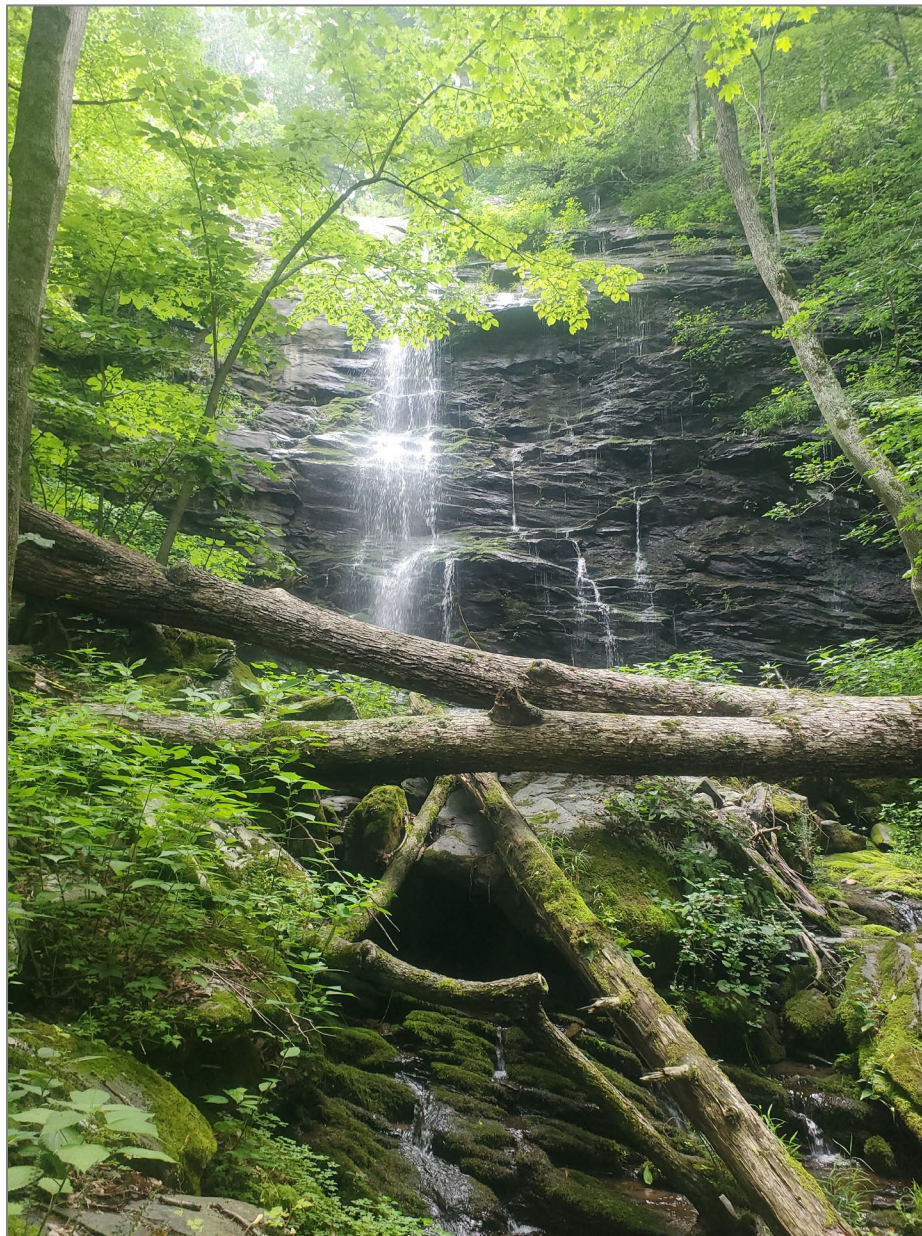








Inventory of Rare Bryophytes to Inform High-Use Recreation Site Management in Shenandoah National Park



Big Creek Falls with bryophytes covering rocks, downed logs, live trees, and the falls themselves.
NPS / SHERSHEN

Inventory of Rare Bryophytes to Inform High-Use Recreation Site Management in Shenandoah National Park

Science Report NPS/SR—2026/420

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Abstract

We surveyed bryophyte communities at 36 sites containing either waterfalls, rivers, wetlands, or rock outcrops in Shenandoah National Park in Virginia to determine the location and distribution of rare bryophytes and to explore whether human disturbance negatively impacted bryophyte communities. An intentional meander through the 36 sites was conducted to collect and document all unique species. In addition, we examined overlapping transect lines to calculate species level bryophyte cover at 16 of the sites, eight containing water features and eight with rock outcrops with varying levels of human disturbance. We found 247 species, three of which were rare at the global or state level, one that was a new state record for Virginia, and 76 of which were new to the park compared to historical specimens and records from the park. We found that visitation intensity (level of disturbance) did not significantly impact bryophyte diversity or percent cover at either site type. However, we observed high levels of bryophyte community dissimilarity between disturbed and undisturbed sites, and these sites clustered independently from one another in both rock outcrops and water feature sites. This suggests that human disturbance impacts the bryophyte community composition; however, the number of unique species and their abundance is not different between disturbed and undisturbed sites. This may be because some species can tolerate disturbances, and human foot traffic may create opportunities for more disturbance-resilient species to occupy the space, as these species face less competition from disturbance-sensitive species that typically share the same niche. Investment in the preservation of bryophyte biodiversity within the park should be targeted towards sites with low levels of disturbance and those housing rare species, to ensure disturbance-sensitive and rare species' habitat is protected from human trampling damage.

Acknowledgments

This project was made possible through the support from the National Park Service Inventory and Monitoring Division. Thanks to Isabel Hildesheim for fieldwork assistance, Liz Halasz for species identifications and fieldwork assistance, and Alexis Powell, Tessa Nuchols, Seth Shaw, Josh Kreis, and Garrett Billings for specimen curation assistance.

Introduction

Anthropogenic disturbance, specifically driven by tourism, can negatively impact biological communities across habitat types (Li et al. 2005; Ballantyne and Pickering 2012; Wolf et al. 2013; Malik et al. 2016; Machado et al. 2017; Wilson and Verlis 2017; Marcella et al. 2017; Araujo et al. 2017; Rodway-Dyer and Ellis 2018, Niu and Cheng 2019). Bryophytes are no exception to this trend and have also been shown to be sensitive to disturbances (Cobb et al. 2001; Fenton and Krego 2005). In spite of their small size bryophytes play crucial roles in the ecosystems they inhabit by enhancing soil stability (Gao et al. 2020), which reduces nutrient run-off (Silva et al. 2019; Van Miegroet et al. 2007), as well as providing habitat for macroinvertebrates (Ziesche and Roth 2008; Coyle 2009) and microorganisms (Bartels and Nelson 2007). Within Shenandoah National Park (SHEN) in Virginia, park staff noted trampling damage to bryophyte communities in areas with high visitor use (pers. comm. Wendy Cass 2023). However, little research on bryophyte communities within the park has been undertaken, and historical collections may not represent the current state of these sensitive communities and how they are responding to anthropogenic disturbance.

This study aimed to survey the bryophyte communities across SHEN, with a focus on rock outcrops and sites with water features, to assess the impact of visitor use and human foot traffic on bryophyte diversity and abundance at sites with varying levels of visitation intensity. Additionally, we aimed to document species that are rare to the region to support the park's mission of preserving biodiversity. We predicted that relatively undisturbed sites would harbor more diverse communities with higher levels of bryophyte coverage compared to disturbed sites. We also predicted that when we compared disturbed and undisturbed sites, they would display high levels of community dissimilarity. We also expected that environmental variables such as elevation, slope, aspect, and canopy cover could influence community composition across the park, as prior work has shown these variables to be drivers of bryophyte diversity and abundance (Cacciatori et al. 2022; Dearborn and Danby 2017; Shershen et al. 2024).

Methods

Park staff selected 36 sites for surveys, representing both wet (waterfalls, rivers, wetlands) and dry (rock outcrops) areas across a gradient of expected visitor use (low/medium to high; Figure 1; Table 1). At each site, researchers conducted a systematic, timed meander in areas most likely to harbor unique bryophyte species (described in the “Site surveys” section below). Researchers conducted quantitative surveys along transect lines to determine the effects of anthropogenic disturbance on bryophyte diversity and abundance at a subset of sites that were paired based on visitor use (described in “Disturbance impact surveys” section below).

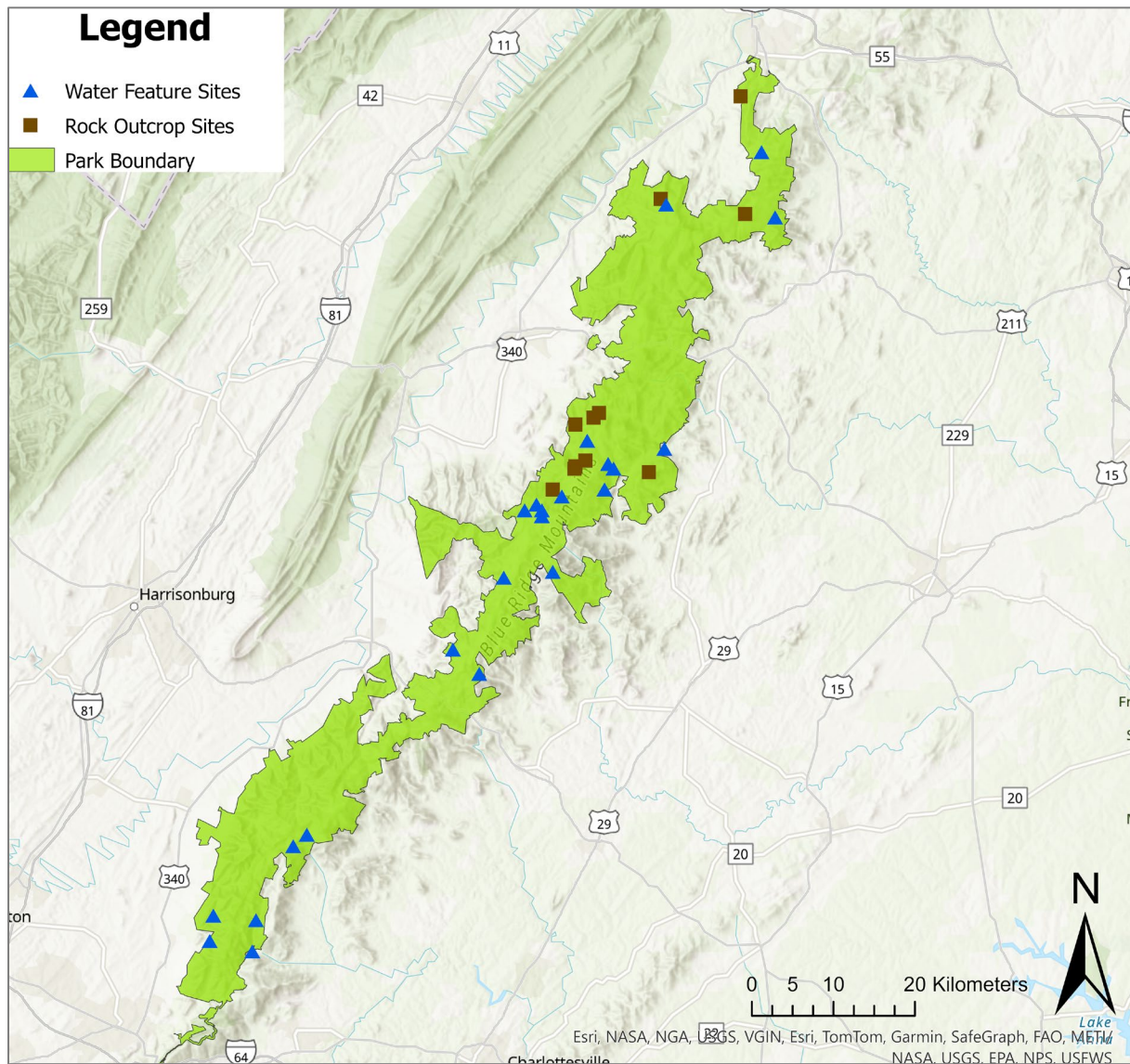


Figure 1. Map indicating the locations of the sites surveyed during the summer of 2023 in Shenandoah National Park. Blue triangles represent water feature sites and brown squares represent rock outcrop sites.

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Table 1. Sites surveyed, location, site type, and visitor use level. Within each site type, four sites with high visitor use were paired with four sites with medium/low visitor use. These 16 sites were surveyed for bryophytes using transect lines to determine the effects of anthropogenic disturbance on diversity and abundance. The number and length of the transect lines surveyed, as well as their configuration relative to the site feature, is described. Sites that were not included in the pairing and were not sampled with transects are indicated with NA.

Site Name	GPS Coordinates	Site Type	Level of Visitor Use	Site Pairing	Number and Length of Transects	Site Configuration
Big Branch	38.165986, -78.746373	waterfall	Low	NA	NA	NA
Big Creek	38.465864, -78.481263	waterfall	Low	Rose River	Three 10 m transect lines, 3 m apart	Parallel to the water feature
Big Meadows North	38.525188, -78.437833	wetland	Medium	NA	NA	NA
Big Meadows South	38.515015, -78.431091	wetland	Medium	NA	NA	NA
Cedar Run Falls	38.538075, -78.364126	waterfall	High	NA	NA	NA
Cool Spring Hollow	38.148043, -78.797422	wetland	Low	NA	NA	NA
Crescent Rock	38.562538, -78.384087	outcrop	High	Hawksbill Upper Outcrop	Three 10 m transect lines, 2.7 m apart	Parallel to the cliff face
Dark Hollow	38.519245, -78.423333	waterfall	High	NA	NA	NA
Dickey Ridge	38.875238, -78.212683	outcrop	Low	NA	NA	NA
Doyles River	38.241071, -78.691632	waterfall	Medium	South River	Three 10 m transect lines, 2 m apart	Perpendicular to water feature
Dry Run	38.399928, -78.530261	waterfall	Medium	NA	NA	NA
Franklin Cliffs Overlook	38.547651, -78.420728	outcrop	High	Hawksbill Amphitheater	Ten 3 m transect lines, 3.2 m apart	Perpendicular to the cliff face
Hawksbill Upper Outcrop	38.555394, -78.395597	outcrop	Low	Crescent Rock	Five 6 m transect lines, 3 m apart	Parallel to the cliff face

Table 1 (continued). Sites surveyed, location, site type, and visitor use level. Within each site type, four sites with high visitor use were paired with four sites with medium/low visitor use. These 16 sites were surveyed for bryophytes using transect lines to determine the effects of anthropogenic disturbance on diversity and abundance. The number and length of the transect lines surveyed, as well as their configuration relative to the site feature, is described. Sites that were not included in the pairing and were not sampled with transects are indicated with NA.

Site Name	GPS Coordinates	Site Type	Level of Visitor Use	Site Pairing	Number and Length of Transects	Site Configuration
Hawksbill Amphitheater	38.395927, -78.395927	outcrop	Low	Franklin Overlook	Three 10 m transect lines, 2 m apart	Perpendicular to the cliff face
Hughes River	38.574709, -78.298006	stream	High	Moorman's River	Five 6 m transect lines, 2.5 m apart	Parallel to the river
Jones River	38.229656, -78.705633	waterfall	Medium	NA	NA	NA
Jordan River	38.771401, -78.171168	waterfall	Medium	NA	NA	NA
Lands Run	38.828386, -78.189690	waterfall	Medium	NA	NA	NA
Lewis Springs	38.520316, -78.450320	waterfall	High	NA	NA	NA
Limberlost	38.575961, -78.376748	wetland	High	NA	NA	NA
Little Stony Man Disturbed	38.603734, -78.371368	outcrop	High	Little Stony Man Undisturbed	Five 6 m transect lines, 2.5 m apart	Perpendicular to the cliff face
Little Stony Man Undisturbed	38.603146, -78.369225	outcrop	Low	Little Stony Man Disturbed	Six 5 m transect lines, 2.5 m apart	Perpendicular to the cliff face
Millers Head Disturbed	38.593275, -78.394425	outcrop	High	Miller's Head Undisturbed	Five 6 m transect lines, 2 m apart	Perpendicular to cliff face
Millers Head Undisturbed	38.593228, -78.393999	outcrop	Low	Miller's Head Disturbed	Two 15 m transect lines, 4 m apart	Perpendicular to cliff face
Moorman's River	38.159446, -78.747331	stream	Medium	Hughes River	Five 6 m transect lines, 2 m apart	Parallel to the river
North Marshall	38.774699, -78.207383	outcrop	High	NA	NA	NA

Table 1 (continued). Sites surveyed, location, site type, and visitor use level. Within each site type, four sites with high visitor use were paired with four sites with medium/low visitor use. These 16 sites were surveyed for bryophytes using transect lines to determine the effects of anthropogenic disturbance on diversity and abundance. The number and length of the transect lines surveyed, as well as their configuration relative to the site feature, is described. Sites that were not included in the pairing and were not sampled with transects are indicated with NA.

Site Name	GPS Coordinates	Site Type	Level of Visitor Use	Site Pairing	Number and Length of Transects	Site Configuration
Old Rag	38.552609, -78.314475	outcrop	High	NA	NA	NA
Overall Run Barren	38.787257, -78.301663	outcrop	Low	NA	NA	NA
Overall Run Falls	38.784611, -78.300184	waterfall	High	NA	NA	NA
Rip Rap Swimming Hole	38.170848, -78.795658	stream	High	NA	NA	NA
Rose River	38.531667, -78.409319	waterfall	High	Big Creek	Six 5 m transects, 2 m apart	Perpendicular to waterfall, near stream edge going towards trail
South River	38.380180, -78.502340	waterfall	High	Doyle's Run	Three 10 m transect lines, 3 m apart	Perpendicular to the river
Staunton River	38.461106, -78.409509	stream	Medium	NA	NA	NA
Stony Man Seep	38.599933, -78.375038	outcrop	Low	NA	NA	NA
Tim's River	38.556768, -78.353188	waterfall	Medium	White Oak	Three 10 m transect lines, 3 m apart	Perpendicular to waterfall, running through the stream
White Oak	38.555858, -78.353188	waterfall	High	Tim's River	Three 10 m transect lines, 3 m apart	Perpendicular to waterfall, running through the stream

Site Surveys

To determine the bryophyte diversity at each site, researchers walked systematically across the site to record and collect as many unique species as possible while also noting the substrate they inhabit. Survey time was standardized at 30 minutes for two researchers, for a minimum total of one person hour of surveying per site. If new species were continually being found, researchers continued to search for an additional 30 minutes or until no new species were documented. Researchers noted the start and end time of the search and documented their locations using GPS tracks or perimeter mapping to document the area searched using a Bad Elf GNSS Surveyor (Bad Elf LLC, West Hartford, AZ). Surveyed sites varied in size from 228 m² (Miller's Head Disturbed) to 20,512 m² (Big Creek). However, due to equipment malfunction, some surveyed sites do not have area data and others may be inaccurate. A 25 cm² sample was collected for bryophyte species that could not be identified in the field. After collection, each additional time this species was observed it was noted but not collected to minimize habitat disturbance. If the taxon was suspected to be a rare species, then less than 15% of the patch was collected to minimize the impact. Specimens were deposited for long-term storage primarily at the University of Tennessee Knoxville Herbarium (TENN). Duplicates of rare species were deposited in the SHEN Herbarium.

Disturbance Impact Surveys

In addition to the site surveys, eight water feature sites and eight rock outcrop sites were surveyed for bryophytes using transect lines to determine the effects of anthropogenic disturbance on bryophyte diversity and abundance. Sites with high visitor use were paired with those that have medium/low visitor use (as defined by the park staff based on personal observations), hereafter referred to as disturbed and undisturbed sites respectively, maintaining elevation, aspect, geologic substrate, and site type (rock outcrop or water feature) constant between pairings as much as possible. At each site, a 10 × 10-meter plot (or alternate configuration with the same area) was established in an area that was safe for researchers to maneuver for extended periods of time and was within the bounds of the site survey. Plot location was standardized so that it was centered over the feature of interest (rock outcrop or water feature).

Once the plot was established, transect lines were laid down, with at least two meters spacing between each line and with the transect lines summing to 30 meters in total for each site. The configuration of these transects was determined on a site-by-site basis as sites varied in size and in terms of researchers' ability to safely navigate through the site. The transects were arranged so that the transect survey covered a majority of the site's feature of interest (e.g., main waterfall or rock outcrop). Along these transect lines, any bryophyte species that touched the line and the length of the line that the species touched (to the nearest centimeter) were recorded. The habitat and substrate were also recorded for each species. Habitat focused on the site level description, such as waterfall, rock outcrop, wetland, or river. Substrate focused on the surface the bryophyte was growing on and included rock, live tree, downed tree, decaying wood, soil, and leaf litter, along with descriptors that further aided in species identification such as the moisture level (ranging from dry to moist to submerged). Additional covariates collected for each site included canopy density, as measured from a fish-eye photo, with each photo taken as close to the plot centroid as possible. These photos were

converted into binary pixel images and then analyzed to calculate the gap fraction of the canopy using ImageJ (Schneider et al. 2012) and Hemispherical (Beckschäfer 2015).

Statistical Analyses

All analyses were performed in R version 4.3.2 (R Core Team 2021). A linear mixed effect model was used to determine if alpha diversity for the site survey and abundance for the disturbance impact survey were predicted by fixed effects such as elevation, slope, aspect, visitation intensity, and gap fraction and to test for any interactions between them. Sampling time was also included as a random effect for the site survey model for alpha diversity, but not for the disturbance impact survey model for abundance, since we standardized sampling effort using 30 m of transect line at each site. All models were reduced using a backward stepwise AIC function and then the reduced models were analyzed using an ANOVA to determine if any predictor variables significantly influenced the response variables.

To determine if the bryophyte communities were impacted by human disturbance, alpha diversity and absolute percent cover (abundance) were compared between disturbed and undisturbed sites for rock outcrops and water features using paired t-tests. Pairwise dissimilarity was calculated over three different Hill numbers, a metric that standardizes commonly used diversity metrics so that they can be compared between sites, using the hillR package (Li 2018). Dissimilarity ranges from 0 to 1, wherein 0 indicates the paired sites are the same in terms of their bryophyte community (0% different), and 1 indicates that they are completely dissimilar (100% different). The more dissimilar the communities were, the more likely human disturbance has influenced their community composition, since sites were paired based on similar geology, elevation, and aspect. Nonmetric multidimensional scaling (NMDS) plots were also generated using the vegan package (Dixon 2003) to visualize how dissimilar the communities were between the sites and to determine if the disturbed and undisturbed sites cluster. If rare species were present at both the disturbed and undisturbed sites, paired t-tests were used to test whether there was a difference in the abundance of rare species between sites.

Rare Species Population and Habitat Assessment

In June 2025, we returned to the sites where rare bryophyte species had been documented in 2023 to carry out more detailed species population and habitat assessments. For the population assessment the sexual condition and plant health were recorded, and each patch of a rare species was counted and then the patch area was measured to the nearest square centimeter to estimate the population size within each site. The habitats of the rare species were assessed by determining the vascular plant community type, light level, detailed microhabitat description, substrate, moisture state, habitat quality, and potential threats to the rare species. Plant community types were assigned using the categories in a technical report from the Virginia Department of Conservation and Recreation (Fleming and Patterson 2021). Light level was estimated using a continuous percent shade cover that each rare species was found growing in. If different patches of the same rare species had significantly different light levels, then both percentages were noted. Microhabitat descriptions included the specific locations of the rare bryophyte patches in each habitat, the location of the patches on its substrate, and associated vascular plant species. The moisture state included descriptions of water

permanence, distance from any water sources, and the extent that the patches were submerged. To assess habitat quality, the number of unoccupied microhabitats at each site that the rare bryophyte species had the potential of colonizing were counted and used along with the number of occupied microhabitats to calculate the percentage of occupied sites. Also, the amount of anthropogenic disturbance that was present, such as trash, trampling, and pollution, was noted. Potential threats were evaluated by the proximity of the rare species to human trampling, the likelihood of pollution, or the stability of the natural habitat.

For the rare bryophyte species located during this survey, a field guide was developed to help the park identify these species and the habitats with the potential to harbor these rare species in other areas of the park not surveyed during this project.

Results

Across all sites we found 247 species with 76 of those being new observations for the park. Sites with rock outcrops harbored 148 species and sites with water features 193 species. The species were documented through 984 collections, 622 of which contained enough plant material to be curated into specimens and deposited in the TENN herbarium (TENN-B-0140823 – TENN-B-0140945, TENN-B-0140969 – TENN-B-0141466), with duplicates of some collections sent to the SHEN herbarium (SHEN004700 to SHEN004702). The records for all these specimens can be accessed via the [Consortium of Bryophyte Herbaria \(https://bryophyteportal.org/portal/\)](https://bryophyteportal.org/portal/).

Rare Species

We found three species that were listed as rare at either the global or state level and one species that was a new state record for Virginia (NatureServe 2024; Consortium of Bryophyte Herbaria 2025; Table 2), including *Aneura sharpii* Inoue & N.G. Mill. (GNR, S1), *Cephaloziella spinicaulis* Douin (G3, S1), *Lophoziopsis excisa* (Dicks.) Konstant. & Vilnet (G5, SNR), and *Sphenolobopsis pearsonii* (G4, S1).

Table 2. Rare species found within the park. For each species, the sites where they were documented and the year are indicated, along with their global and state rank rarity as determined by [NatureServe \(https://www.natureserve.org/nsexplorer/about-the-data/statuses/conservation-status-categories\)](https://www.natureserve.org/nsexplorer/about-the-data/statuses/conservation-status-categories) and the specimen catalog numbers. NatureServe codes are the calculated rarity of a species at the global (G) and state (S) levels. These scale from 1 to 5, with 1 being critically imperiled and 5 being secure. Not ranked (NR) refers to a species that has not been ranked at that level.

Species	Site and Year Observed	NatureServe Ranking	Specimen Catalog Numbers
<i>Aneura sharpii</i> (thalloid liverwort)	Dry Run (38.39991°N 78.52892°W); 2023	GNR = Unranked S1 = Critically Imperiled	TENN-B-0139185 SHEN004700
<i>Cephaloziella spinicaulis</i> (leafy liverwort)	Little Stony Man Undisturbed (38.60307°N 78.36831°W); 2023 & 2025	G3 = Vulnerable S1 = Critically Imperiled	TENN-B-0139186 TENN-B-0139194 SHEN004701
<i>Lophoziopsis excisa</i> (leafy liverwort)	Little Stony Man Disturbed (38.60295°N 78.36818°W); 2023 Little Stony Man Undisturbed (38.60307°N 78.36831°W); 2025	G5 = Secure SNR = Unranked Closest states with ranking are North Carolina = S1 and Pennsylvania = S2S3.	TENN-B-0141115 SHEN004702
<i>Sphenolobopsis pearsonii</i> (leafy liverwort)	Little Stony Man Undisturbed (38.60307°N 78.36831°W); 2025	G4 = Apparently Secure S1 = Critically Imperiled	TENN-B-0139195 SHEN004702

Population and Habitat Assessment

Three of the rare bryophyte species located during this study were found at only one site each and one was found at two sites. Since these species were not present at both disturbed and undisturbed

sites, paired t-tests could not be used to test whether there was a difference in the abundance of the rare species between sites.

Aneura sharpii was found at Dry Run (38.39991°N 78.52892°W) in 2023 as a single contiguous patch 0.3 m² in area (TENN-B-0139185; SHEN004700). It was growing on a rockface at least 2 m above a stream. This patch of *A. sharpii* was not relocated in 2025 and no other patches of *A. sharpii* were found after two thorough searches of the site. Since this species was not relocated in 2025, a full habitat assessment could not be carried out. This site's vascular plant community type is a central Appalachian montane rich boulder field forest. The habitat quality is high, since the site is off trail and shows no signs of anthropogenic disturbance. However, the area where *A. sharpii* was found in 2023 was surrounded by multiple fallen trees that created gaps in the canopy and blocked the side stream below the rockface, which was covered in poison ivy (*Toxicodendron radicans*). Natural tree falls, due to the rocky substrate and steep slope that result in canopy opening, are considered the greatest threat to the population of *A. sharpii*. Open canopy areas change the microhabitat, both decreasing the shade and the moisture level, which is likely to have had a negative impact on this species.

Cephaloziella spinicaulis, *Lophoziopsis excisa*, and *Sphenolobopsis pearsonii* were all found at the Little Stony Man Undisturbed site (38.60307°N 78.36831°W). *Lophoziopsis excisa* was also found at the Little Stony Man Disturbed site (38.60295°N 78.36818°W). They were all collected without sex organs (gametangia) and based on previous collections this is typical for *C. spinicaulis* and *S. pearsonii*, however, typically *L. excisa* is found with sex organs (Hicks 1992; Schuster 1969). These three species are all physically very small and were only found scattered amongst other bryophytes (*Andreaea rothii*, *Dicranum fulvum*, *Scapania undulata*, and *Schistidium rivulare*). Patches of these physically larger bryophytes must be collected and examined microscopically to determine if these rare species are present.

The *C. spinicaulis* and *S. pearsonii* populations appear healthy. They were each found growing in two separate patches on the rockface at least 10 m from each other. The patches of bryophytes these rare species were growing in were 16 to 32 cm² (TENN-B-0139186, TENN-B-0139194, TENN-B-0139195, SHEN004701, SHEN004702). The rare bryophytes made up 1–5% of the plant biomass composing these patches. *Lophoziopsis excisa* was found growing in two patches of larger bryophytes that were 4 to 16 cm² (TENN-B-0141115, SHEN004702). The plants were also found sparsely scattered amongst other larger bryophytes also composing 1–5% of the plant biomass of the patch and appeared healthy. The *L. excisa* populations are likely to persist since it is a pioneer species that is one of the first to colonize rock (Schuster 1969), and there are many bare rock shelves and crevices that are open for colonization at both Little Stony Man sites.

The patch of *L. excisa* growing at the Little Stony Man Disturbed site was found at the southwest end of the overlook on thin soil and with a light level of at least 50% shade (TENN-B-0141115). The vascular plant community type at the Little Stony Man Disturbed site is a central Appalachian high-elevation heath barren / pavement. The vascular plant community type at the Little Stony Man Undisturbed site is a central Appalachian northern hardwood forest (yellow birch - northern red oak

type). The patch of *L. excisa* from the Little Stony Man Undisturbed site, which also included *S. pearsonii* (SHEN004702), was growing on thin soil on a horizontal rock shelf under a clump of grass which kept them moist and resulted in a light level of approximately 80% shade. The other *S. pearsonii* patch (TENN-B-0139195) was growing in a more open area of approximately 25% shade and the *C. spinicaulis* patches (TENN-B-0139186, TENN-B-0139194, SHEN004701) were growing in around 75% shade. The patches from the Little Stony Man Undisturbed site were growing in rock crevices that were persistently moist from ground water dripping onto the patches, though the water was not pooling.

The habitat quality at the Little Stony Man Undisturbed site was medium since there were about 50–75 rock crevices where bryophytes were growing and the rare species could potentially occupy. However, there were signs of human disturbance from rock climbers near where the rare bryophytes were found. The two greatest threats to these rare species at the Little Stony Man Undisturbed site are trampling and invasive species. The trampling would be due to the use of part of the site for rock climbing and the close proximity to a trail. A small patch of the invasive Japanese stilt grass (*Microstegium vimineum*) was found at the site which threatens invasion of the suitable habitat for all of the rare liverwort species and extirpation due to competition.

The habitat quality at the Little Stony Man Disturbed site was medium-high since there were many areas of shaded rock or thin soil covering rock along the border of the vascular plant vegetation where *L. excisa* could colonize. While there is extensive disturbance due to trampling at this site, it could contribute to the persistence of *L. excisa* at this site since trampling likely decreases competition keeping the rock and soil bare for colonization. A threat to the *L. excisa* population at Little Stony Man Disturbed is pollution, since some trash was observed at the site.

Predictors of Bryophyte Community Composition

Upon examination of the data generated from our GPS monitored surveys, the survey areas recorded for several of the larger sites appeared to be dramatically smaller than the area known to be surveyed (e.g., White Oak was recorded to have been surveyed for only 10 m², while a larger area was known to have been sampled). Thus, survey area was not included in our models due to our concerns regarding the accuracy of the GPS measurements.

Site Surveys: Alpha Diversity

After examining the AIC values for multiple versions of the linear mixed effects models, sampling time was dropped, and all the models were reduced to linear fixed effect models. The only models where the slope was significantly different than zero were alpha diversity across all sites ($F_{1,17} = 2.92$, $p = 0.017$) and alpha diversity across all water feature sites ($F_{8,14} = 3.93$, $p = 0.012$; Table 3). Bryophyte alpha diversity across all site surveys was significantly predicted by gap fraction ($F_{1,17} = 16.83$, $p = 0.0007$), elevation ($F_{1,17} = 7.95$, $p = 0.012$), and slope ($F_{1,17} = 5.84$, $p = 0.027$). Aspect ($F_{7,17} = 1.04$, $p = 0.44$) and the interaction between aspect and slope ($F_{7,17} = 1.66$, $p = 0.18$) were retained in the model; however, they were not significant predictors. This model explained a portion of the variance (Adjusted $R^2 = 0.49$). As gap fraction (canopy openness) and elevation increased, diversity decreased, while as slope increased diversity also increased. Alpha diversity of the water feature sites was significantly predicted by slope ($F_{1,14} = 11.29$, $p = 0.005$) and aspect ($F_{7,14} = 2.87$, p

= 0.044). This model explained a similar level of variance compared to the model with all site types included (Adjusted $R^2 = 0.52$). As the slope increased, diversity increased. We also observed lower diversity at western and southwestern aspects. All model results are shown in Table 3 and Table 4.

Table 3. Description of the linear models used to determine predictors of diversity and abundance. This includes response variables for a given model; the predictor variables retained in the model; the F -stat, degrees of freedom, and p -value of the ANOVA; and the adjusted R^2 of the model.

Response Variable	All Predictor Variables of Final Model	F -stat	df	p -value	Adjusted R^2
Alpha Diversity (all sites)	Gap fraction + Elevation + Slope + Aspect + Aspect:Slope	2.915	15, 19	0.017	0.49
Alpha Diversity (rock outcrop)	Visitor Use Intensity + Gap Fraction + Slope + Aspect	2.98	2, 9	0.28	0.62
Alpha Diversity (water feature)	Slope + Aspect	3.93	8, 14	0.012	0.52
Percent Cover (all paired sites)	Gap Fraction + Slope + Aspect + Slope:Aspect	5.51	3, 12	0.093	0.78
Percent Cover (paired rock outcrop)	Gap Fraction + Slope + Aspect + Slope:Aspect	6.94	2, 5	0.13	0.81
Percent Cover (paired water feature)	Slope + Aspect + Slope:Aspect	15.34	1, 6	0.19	0.92

Table 4. Description of the linear models used to determine predictors of diversity. This includes response variables for a given model, the predictor variables retained in the model, the F -stat and p -value associated with the predictor variable in the ANOVA, and the estimates of the regression coefficients of the predictor variables that indicate the direction and magnitude of the effect each predictor had on the response variable.

Response Variable and All Predictor Variables of Final Model	Predictor Variable	F -stat	p -value	Regression Coefficients (Direction and Magnitude of Predictor Effects)
Alpha Diversity (all sites) ~ Gap Fraction + Elevation + Slope + Aspect + Slope:Aspect	Gap Fraction	16.83	0.0007	-0.24
	Elevation	7.95	0.012	-0.0072
	Slope	5.84	0.027	0.033
	Aspect	1.04	0.44	North: -0.74 Northeast: 0.29 Southeast: -4.23 South: -23.69 Southwest: -15.15 West: -29.99 Northwest: -8.99

Table 4 (continued). Description of the linear models used to determine predictors of diversity. This includes response variables for a given model, the predictor variables retained in the model, the *F*-stat and p-value associated with the predictor variable in the ANOVA, and the estimates of the regression coefficients of the predictor variables that indicate the direction and magnitude of the effect each predictor had on the response variable.

Response Variable and All Predictor Variables of Final Model	Predictor Variable	<i>F</i> -stat	p-value	Regression Coefficients (Direction and Magnitude of Predictor Effects)
Alpha Diversity (all sites) ~ Gap Fraction + Elevation + Slope + Aspect + Slope:Aspect (continued)	Slope:Aspect	1.66	0.18	Slope:North: 0.011 Slope:Northeast: -0.15 Slope:Southeast: 0.12 Slope:South: 0.27 Slope:Southwest: 0.18 Slope:West: 11.68 Slope:Northwest: 0.12
Alpha diversity (rock outcrop) ~ Visitor Use Intensity + Gap Fraction + Slope + Aspect	Visitor Use Intensity	0.83	0.54	High: 24.89 Medium: -6.95 Low: -12.9
	Gap Fraction	5.38	0.15	-0.25
	Slope	3.14	0.21	0.22
	Aspect	3.33	0.25	Northeast: -14.72 South: 4.79 Southwest: 8.18 West: 25.54 Northwest: -6.34
Alpha diversity (water feature) ~ Slope + Aspect	Slope	11.29	0.005	0.038
	Aspect	2.87	0.044	North: -0.98 Northeast: 0.03 Southeast: 2.8 South: 5.58 Southwest: -13.52 West: -10.39 Northwest: 5.51

Disturbance Impact Surveys: Alpha Diversity and Percent Cover

Alpha diversity between disturbed and undisturbed sites was not significantly different for rock outcrop ($t_3 = -0.27$, $p = 0.8$) or water feature sites ($t_3 = 0.87$, $p = 0.45$; Figure 2). Percent cover between disturbed and undisturbed sites was also not significantly different for rock outcrop ($t_3 = -1.24$, $p = 0.3$) or water feature sites ($t_3 = -0.26$, $p = 0.81$; Figure 3).

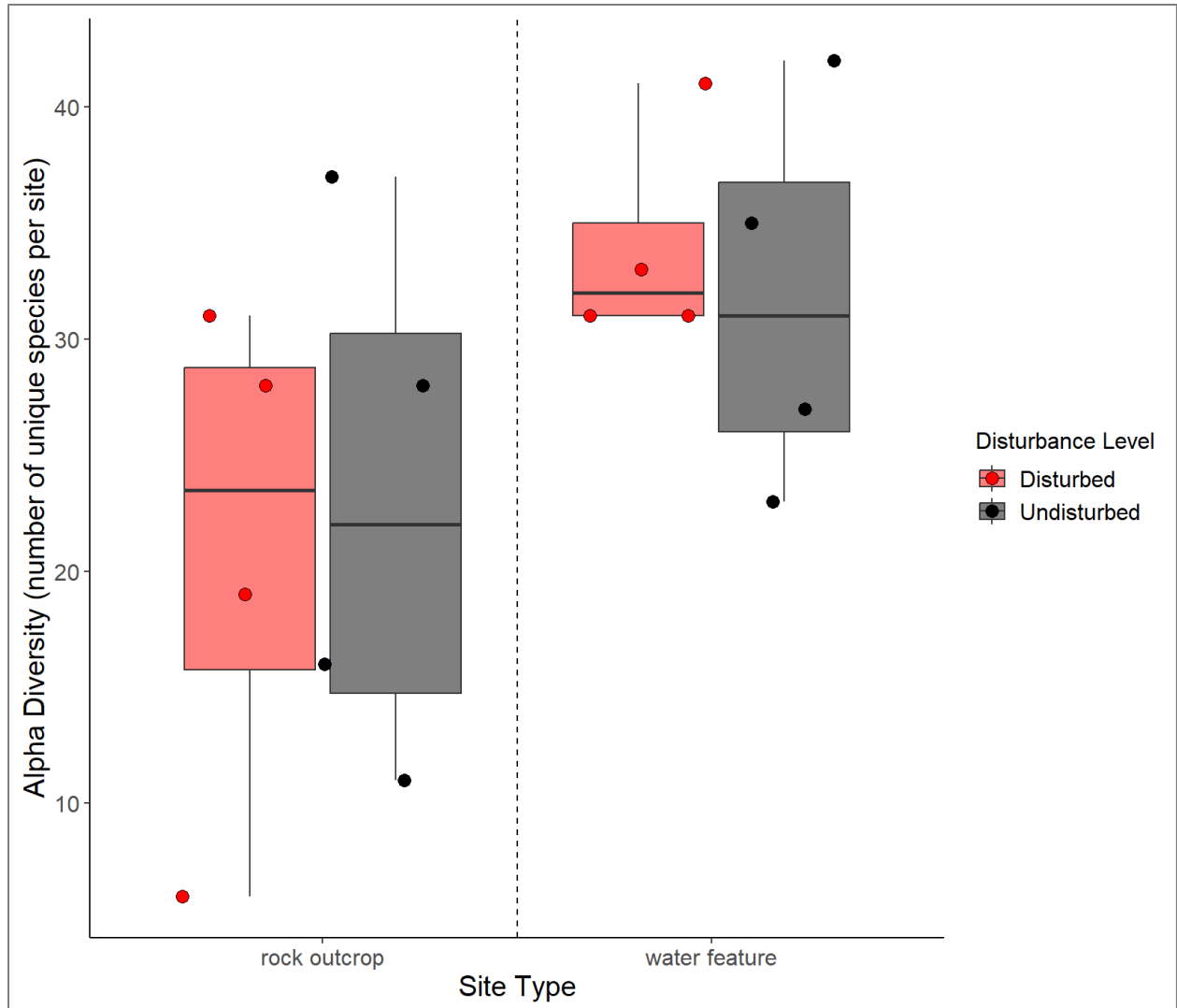


Figure 2. Alpha diversity comparing disturbed and undisturbed sites with either rock outcrops or water features from data collected using the transect surveys. Individual points represent a single site surveyed with red representing disturbed and black representing undisturbed sites. The midline represents the median while the whiskers represent the data falling outside of the interquartile range. Neither rock outcrops ($t_{5.9} = -0.278$, $p = 0.79$), nor water features ($t_{4.6} = 0.52$, $p = 0.623$) had significantly different levels of alpha diversity between disturbed and undisturbed sites.

NPS / SHERSHEN

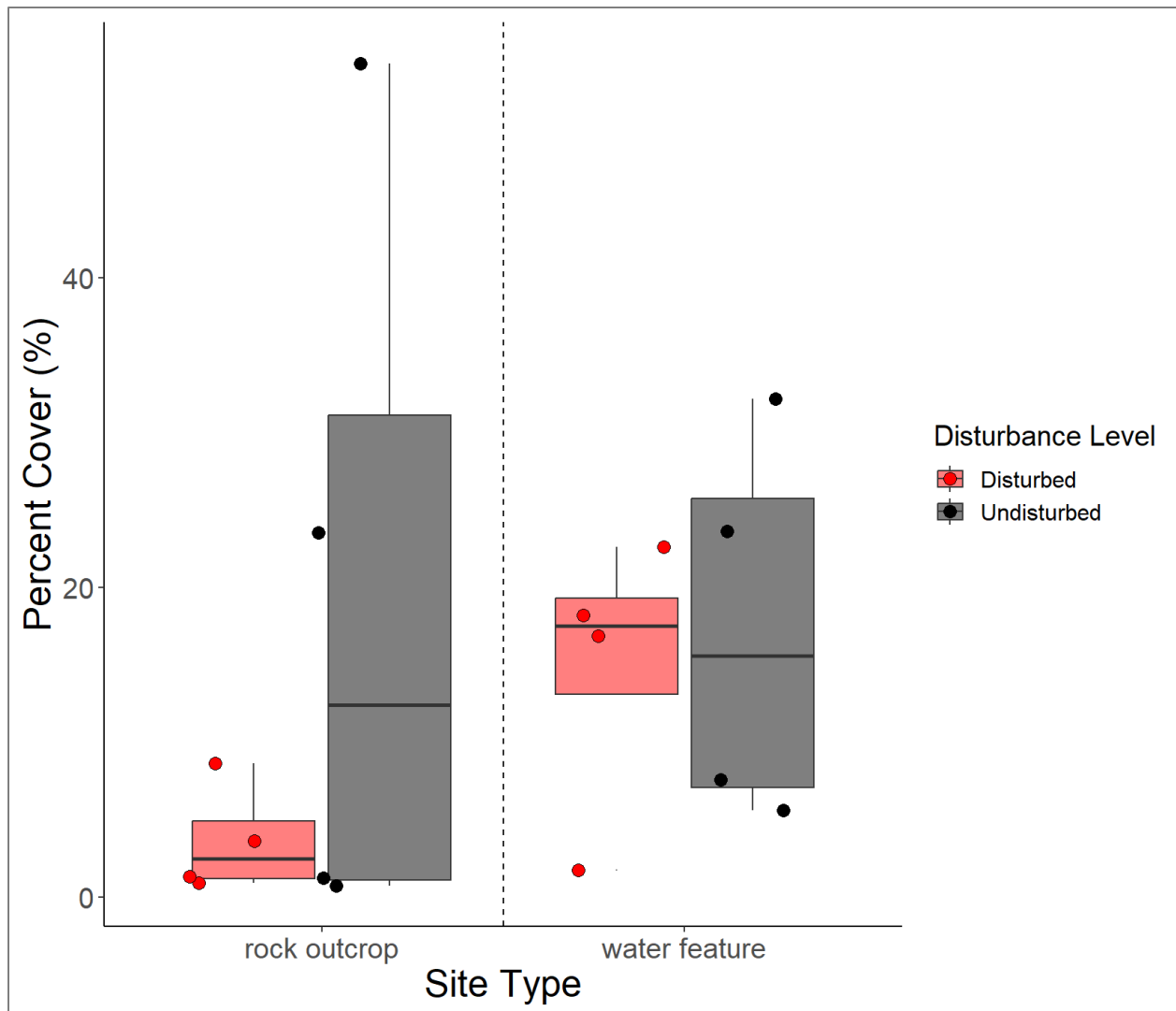


Figure 3. Absolute percent cover comparing disturbed and undisturbed sites for both rock outcrops and water features using transect surveys. Individual points represent a single site surveyed with red and black representing disturbed and undisturbed sites respectively. Whiskers represent the data that falls outside of the interquartile range while the midline represents the median. Neither rock outcrops ($t_{3,1} = -1.28$, $p = 0.287$), nor water features ($t_{5,4} = -0.30$, $p = 0.77$) had significantly different levels of percent cover between disturbed and undisturbed sites.

NPS / SHERSHEN

Disturbance Impact Surveys: Community Dissimilarity

The average dissimilarity between disturbed and undisturbed sites was above 60%, regardless of the site type or the Hill number (order of q) at which dissimilarity was examined (Figure 4). As the order of q increased, which places more weight on abundance, the average dissimilarity of the rock outcrop sites increased, while the average dissimilarity of water feature sites remained relatively constant. A notable exception to this trend occurred at the Millers Head rock outcrop sites, where dissimilarity between disturbed and undisturbed sites decreased with higher q values. NMDS analysis revealed that disturbed sites clustered together irrespective of site type, as did the undisturbed sites (Figures 5,

6). Stress values, measures of how well the ordination summarizes the distances between samples, was 9.19×10^{-5} for rock outcrops and 0.07 for water features, indicating a good (rock outcrops) and fair (water features) goodness-of-fit.

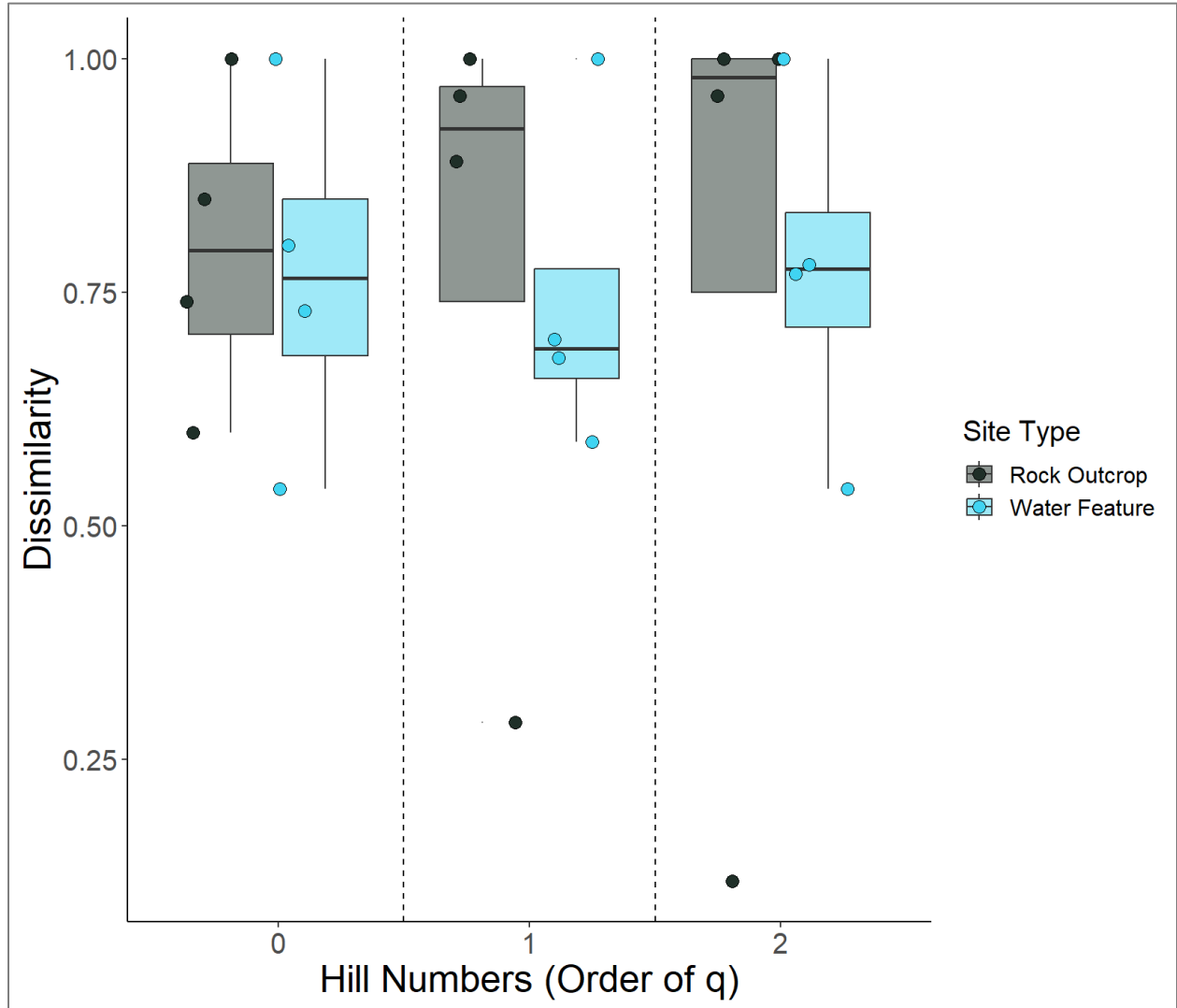


Figure 4. Dissimilarity values, where zero is 100% similar and one is 100% dissimilar, across various Hill numbers comparing paired disturbed and undisturbed rock outcrop (black) and water feature (blue) sites. Whiskers represent data that falls outside the interquartile range, midline represents the median, and outliers are points plotted above or below the whiskers. Individual points represent the comparison of two paired sites surveyed. Change in diversity is evaluated over Hill numbers ($q = 0$, species richness; $q = 1$, Shannon's diversity; $q = 2$, Simpson's diversity).

NPS / SHERSHEN

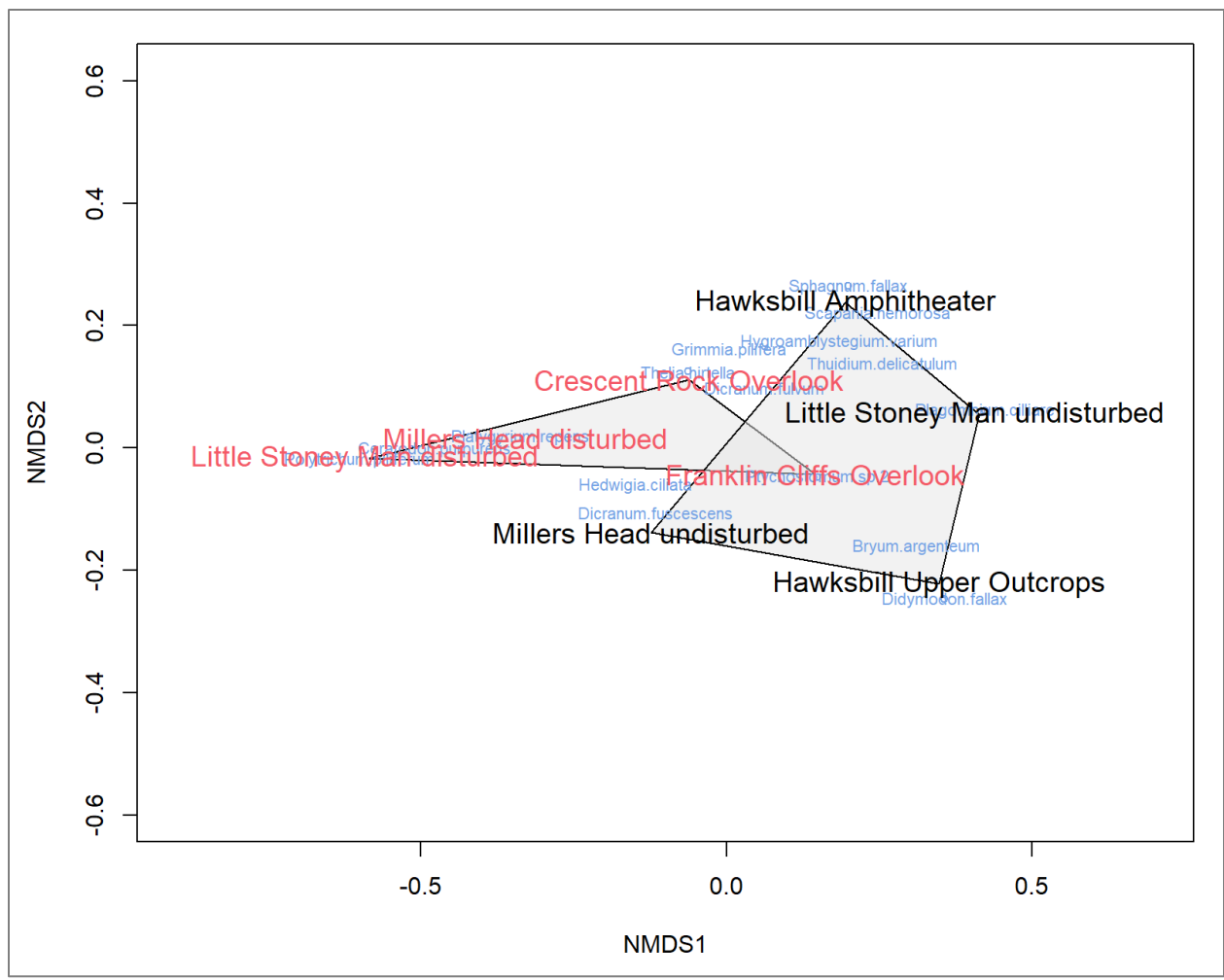


Figure 5. NMDS plot depicting how similar communities are at the paired rock outcrop sites. Disturbed sites are in red and undisturbed sites are in black with species in blue. The closer a species is to a given site, the more abundant it is relative to the other sites and thus these species may be drivers of dissimilarity between sites.

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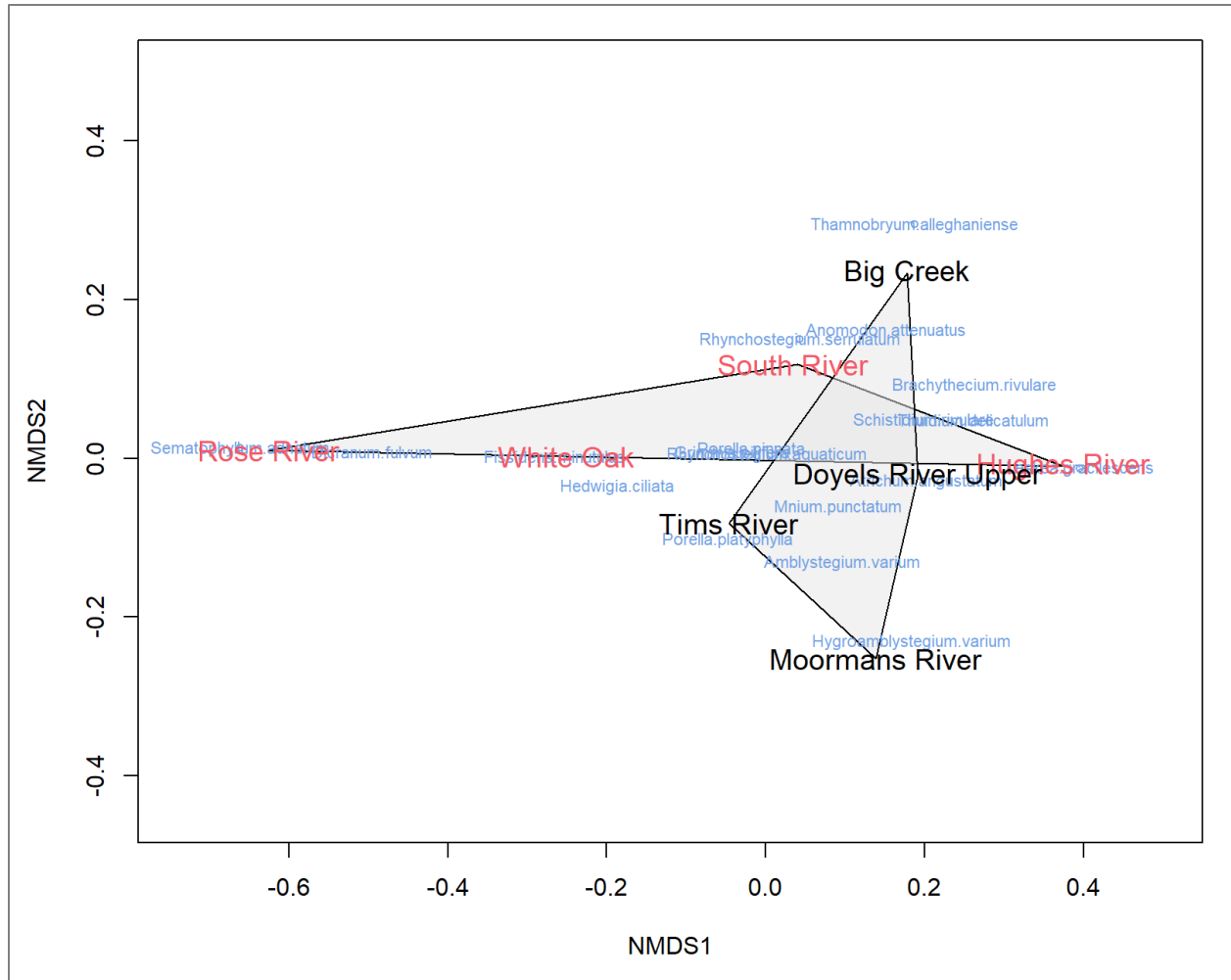


Figure 6. NMDS plot depicting how similar communities are at the paired water feature sites. Disturbed sites are in red and undisturbed sites are in black with species in blue. The closer a species is to a given site, the more abundant it is relative to the other sites and thus these species may be drivers of dissimilarity between sites.

NPS / SHERSHEN

Herbarium Curation

During the 2025 fieldwork at Shenandoah National Park the curation of the park’s herbarium was improved. The herbarium was registered with Index Herbariorum, which is the international registry for plant natural history collections, under the acronym SHEN (<https://sweetgum.nybg.org/science/ih/herbarium-list/?NamOrganisationAcronym=SHEN>). The SHEN herbarium also joined the Consortium of Bryophyte Herbaria (CBH) as a participating Collection (<https://bryophyteportal.org/portal/collections/misc/collprofiles.php?collid=186>). Then all the bryophyte specimens in the SHEN herbarium were transported to the TENN herbarium in Knoxville, Tennessee to be barcoded, imaged, and databased. The data for these 703 specimens (SHEN003997 to SHEN004699) was added into the CBH database, so that these records are now publicly available for future studies of bryophyte communities in Shenandoah National Park and more broadly across the landscape.

Discussion

Gap fraction, elevation, and slope were found to be significant drivers of alpha diversity for the site surveys. Contrary to our predictions, bryophyte diversity and abundance did not differ significantly between disturbed and undisturbed sites (Figures 2, 3). However, these findings describe the number of species and total bryophyte cover separately, whereas community composition examines them together. When we combine the two to understand differences in species composition between disturbed and undisturbed sites, regardless of site type, our data suggests that disturbance level may impact bryophyte community composition (Figures 4, 5, 6).

Rare Species

We found three species that were listed as rare at either the global or state level and one species that was a new state record for Virginia (NatureServe 2024; Consortium of Bryophyte Herbaria 2025; Table 1). *Sphenolobopsis pearsonii* has a scattered global distribution, but is uncommon in the United States, *Lophozia excisa* is common in tundra, alpine, and boreal regions with rare disjunct populations from Maine to North Carolina at high elevations in the Appalachians, and *Aneura sharpii* and *Cephaloziella spinicaulis* are endemic to the southern Appalachians. The sites where these species occur (Table 1) should be monitored to ensure their populations persist or potentially recover, as in *A. sharpii*. Many bryophyte taxa, including these rare species, can typically only be identified to the genus level in the field and a light microscope is needed to identify them to the species level. The guide to the rare bryophytes produced as part of this report will aid park staff in identifying these species to genus level in the field and to the species level under the microscope (Budke et al. 2026).

Cephaloziella spinicaulis, *L. excisa*, and *S. pearsonii* all occurred together at Little Stony Man Undisturbed, which is the cliff face below the upper Little Stony Man cliffs trailside vista (Little Stony Man Disturbed; Table 1). There is currently a sign permitting rock climbers to scale the rocks in the area where all three of these species are growing. Rock climbing has been shown to negatively impact plant community diversity and composition through trampling, gardening (displacing bryophytes from rock crevices for hand holds), and changing the pH of rocks with climbing chalk which creates an unsuitable habitat for bryophytes (Harrison et al. 2022; Tessler and Clark 2016; Hepenstrick et al. 2020). In order to protect these rare bryophytes, we recommend reducing the potential for human impact (Söderström 2006) by replacing this sign with one that prohibits gardening of climbing routes or rock climbing altogether in this area. The sign could also educate visitors about the rare and sensitive bryophytes they are protecting by avoiding climbing in this area and instead encouraging rock climbing in other approved areas of the park. Public education is an important part of conserving bryophytes since they are small and often overlooked (Hallingbäck and Tan 2010; Hallingbäck and Hodgetts 2000). Additionally, building a fence along the base of the cliff face would reinforce the rock-climbing prohibition and discourage hikers from approaching this area and disturbing the rare bryophytes. Due to the presence of Japanese stilt grass (*Microstegium vimineum*), the park should monitor the site for invasives and remove them when possible (Hallingbäck and Hodgetts 2000).

Lophozia excisa was the only rare species found at the Little Stony Man Disturbed site. Given its ruderal life-history strategy, trampling at this site may help to maintain the population rather than harming it (Schuster 1969). Most of the trampling occurs in the full sun area of the site, which is likely too hot and dry for *L. excisa* to colonize. *Lophozia excisa* has been observed to regularly produce gametangia (Schuster 1969), with the resulting sporophyte development and spore production potentially benefitting its persistence at the site. While trampling due to visitors is likely not to pose a significant threat to the *L. excisa* population at Little Stony Man Disturbed, trash pollution left by visitors could. Only a small amount of trash was observed at this site; however, “leave no trace” should continue to be stressed to visitors to preserve the habitat for this rare bryophyte.

Aneura sharpii was the only rare species found at Dry Run and this species was only found at this single site. Dry Run is not easily accessed by park visitors since it is not located near hiking trails. However, it is used by park staff for search-and-rescue training. To avoid trampling or disturbing patches of *A. sharpii* during these trainings, we recommend that park staff survey the area using the guide to the rare bryophytes (Budke et al. 2026) produced as part of this project to determine if *A. sharpii* is present where the training is intended to take place and avoid areas where it is growing. The other greatest threat to the *A. sharpii* population at Dry Run is gap formation in the tree canopy due to the steep and rocky terrain. Fallen trees or defoliation, leading to gaps in the tree canopy, typically increase solar radiation, mean temperature, and temperature fluctuations, and decrease relative humidity and surface soil moisture at ground level (Roberts 2004). *Aneura sharpii* is only found in wet, shaded habitats (Consortium of Bryophyte Herbaria 2025; Hicks 1992), so a change in these conditions could be lethal for this liverwort. Of the few specimens of *Aneura sharpii* ever collected, even fewer have been found with sexual reproductive organs or sporophytes (Consortium of Bryophyte Herbaria 2025), which could mean that its primary mode of dispersal and population regeneration is vegetative growth. Given that observation, it could be difficult for *A. sharpii* to colonize nearby rocks with suitable habitat that are not joined to or touching the one it currently inhabits. The ecology of *A. sharpii*, including its life-history strategy, remains unexplored (Inoue and Miller 1985). Given its habitat, it could be a ruderal species adapted to forest disturbance regimes and thus likely to recover from canopy gaps, such as those formed by downed trees between 2023 and 2025. Alternatively, it could be a competitive species that will become extirpated by disturbance and stress. Due to this knowledge gap and the relatively short timeframe in which Dry Run’s population of *A. sharpii* decreased from a patch 0.3 m² in 2023 to undetectable in 2025, we recommend that the park monitors the site for *A. sharpii* every two to three years (Roberts 2004) to determine if the population has been extirpated or is regenerating post-disturbance.

Environmental Variables

Canopy Cover

Bryophytes are sensitive to changes in canopy cover. As the number of canopy gaps increase the abundance and number of bryophyte species typically decrease (Halpern et al. 2014; Shershen et al. 2024). Based on this, it is not surprising that the number of species at our sites significantly decreased as gap fraction increased (Table 4). This observation may be due to the influence of gap

size on the abiotic conditions of the understory, where more open canopies have higher levels of solar radiation, which increases air temperature. Larger gaps also have higher soil moisture as there are fewer roots drawing up water from the soil matrix through transpiration (Gray et al. 2002). However, since bryophytes lack true roots to draw up water from the soil and instead rely on external water such as dew and rainfall for their supply, additional soil moisture has a lower impact on them. This is less concerning for vascular plants which can use water from the soil matrix, not just external water supply. In contrast, studies have found vascular plant diversity increases with gap size (Degen et al. 2005). This suggests that if bryophyte conservation is the goal, implementing conservation strategies that focus on increasing canopy cover may be beneficial (Berdugo and Dovciak 2019). That said, future work determining if there is a correlation between the abundance of specific tree species and increased bryophyte diversity could aid in narrowing down what tree species could be planted to better preserve bryophyte diversity.

Elevation, Slope, and Aspect

Elevation has been found to positively correlate with bryophyte diversity, which is a trend that is opposite in vascular plants (Dearborn and Danby 2017; Auld et al. 2022; Cacciatori et al. 2022; Shershen et al. 2024). However, our observations at SHEN did not find a positive correlation between elevation and bryophyte diversity. The relationship between elevation and diversity was slightly negative. Elevation was only a significant predictor when all sites were examined together but was dropped from the models when analyzing water features separately. Considering this, other variables such as gap fraction may be more important to consider when designing and implementing bryophyte conservation practices in SHEN.

In other studies slope has been shown to negatively impact bryophyte diversity (Horvat et al. 2017), however, our data indicated higher bryophyte diversity with increased slope. This aligns more closely with literature regarding vascular plants wherein slope initially increased vascular plant diversity, however, above a slope of 25 degrees, diversity declined (Zhang et al. 2018). Our sites ranged from 0 to just under 60 degrees. These maximums represent the sheer wall-faces of the rock outcrops or waterfalls, not necessarily the landscape we were able to traverse. However, those sites with steeper slopes also had a more diverse range of slopes. As such, bryophytes may experience a tipping point similar to vascular plants, but they may have a higher tolerance level. It may be that steeper slopes can only be colonized by specific species of bryophytes that are not found on shallower slopes, thus increasing the diversity when the steeper slopes are sampled. This would explain why we observe higher diversity at steeper sites.

Another possibility is that there are fewer park visitors disturbing the bryophyte communities on steeper slopes since only experienced hikers and those with specialized equipment may be able to disturb such communities. This idea is supported by our data from the rock outcrop sites, whereas visitor use increased, diversity decreased, while as slope increased, diversity also increased. Even though neither of these predictors were significant, they still provide insight as to what may be going on in Shenandoah rock outcrops.

The positive relationship between increasing slope and diversity was significant for water feature sites. The models explained a majority of the variance, however, other factors such as the water flow rate, which we did not measure in this study, could be important in determining diversity. Slope and water flow rate are known to be positively correlated yet the relationship between flow rate and diversity has been little studied, with Slack and Glime (1985) mainly focusing on within stream differences, not between site differences. They did note that streams with different flow rates supported different species, but more work would be needed to determine if the interaction of water flow and slope predict bryophyte diversity within SHEN.

Aspect has also been shown to influence bryophyte diversity, with southern facing slopes being less diverse in the northern hemisphere (Åström et al. 2007). We found that south and southwest facing slopes negatively impacted bryophyte diversity at water feature sites. However, the small sample size of sites included in this study means that a limited number of different aspects were included. A future study with more sites across diverse slope aspects could enhance our understanding of this relationship. Previous studies have shown that different aspects promoted diversity of different kinds of vascular plants, with forbs and sedges increasing in abundance on southern facing slopes, while shrubs increased on northern facing slopes (Zhang et al. 2022). This could explain why bryophytes are less diverse on southern facing slopes, as they are unlikely to outcompete forbs and sedges for space whereas some species can take advantage of the shady areas beneath the shrubs. It is likely that the microclimates of these aspects, along with the differences in vascular plant communities, are driving the differences in bryophyte assemblages. Future work could examine if vascular plant communities and microclimate conditions predict bryophyte diversity and if those correlate to different aspects.

Disturbance and Dissimilarity

By examining both diversity and abundance in tandem, we can determine whether bryophyte communities as a whole are different as a result of anthropogenic disturbance. We observed high levels of dissimilarity across both site types when comparing disturbed and undisturbed sites, with the notable exception of Millers Head (Figure 4). In addition, despite some overlap in disturbed and undisturbed sites in our NMDS plots, we see the communities of similar disturbance levels cluster together (Figures 5, 6). The overlap in rock outcrop sites may be explained by the undisturbed Millers Head site being similar to the disturbed site, as seen with the low dissimilarity values (Figure 4). The overlap in water feature sites may be due to the Hughes River and Moorman's River pairing which had lower levels of dissimilarity than the other pairings (Figure 4) but not as low as the Millers Head pairings. These sites were selected based on perceived visitor use, which may not correlate to realized disturbance levels. It may be that Hughes River and Moorman's River sites are not distinct enough regarding disturbance levels as previously thought, despite having differing visitation intensities. All other site pairings displayed both high levels of dissimilarity and clustered apart from their partner, suggesting that both the species and how abundant they are in these communities are distinct. Since we standardized site pairings for environmental variables that have been shown to influence bryophyte communities either directly or indirectly, this leads us to conclude that some other factor is driving the observed differences. We paired these sites based on visitor use as a proxy

for disturbance level, and it is highly probable that such anthropogenic disturbance is driving the observed differences between paired sites.

Studies have shown that trampling and tourism related disturbance can alter the community composition of a landscape for vascular plants, where the more frequent the trampling and the larger the area of impact, the less diverse the communities become (Pickering and Hill 2007). Others have shown that the functional trait diversity declines with increased trampling as well, lending further support to this case (Li et al. 2023). Rare species are especially prone to the negative effects of human trampling and tourism disturbance, as seen in Europe where 194 of the 462 species within the IUCN Red listings were associated with such activities (Ballantyne and Pickering 2013).

Trampling damage to bryophytes is not as well studied compared to vascular plants, and results indicate varying effects. Hamburg et al. (2008) found that bryophyte diversity and abundance declined on urban trails experiencing trampling. They attributed this decline to trampling induced changes in the microclimate and suggested implementing 50-meter buffer areas at a minimum around trails to ensure that species sensitive to disturbance have suitable habitat to maintain their populations. This minimum buffer zone may need to be increased depending on the frequency of trail use and the level of concern for the species. Other studies examining *Sphagnum* noted its high sensitivity to trampling (Ketchledge 1971), with species such as *Sphagnum rubellum* only tolerating up to 80 tramples in a montane heath community in Scotland (Bayfield 1971). Such trespassing can have lasting effects, with footprints in sphagnum bogs persisting for up to 30 months (Slater and Agnew 1977). Other species can take up to 5 years to recover from trampling (Westhoff 1967). That said, mosses underneath other mosses in a spruce forest have been shown to be more resilient to trampling than those exposed in a mat (Kellomaki 1973). Studlar (1980) found that trails had higher bryophyte diversity compared to trail adjacent plots, however, the species that increased the diversity were more common taxa. This may suggest that common species are more resilient to trampling damage, however, no study to our knowledge has examined whether trampling disturbance more greatly impacts rare species.

Conclusion

Several environmental variables, especially gap fraction, were predictors of bryophyte diversity and abundance. We also found that despite similar species counts and total bryophyte cover, the overall composition of disturbed sites was different than that of undisturbed sites as seen in the levels of dissimilarity and NDMS plots. These differences were likely driven by anthropogenic disturbance, such as trampling damage which can alter the abiotic conditions of the disturbed area. Our results suggest that canopy conservation may also benefit the bryophyte communities in the understory, as sites with higher canopy cover had higher diversity and decreased canopy cover appeared to have a negative impact on a rare bryophyte population. Other efforts should be made to monitor the populations of rare species and add signage around the sites where they are found to reduce human impact. Future work could explore transplanting lab-grown populations of rare species into suitable habitats, as well as determining suitable microclimates for these species in order to maximize the success of transplanted populations. General work exploring the relationship between tree species occupying the canopy and bryophyte diversity could also aid in the overall bryophyte community conservation work within the park.

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