanthelium 2</i>	<i>Cephaloziella sp.</i>	<i>Leptogium chloromelum</i>
<i>Dicchanthelium 3</i>	<i>Diplophyllum apiculatum</i>	<i>Leptogium lichenoides</i>
<i>Dicchanthelium aciculare¹</i>	<i>Frullania riparia</i>	<i>Melanelia culbersonii</i>
<i>Dicchanthelium aff. Commutatatum</i>	<i>Scapania nemorea</i>	<i>Melanelia disjuncta</i>
<i>Dicchanthelium boscii</i>		<i>Melanelia panniformis</i>
<i>Dicchanthelium depauperatum</i>		<i>Melanelia soresdiata</i>
<i>Dicchanthelium dichotomum</i>		<i>Micarea peliocarpa</i>
<i>Dicchanthelium latifolium</i>		<i>Nostoc</i>
<i>Dicchanthelium villosinum</i>		<i>Ochrolechia sp.</i>
<i>Diospyros virginiana</i>		<i>Panaparmelia alabamensis</i>
<i>Elymus hystrix</i>		<i>Paraparmelia alabamensis</i>
<i>Epigaea repens</i>		<i>Parmelia squarrosa</i>
<i>Erechtites hieracifolius</i>		<i>Parmelinopsis minarum</i>
<i>Eurybia divaricata</i>		<i>Parmotrema</i>
<i>Fraxinus quadrangulata</i>		<i>Peltula sp.</i>
<i>Galax urceolata</i>		<i>Pertusaria amara</i>
<i>Galium aparine</i>		<i>Pertusaria plittiana</i>
<i>Gaylussacia baccata</i>		<i>Pertusaria rubefacta</i>
<i>Glautheria procumbens</i>		<i>Phaeophyscia adiaastola</i>

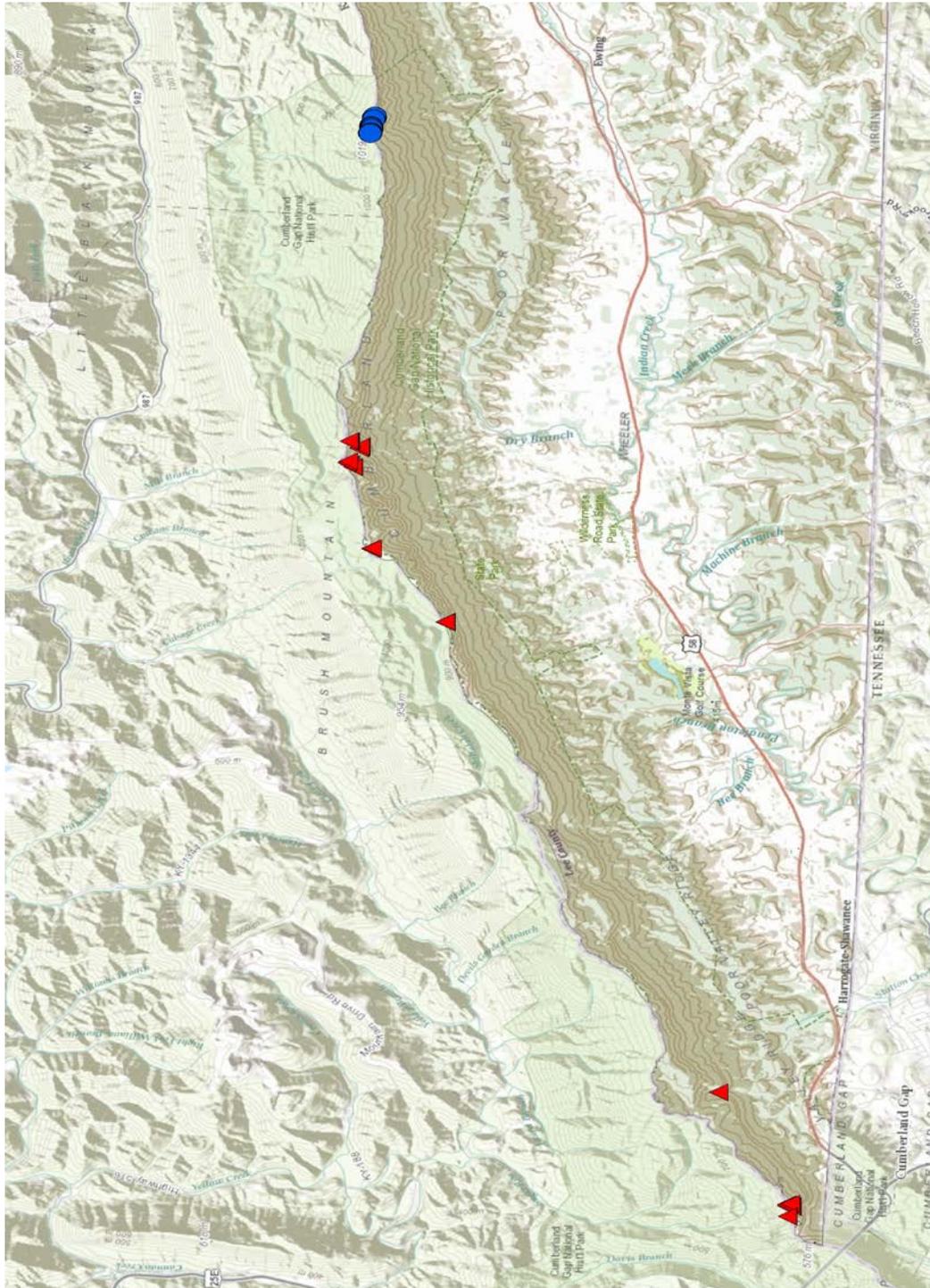
Hamamelis virginiana
Helianthus cf. microcephalus
Heuchera americana
Heuchera cf. parviflora
Houstonia longifolia
Huchera americana
Hydaticea petiolaris
Impatiens capensis
Kalmia latifolia
Lysimachia quadrifolia
Maianthemum racemosum
*Melampyrum lineare var. latifolium*²
Mitchella repens
Nyssa sylvatica
Osmundastrum cinnononea
Ostrya virginiana
Oxalis grandis
Oxydendrum aboreum
Oxydendrum arboreum
Packera obovata
Pellaea atropurpurea
Persicaria cf. longiseta
Philadelphus hirsutus
Pinus virginiana
Pityopsis graminifolia
Poaceae
Polmnia canadensis
Polygala senega
Polygonatum biflorum var. biflorum
Quercus alba

Phaeophyscia ciliata
Phaeophyscia sciastra
Phlyctis argena
Physcia aipolia
Physcia subtilis
Physciella chloantha
Physciella melanchra
Physonica
Pleopodium flavum
Polysporina simplex
Protoblastenia rupestris
Ramalina obtusata
Ramalina pollinaria
Rhizocarpon badioatrum
Rhizocarpon disporum
Rhizocarpon hochstetteri
Rhizocarpon obscuratum
Sarcogyne regularis
Trentephtia sp.
Tripe rugosa
Umbilicaria mammulata
Umbilicaria virginis
Usnea amblyoclada
Usnea halei
Verrucaria calciseda
Xanthoria sorediata

Quercus montana
Quercus rubra
Quercus velutina
*Rhododendron carolinianum*³
Rhododendron maximum
Rhus copallina
Rubus cf. pensylvanicus
Sassafras albidum
Sedum ternatum
Silene rotundifolia
Smilax glauca
Smilax rotundifolia
Solidago caesia
Solidago flexicaulis
Symphotrichum oblongifolium
Thalictrum thalictroides
Toxicodendron radicans
Vaccinium cf. pallidum
Vaccinium cf. parviflora
Vaccinium corymbosum
Vaccinium fuscatum
Vaccinium stamineum
Vaccinium corymbosum
Viola cf. blanda
Viola cf. sororia
Viola hastata

1. Endangered
2. Threatened
3. New State Record/Disjunct
4. Arctic and Boreal Disjunct

Appendix B - Enlarged Map



Biographical Sketch

Justin Harkey earned his Bachelor of Science Degree in Biology from Appalachian State University, Boone, NC. After graduation, Justin went directly into graduate school under the direction of Dr. Gary Walker. His thesis research focused on looking at vegetational communities on cliff systems in Cumberland Gap National Historical Park, including locating and mapping the extent of rare, endangered, and arctic and boreal disjunct species. This project was funded through a cooperative agreement between ASU and the National Park Service called the Southern Appalachian Cooperative Ecosystem Studies Unit. He received his Master of Science Degree in Evolutionary Biology and Ecology in May 2013.