

Environmental determinants of bryophyte community change over time

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Abstract

Environmental factors mediating community change over time have been well documented for vascular plants, but not for their non-vascular relatives, bryophytes. Elevation is one variable that has been explored regarding bryophyte community change wherein as elevation increases, bryophyte communities increase in diversity and abundance, whereas diversity and abundance decline for vascular plant communities. This begs the question, how might other environmental variables such as slope and aspect influence bryophyte communities, and how might these variables drive community changes over time? Our study focused on bryophyte communities in high elevation, spruce-fir zones in the Great Smoky Mountains National Park (GSMNP), located in the Southeastern United States to answer this question. Plots established in 2007 were revisited and reinventoried in 2020. Comparisons were drawn to determine whether changes in bryophyte coverage corresponded to canopy cover change and environmental factors including elevation, slope, and aspect. Diversity and abundance at the two timepoints were analyzed. Alpha diversity and turnover across orders of q were compared for different elevation zones. Bryophyte alpha diversity at $q = 0$ significantly declined over time in association with elevation, but at $q = 2$, changes in alpha diversity varied according to changes in gap fraction, a measure of canopy cover, and slope. Bryophyte coverage remained stable except in the highest elevation zone dominated by fir trees where there was a decline in coverage predicted by aspect. There were high rates of turnover across all elevation zones regardless of Hill number. In contrast with other studies which examine how environmental variables mediate community changes at $q = 0$, the species richness of a community, our study shows that the environmental drivers of bryophyte community change vary depending on how abundance is weighted.

KEY WORDS

aspect, bryophyte, canopy cover, community composition, high elevation, hill numbers, slope, turnover

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INTRODUCTION

Vegetation communities can change as a consequence of various pressures and disturbances (Leßmeister et al., 2019; Meng et al., 2015; Wilson & Nilsson, 2009). Changes can be relatively brief wherein a community reverts to a previous stable state, such as communities recovering after a fire (Meng et al., 2015). Alternatively, changes may persist, thereby shifting the distributions of community members to track favorable conditions (Jacobson et al., 1987), or when species are lost because of community disassembly (Lindo et al., 2012; Zavaleta et al., 2009). Environmental variables, such as elevation, slope, and aspect, have been shown to mediate vascular plant

community changes over time (Auld et al., 2022; Bale et al., 1998; Bennie et al., 2006). However, how environmental variables such as slope, aspect, elevation, and canopy cover interact to influence bryophytic communities over time has not been studied extensively.

Bryophytes, particularly mosses and liverworts, are major understory community members in temperate montane forests (Chen et al., 2017), like those in the southern Appalachians including in the Great Smoky Mountains National Park (GSMNP) (Davison et al., 1999; Smith et al., 1991; Stehn et al., 2010a, 2010b) (Figure 1A). Across ecosystems, bryophytes provide key ecosystem services such as enhancing soil stability (Gao et al., 2020) which reduces nutrient run-off (Silva et al., 2019;

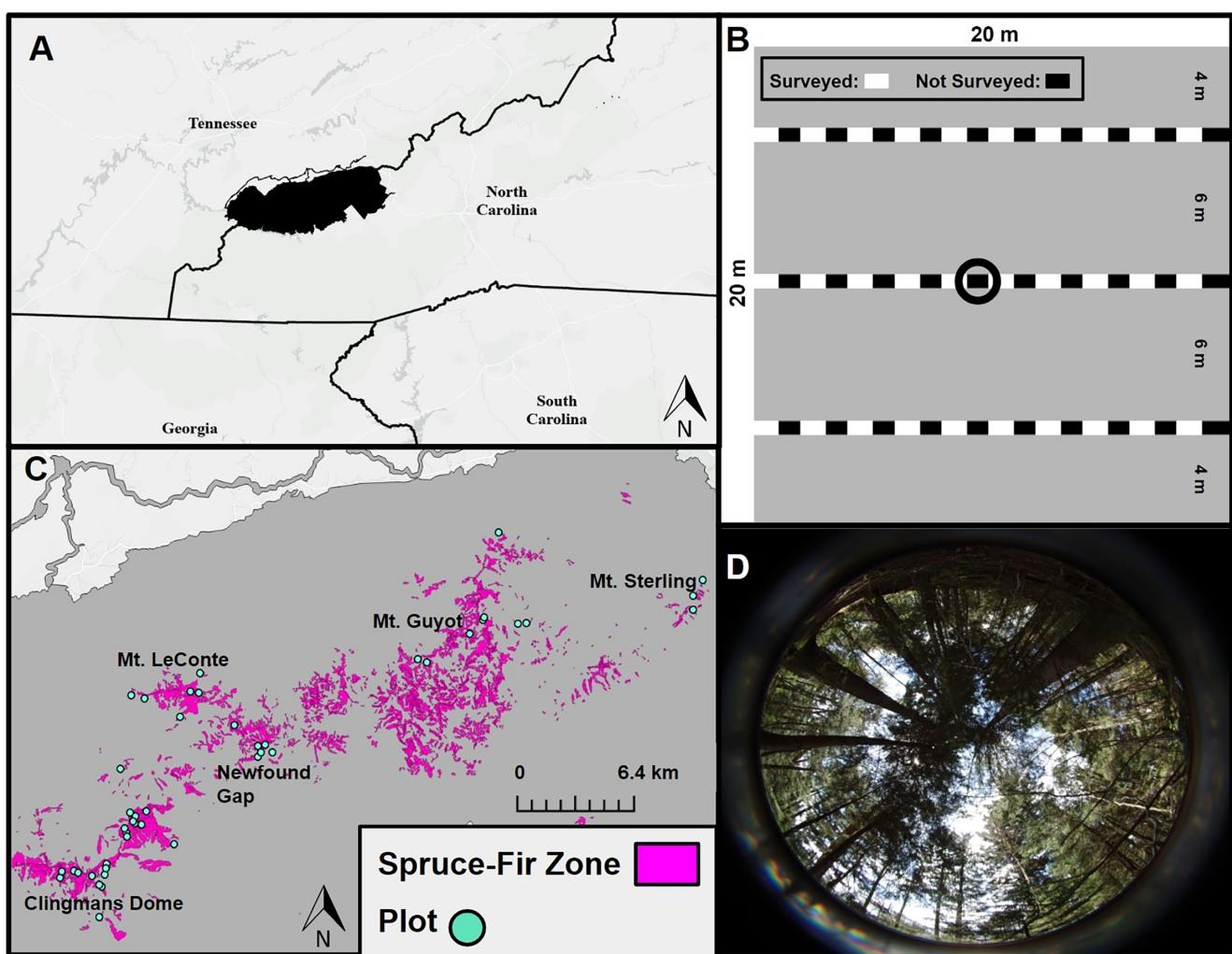


FIGURE 1 (A) Location of the Great Smoky Mountains National Park highlighted in black. (B) Sampling design for community composition in each 20 × 20-m plot. Each checkered line represents a 20-m transect line across the plot, spaced out 6 m from one another and 4 m from the edge of the plot. The white blocks represent the 10 m where bryophytes were surveyed. The black blocks represent the alternating 10 m where bryophytes were not surveyed. Thus, a total of 30 m was sampled per plot. The black circle in the center represents the location where the fish-eye photo was taken in each plot as well as the central point for tree community composition data collection. (C) Map of the Great Smoky Mountains National Park with the spruce, spruce-fir, and fir zones in magenta, and the 45 plots surveyed in 2020–2021 in light green. (D) Example of a fish-eye photo taken at the center of each plot; photo credit: Eric Shershen.

Van Miergot et al., 2007), and providing habitat for macroinvertebrates (Coyle, 2009; Ziesche & Roth, 2008) as well as microorganisms (Bartels & Nelson, 2007). Ecosystems may experience a loss of ecosystem functions due to insufficient knowledge regarding the drivers of bryophyte community change over time.

Environmental variables are known to impact bryophyte communities over spatial gradients at a single point in time. It has been shown that as elevation increases, bryophyte diversity increases (Dearborn & Danby, 2017), whereas slope has the opposite effect (Horvat et al., 2017). Aspect has also been shown to influence bryophyte community composition (Åström et al., 2007). Other determinants of bryophyte community composition that are more dynamic include canopy cover and temperature (Halpern et al., 2014; van Zuijlen et al., 2022; Walker et al., 2006). However, many of these static abiotic variables have been shown to interact and or correlate with these dynamic variables (Cacciatori et al., 2022; Gray et al., 2002; Griffiths et al., 2009; Phan et al., 2018; Ritter et al., 2005; Sospedra-alfonso et al., 2008), creating complex systems wherein all components warrant further examination to determine their effects on bryophyte communities over time.

Most prior work examining how environmental variables shape bryophyte communities over time has focused on experimentally altering conditions to simulate climate change (Alatalo et al., 2015; Scarpitta et al., 2017; van Zuijlen et al., 2022). There has been only one study to our knowledge that has examined how environmental variables mediate bryophyte community change over time focused on elevation and tree stand dynamics (Cacciatori et al., 2022). This study found contrasting results compared with vascular plant studies of elevation impacting communities over time (Auld et al., 2022). It follows that if bryophyte community responses differ in respect to one environmental variable, that responses to other variables might also differ. Our study addresses this knowledge gap by examining how environmental variables, including elevation, slope, aspect, and canopy cover, mediate observed changes in bryophyte community composition over time.

Here we address the following questions to advance understanding of bryophyte community compositional change: (1) How do bryophyte alpha and beta diversity change over time? (2) How does the abundance of bryophytes change over time? (3) Do environmental variables (e.g., canopy cover, elevation, slope, and aspect) elicit changes in bryophyte community composition? To achieve these objectives, we compared bryophyte community composition from the GSMNP over a 12-year period, which prior work suggests is sufficient to detect changes in bryophyte abundance and community composition (Fenton et al., 2003). We hypothesized that

bryophyte species richness and abundance had declined over time in response to changes in canopy cover, which has been shown to influence bryophyte communities (Halpern et al., 2014). As it has been shown that bryophyte communities are distinct along elevational (Stehn et al., 2010a) and aspect gradients at one timepoint (Åström et al., 2007), we accordingly, hypothesized that elevation and aspect would be significant predictors of bryophyte community compositional change over time as well. To the best of our knowledge, no prior work has examined whether bryophyte community composition varies across slope gradients above 20%. The maximum slope gradients within our plots were ~75% and did not greatly vary. As such, we hypothesized that slope would not contribute to any changes to the bryophyte communities. To better predict how bryophyte communities will change in the future and thus preserve the ecosystem functions they provide, it is imperative to understand how environmental variables impact their communities.

METHODS

Study site

Across the southern Appalachian Mountains of the eastern United States, plant communities are influenced by an array of abiotic and biotic factors. Peaks of the southern Appalachians are dominated by red spruce trees (*Picea rubens* Sargent) from 1370 to 1646 m, red spruce and Fraser fir (*Abies fraseri* Poiret) trees from 1646 to 1860 m, and almost exclusively Fraser fir trees from 1890 m to the highest elevations at 2024 m (Whittaker, 1956). A major biotic disturbance for the high-elevation southern Appalachian ecosystems was the arrival of an invasive European insect, *Adelges piceae* Ratz. (balsam woolly adelgid [BWA]). First found in the southeastern United States in the 1950s (Spears, 1958), BWA has resulted in the death of >90% of Fraser fir trees across the southern Appalachians (Dull, 1988). In two recent studies, both Smith and Nicholas (2000) and Kaylor et al. (2016), showed that Fraser fir trees have recovered by increasing in abundance, specifically in the understory, but these gains have not reached preinvasion levels. Nonetheless, recent changes in Fraser fir canopy have most likely influenced the community composition of understory herbaceous plants, especially bryophytes.

Sampling

We conducted a comparative analysis of bryophyte community composition in GSMNP. One set of data was collected in 2007/2008 (Stehn et al., 2010a) and the other

was collected in 2020/2021, representing a time span of 12–13 years. In 2007/2008, 60 plots were established ranging in elevation from 1262 to 1964 m. Plots were no more than 500 m off of roads or trails, and had an over-story dominated by either Red Spruce, Fraser Fir, or a combination of the two species. During the summers of 2020 and 2021, 45 of the 60 established plots (Stehn et al., 2010a, 2010b) were resurveyed. The other 15 plots studied in 2007/2008 were excluded from the 2020/2021 survey due to safety concerns with site accessibility and to reduce habitat disturbance to the endangered spruce-fir moss spider (*Microhexura montivaga*; Crosby and Bishop) (U.S. Fish and Wildlife Service, 2019). The 45 plots surveyed in 2020/2021 ranged in elevation from 1428 to 1963 m, which overlaps with a broad range of the elevations surveyed in 2007/2008.

Sampling methods in 2020/2021 plots replicated those of the 2007/2008 study, and were located using GPS coordinates (Stehn et al., 2010a). Within each 20 × 20-m plot, bryophyte abundance was measured via the line-intercept method along three 20-m transect lines spaced 6 m apart, perpendicular to the slope of the plot. Bryophytes were surveyed along every alternating meter on a transect line for a total of 30 m per plot (Figure 1B). Coverage was recorded to the nearest centimeter as the length of (1) bryophyte by species, (2) bare soil, (3) rock, (4) decaying wood, (5) live tree, (6) litter, or (7) lichen cover along the transect line. Additionally, substrate and habitat description (e.g., dry streambed) were recorded for each bryophyte sample that was collected to aid in identification. At every plot, 4 cm² of each unique bryophyte species was collected for species identification to create a voucher specimen. The specimens were collected from the edge of the bryophyte mats to reduce disturbance to spruce-fir moss spider habitat. All specimens were identified to species using either *The Flora of North America* (Flora of North America Editorial Committee, 1993), *The Mosses of Eastern North America* (Crum & Anderson, 1981), or *Guide to the Liverworts of North Carolina* (Hicks, 1992). Certain specimens from 2007/2008 were referenced to ensure especially challenging species were paired correctly and to ensure nomenclature changes did not influence abundance comparisons. Specimens from 2020/2021 were deposited in the University of Tennessee Herbarium (TENN) (catalog TENN-B-0132932 – 0133272) in Knoxville, Tennessee.

Canopy cover and tree community composition were collected at both timepoints; however, the methodologies differed. In 2007/2008, a fish-eye photo was taken at the midpoint of each of the three 20-m transect lines per plot. Owing to a lack of field assistants resulting from COVID-19 restrictions in 2020/2021, we took a single fish-eye photo per plot at the midpoint of the middle transect line. The middle transect photos were used to

assess changes in gap fraction, a way to examine canopy cover, over time. As such, when we examined tree community composition, we focused on the trees captured within our fish-eye photo utilizing the point-quarter method (Khan et al., 2016). The 2007/2008 study examined every tree within each 20 × 20-m plot with a dbh ≥ 10 cm, which for some plots was >85 trees. The point-quarter methodology used in 2020/2021 divided the plot into four quadrants centered on the midpoint of the middle transect line (Figure 1B). We measured the distance from the central point to the five closest trees per quadrant, while maintaining the 10-cm dbh cutoff, for a maximum of 20 trees per plot. If another tree had canopy branches within the fish-eye photo, the tree was recorded only if there were fewer than five trees already recorded for that quadrant.

Data analysis

Bryophyte community change was assessed in several ways. Bryophyte abundance was calculated as the percentage of total bryophyte cover, across the total 30 m of transect length surveyed in each plot. To determine if abundance changed from 2007/2008 to 2020/2021, we used a paired *t* test to examine the difference in bryophyte abundance in each plot. Individual species abundances were also analyzed using a paired *t* test with a sequential Holms-Bonferroni correction. In order to determine whether alpha diversity changed over time, a paired *t* test was used wherein the alpha diversity value for each plot was considered as an independent sample. Alpha diversity is defined here as the total number of unique species in a given plot. Alpha diversity was calculated over multiple Hill numbers using the diversity function in the vegan package (Oksanen et al., 2016). Hill number diversities vary over orders of parameter *q*, which alters the sensitivity to the abundances of species present when calculating diversity metrics. At *q* = 0, diversity is only examined at the presence and absence levels, or simply species richness. At *q* = 1, diversity is dependent on relative abundance, and is based on the exponential of Shannon's entropy. At *q* = 2, the diversity depends mainly on the common species and is equal to the inverse of Simpson's concentration (Marion et al., 2017). This enables the importance of rarer species to be down-weighted as the order of *q* increases, as well as to compare how the main taxa of a community shift, which typically provide a majority of the ecosystem services in the community. The change in species richness and the change in percent cover were calculated by subtracting the difference in alpha diversity and the amount of bryophyte coverage within a plot between the two time

points, respectively. All analyses were conducted in R version 4.1.2 (R Core Team, 2021).

Gap fraction was calculated by converting the raw fish-eye photos from both timepoints to binary pixel images in ImageJ (Schneider et al., 2012) using the add-on Hemispherical 2.0 (Beckschäfer, 2015). We then compared the number of gap pixels to the total number of pixels to measure gap fraction. The resulting values were normalized by log transformation and then analyzed using a paired *t* test with each plot considered as an independent sample.

General linear models were used to determine whether the response variables, change in abundance and change in alpha diversity (respectively, over various Hill numbers), were influenced by the following predictor variables; elevation, slope, aspect, and change gap fraction. All models were then selected using a backward stepwise Akaike information criterion (AIC) function to determine which predictors, if any, significantly influenced the response variables using an ANOVA.

Beta diversity, defined here as the turnover between the communities at the two timepoints, was analyzed using the R package hillR (Li, 2018) over multiple Hill numbers to determine whether species turnover occurred between the two sampling events. Turnover was calculated over various orders of q after dividing the plots into their elevation zones: spruce, spruce-fir, and fir. To determine whether beta diversity values were significantly different from one another, calculated pairwise turnover rates were compared across each Hill number between elevation zones. Data were log transformed at $q = 0$, and data were arcsine square root transformed at $q = 1$ and $q = 2$. The resulting datasets were then analyzed using an ANOVA followed by a post hoc Tukey test to determine whether there were different turnover rates at different elevations. Tree community turnover was calculated using the hill_taxa_parti_pairwise function in the hillR library in R, tested over various orders of q and across the three elevation zones to determine whether any species turnover had occurred over time. Turnover was then analyzed using an ANOVA followed by a post hoc Tukey

test to determine whether there were different turnover rates at different elevations.

RESULTS

In 2020/2021, we detected 63 species of bryophytes in the spruce, spruce-fir, and fir zones across the GSMNP compared to 98 species in 2008. Comparisons revealed that the numbers of bryophyte species decreased across all functional groups: from 39 to 31 for pleurocarpous mosses, 26 to 25 for acrocarpous mosses, and from 33 to 7 species for liverworts.

Gap fraction and tree community composition

Gap fraction and tree species richness did not significantly change over the 12-year period across all plots regardless of elevation (Table 1). Tree community turnover rates were not significantly different across any of the various Hill numbers.

Abundance

Average bryophyte abundance did not significantly change across the plots over the 12-year period (Figure 2B). When bryophyte abundance was examined by Whittaker's elevation zones, low and medium elevation abundances did not significantly change over time, but high elevation bryophyte abundance significantly decreased (Figure 2D). When individual species abundances are examined, only eight species of bryophytes have significantly decreased (declining species), while the remaining 55 species have not significantly changed (stable species) as shown in Table 2. Only one species significantly increased in abundance (*Hypnum pallescens* (Hedwig) P. Beauvois). The declining species were three pleurocarpous mosses (*Brotherella recurvans* (Michx.), *Bryhnia novae-angliae* (Sull. & Lesq.) Grout, and *Isopterygium tenerum* (Swartz) Mitten), three acrocarpous mosses (*Dicranodontium denudatum* (Brid.)

TABLE 1 Mean gap fraction and change in gap fraction at each of the elevation zones.

Elevation zone	Mean gap fraction			<i>p</i>	df	<i>t</i>
	2007/2008	2020/2021	Change			
Spruce	9.74	13.51	3.77	0.44	7	-0.83
Spruce-fir	10.88	11.00	0.12	0.97	27	-0.038
Fir	10.57	11.10	1.43	0.52	8	-0.67

Note: A paired *t* test was used to compare gap fraction between the two timepoints.

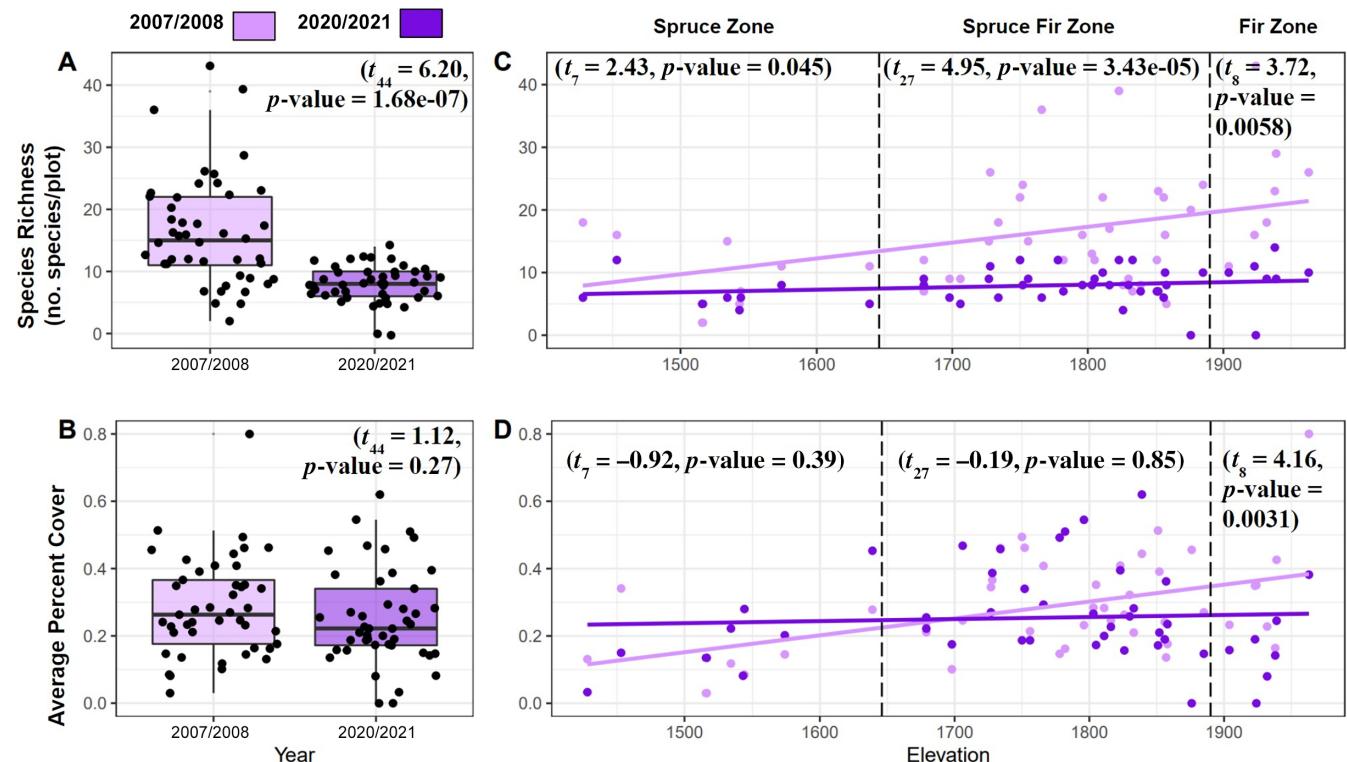


FIGURE 2 Changes in bryophyte species richness and abundance over 12 years in the Great Smoky Mountains National Park. Individual points represent associated plot's measurement for all figures. Whiskers represent variability outside the first and third quartiles, midline represents the median, and outliers are points plotted above or below the whiskers. (A) Species richness significantly declined over time across all plots. (B) Average bryophyte abundance in percent cover across the plots has not significantly declined over time when all plots are considered. (C) Species richness significantly declined across all elevation zones. (D) Average bryophyte abundance in percent cover has significantly decreased over time in the fir zone, but not significantly changed over time in the spruce or spruce-fir elevation zones.

Britt., *Polytrichastrum pallidisetum* (Funck) G.L. Sm., and *Tetraphis pellucida* Hedw.), and two liverworts (*Lepidozia reptans* (Linnaeus) Dum. and *Nowellia curvifolia* (Dicks.) Mitt.).

Richness

Species richness significantly declined over the 12-year period when considering all the plots (Figure 2A), and there were high rates of bryophyte turnover as well. When the plots were divided by their respective elevation zone, as defined by Whittaker (1956), richness significantly declined across all elevation zones with the greatest change occurring in the highest zone (Figure 2C), and this trend was also seen when examined across orders of q (Figure 3). Bryophyte beta diversity varied across time at various orders of q (Hill numbers) and between different elevation zones (Figure 4). As the order of q increased, low elevation turnover increased, but at medium and high elevations, turnover decreased. At $q = 0$, bryophyte communities in the high elevation zone had significantly more turnover

(and thus species loss) between timepoints than communities in the medium elevation zone, while turnover between timepoints in bryophyte communities at low elevation was not significantly different than that at either medium or high elevation. At $q = 1$ and $q = 2$, low elevation communities had significantly more turnover than those at medium elevation, but those at high elevation were not significantly different than those at low or medium elevation communities (Figure 4).

General linear models

Change in overall bryophyte abundance was predicted by elevation ($F_{1,42} = 4.25$, $p = 0.046$) and aspect ($F_{1,42} = 4.35$, $p = 0.043$) and explained some of the variance ($R^2 = 0.185$). For change in species richness, the top AIC model predictors varied across the various orders of q . Change in species richness at $q = 0$ was predicted by elevation ($F_{1,41} = 4.16$, $p = 0.048$), change in gap fraction ($F_{1,41} = 2.33$, $p = 0.13$), and aspect ($F_{1,41} = 3.06$, $p = 0.088$), and this model explained a portion of the variance

TABLE 2 Significantly changing species between the two timepoints with their functional group (FG), percentage of plots the species occupied, and the mean percent coverage in plots where the species was found for each timepoint listed.

Species	FG	2007–2008			2020–2021			Raw p value	Holms- Bonferroni- corrected p value	df	t
		Percentage of plots present	Mean plot coverage (%)	SD	Percentage of plots present	Mean plot coverage (%)	SD				
<i>Brotherella recurvans</i>	P	87	6	3	22	1	3	3.68e-05	0.0018	38	4.67
<i>Bryhnia novae-angliae</i>	P	18	1	0.6	2	0.08	0.2	6.9e-05	0.01	7	5.76
<i>Dicranodontium denudatum</i>	A	62	0.9	0.8	11	0.2	0.5	0.0026	0.025	28	3.3
<i>Hypnum pallescens</i>	P	17	0.07	0.1	38	3	3	8.09e-04	0.01	21	-3.91
<i>Isopterygium tenerum</i>	P	15	0.5	0.2	2	0.02	0.06	0.0032	0.025	6	4.72
<i>Lepidozia reptans</i>	L	62	0.5	0.9	11	0.1	0.4	0.0029	0.025	30	3.24
<i>Nowellia curvifolia</i>	L	76	1	0.9	22	0.3	0.5	5.79e-05	0.0018	33	4.61
<i>Polytrichastrum pallidisetum</i>	A	75	2	4	16	0.2	0.6	0.0038	0.026	35	3.1
<i>Tetraphis pellucida</i>	A	93	0.9	0.7	16	0.2	0.7	1.08e-04	0.0022	40	4.3

Note: Functional groups are as follows: Pleurocarpous (P), Acrocarpous (A), and Liverwort (L). A paired *t* test followed by a sequential Holm's Bonferroni correction was performed to account for multiple comparisons.

($R^2 = 0.205$). At $q = 1$, only change in gap fraction ($F_{1,40} = 5.42$, $p = 0.025$) and slope ($F_{1,40} = 2.83$, $p = 0.1$) were predictors and explained less variance than the $q = 0$ model ($R^2 = 0.143$). At $q = 2$, change in gap fraction ($F_{1,40} = 5.11$, $p = 0.029$) and slope ($F_{1,40} = 5.65$, $p = 0.022$) were predictors of change in species richness and explained similar amounts of variance as the $q = 0$ model ($R^2 = 0.176$).

DISCUSSION

Bryophyte alpha diversity decreased over a 12-year period across the three highest elevation zones in the GSMNP, while bryophyte abundance declined only at the highest elevation zone. As hypothesized based on the literature, the observed changes were weakly influenced by elevation and slope aspect when only considering species richness at $q = 0$ (presence/absence). However, at $q = 1$ change in gap fraction was a significant predictor, and at $q = 2$ (where rare species were down-weighted), both change in gap fraction and slope were significant predictors, contrary to our predictions.

Elevation

In the spruce and the fir zone plots we observed high rates of turnover between time points at $q = 2$, where rare species were down-weighted in importance. This result indicates that common species, which often provide valued ecosystem services (Walker et al., 1999), are changing in abundance and thus increasing turnover rates, which is consistent with the significant loss of alpha diversity without a reduction in bryophyte abundance. It may be that some species that were already dominant in 2007/2008 further increased in abundance while other common species declined. Our models suggest that the observed changes reflect abiotic conditions that alter available niches, although the environmental factors included for consideration are not necessarily the major driving factors. It may be that other abiotic factors such as temperature and humidity are governing the observed shifts in community structure, which we will explore in future studies.

One reason we may have observed these changes in the fir zone is from a homogenization of the canopy and understory microclimate, caused by recovery from BWA.

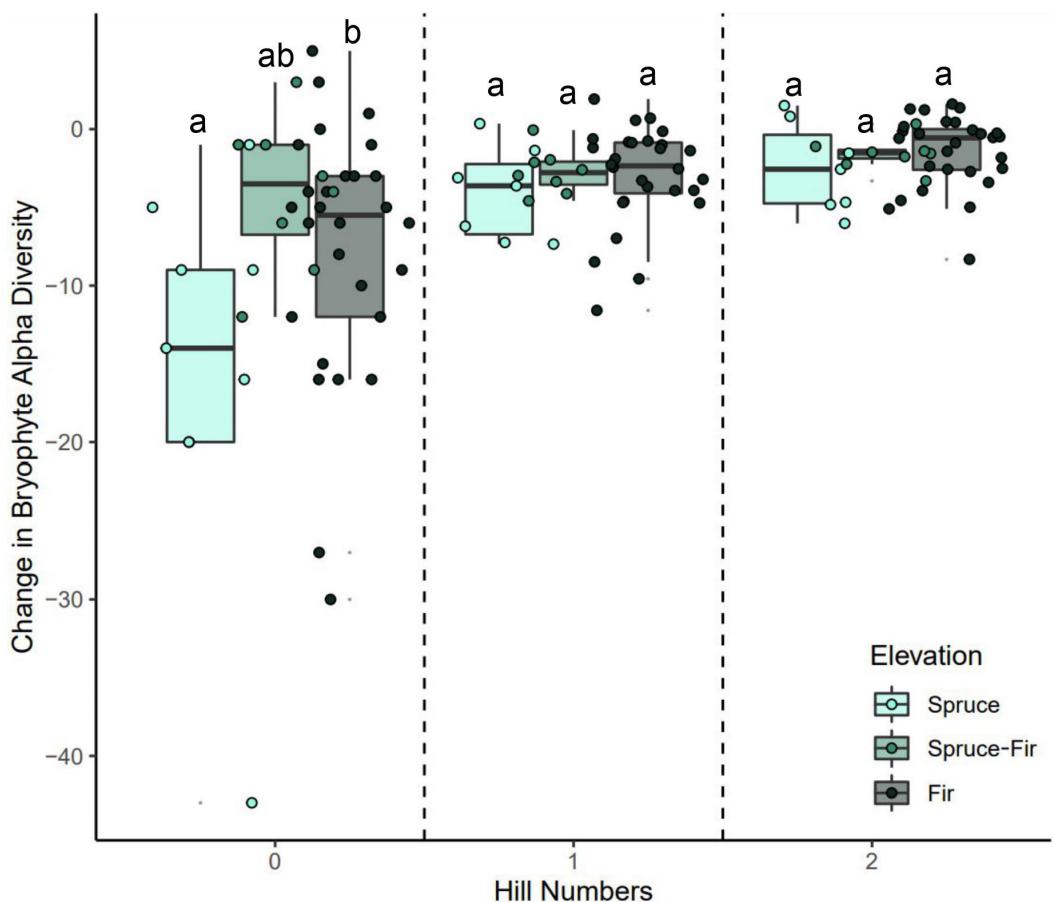


FIGURE 3 Change in bryophyte alpha diversity across the distinct elevation zones. Whiskers represent variability outside the first and third quartiles, midline represents the median, and outliers are points plotted above or below the whiskers. Change in alpha diversity is evaluated over Hill numbers ($q = 0$, species richness; $q = 1$, Shannon's diversity; $q = 2$, Simpson's diversity). Letters denote significant differences at $p < 0.05$ and were determined using a post hoc Tukey test.

For example, a study in Poland found that bryophyte alpha diversity was strikingly elevated in high-elevation forests following mass stand mortality from an invasive pest like BWA (Fudali, 2008). The invasive BWA caused widespread fir mortality on the peaks within the GSMNP (Speers, 1958). Declining alpha diversity and abundance might thus be indicators of recovery from BWA. Notably, several of the species that were dominant in the high-elevation dead forests in Poland, like *T. pellucida*, are among those that were found to have declined in our study. We found that *T. pellucida* was one of four species that significantly declined across our plots over time. This species is commonly found on dead wood (Stehn et al., 2010a), so it may be that as the forest recovers, the availability of downed wood has degraded. Other bryophytes found in healthy forest plots in Poland were also stable in our study plots, which is also consistent with the notion that bryophyte communities of the GSMNP fir zone are recovering from BWA impacts.

As we increased the weight of abundance, the more varied the turnover rates became across the plots in the spruce-fir zones. This may suggest that rare species are the main drivers of change over time in the spruce-fir zone, which is the middle elevation zone of our study. Rare species can often fill similar ecosystem functions as common species but exhibit differences in tolerance to disturbances (Walker et al., 1999). A broader distribution of tolerance can increase the resilience of an ecosystem in the event of disturbances that reduce the abundance of common species (Hernández et al., 2022). Though the possible loss of valued services is of concern, it is important to note that the abundance of bryophytes has not significantly changed, suggesting that ecosystem services bryophytes provide in the spruce-fir zone are possibly being maintained by other species. Other studies have found that common species can often replace rare species, thereby reducing negative impacts an ecosystem would otherwise experience due to species loss (Smith & Knapp, 2003).

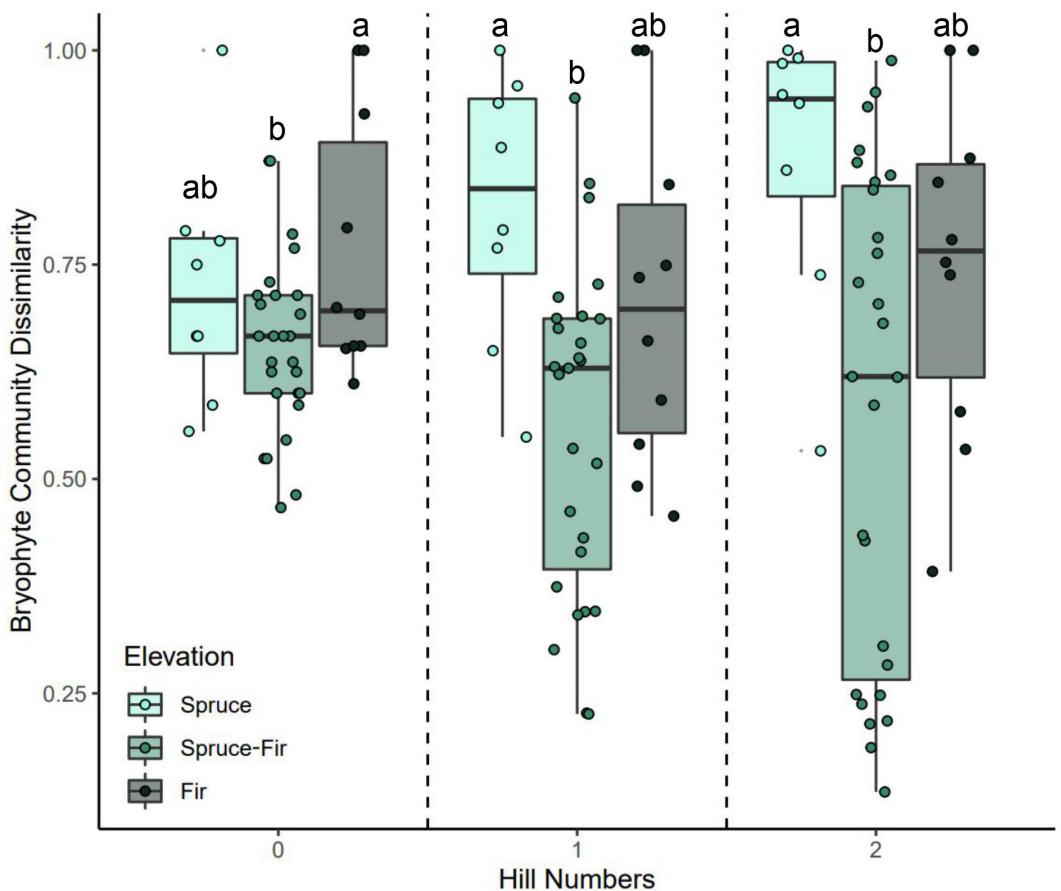


FIGURE 4 Bryophyte turnover across time and elevation zones within the Great Smoky Mountains National Park. Whiskers represent variability outside first and third quartile, midline represents the median, and outliers are points plotted above or below the whiskers. Turnover is evaluated over Hill numbers ($q = 0$, species richness; $q = 1$, Shannon's diversity; $q = 2$, Simpson's diversity). Letters denote significant differences at $p < 0.05$ and were determined using a post hoc Tukey test.

Slope

Slope was only a significant predictor of change in species richness when considering $q = 2$, where rare species were down-weighted. It may be that steepness of a slope does not necessarily influence the richness of a community, but that only certain species thrive or are able to colonize on certain slope percentages, thus increasing their abundance and explaining why slope was a significant predictor of our models at $q = 2$. It may also be that in our study area, rare species are found on certain slope percentages, which would explain our findings at $q = 2$. Other studies have found conflicting results regarding the effects of percent slope on bryophyte richness. For example, one study found that as percent slope increased, the richness of bryophytes decreased (Horvat et al., 2017). Other studies have found that slope is a significant predictor of the presence of certain species (Hespanhol et al., 2011) but not species richness (Hespanhol et al., 2011; Sun et al., 2013). However, these studies examined richness at $q = 0$ which does not preclude the possibility of

broader effects of slope at higher orders of q . Other studies examining bryophyte diversity either focus on slope aspect or the slope percent is examined more qualitatively (e.g., bottom of slope, slope, top of slope; Tilk et al., 2018). As such, future studies should consider both quantifying slope and considering the abundance of species when examining how slope influences bryophyte communities.

Slope aspect

Even though aspect was not a significant predictor, it was retained and increased the variance explained by our top models. Knowledge of how aspect influences plants in the southern Appalachians is limited to studies focusing on individual—and often dominant—tree species (e.g., Busing et al., 1993; Hart & Kupfer, 2011; Kincaid, 2007; Lafon et al., 2019) as opposed to the dozens of bryophytes species examined in our study. It is possible that refocusing on individual species might reveal trends similar to those found for dominant trees, but we do not have

sufficient statistical power to assess individual-level generated models for each species.

Species significantly changing in abundance

Of the eight species with significant declines in abundance (Table 2), three were pleurocarpous mosses. Two of the eight significantly declining species were acrocarpous mosses. The final two significantly declining species were liverworts. *T. pellucida* (an acrocarpous moss), *L. reptans*, and *N. curvifolia* (liverworts) all significantly declined and are substrate specialists occupying downed or decaying wood; while *N. curvifolia* exclusively grows on decaying wood, *T. pellucida* can also grow on rock and at the base of trees (Flora of North America Editorial Committee, 1993). *L. reptans* is commonly found on decaying logs, but may also grow on shady, moist soils. The decline of these substrate specialists could indicate a decline or degradation of downed wood quality concomitant with decay since BWA infestation; however, we do not have the data to test this in our study. The declining pleurocarpous species are not substrate specialists, nor do they share any notable similarities other than their functional group. *B. novae-angliae* and *I. tenerum* prefer moist environments, whereas *B. recurvans* is a substrate generalist (Flora of North America Editorial Committee, 1993). More abiotic habitat data within the plots are required to better understand why these species are declining compared to their more stable community members. The only species which significantly increased in abundance was *H. pallescens* which is a pleurocarpous moss that grows on rocks, base of trees, decaying wood, and forested areas (Flora of North America Editorial Committee, 1993). It is possible that changes to downed wood quality (i.e., progressive decay) have allowed potential relay succession from liverwort species to *H. pallescens* to occur.

Tree community and gap fraction

We did not detect significant changes in canopy cover over time. As our sampling occurred across multiple mountain peaks, this lack of change could be due to the stochasticity of leaf density or stand density across the landscape (Pharo & Vitt, 2000). Tree community turnover was relatively low, suggesting that the tree community has not dramatically changed over time. However, a more intensive survey of the trees present within the plots could better depict any changes in tree structure over time. This is especially true of the age and

size class of fir and spruce trees as their changes in canopy coverage may be the main drivers of the low turnover observed. It may be that the canopy conditions of individual trees or forest structure has changed and led to a cascading change in microclimatic moisture and temperature regimes that affect bryophyte habitat suitability. It has been shown that even sun specks can influence the understory community, and it may be that the understory vegetation is altering the microclimate that the mosses experience underneath them, which would not be captured with fish-eye photography (Pearcy & Way, 2012). The third most common species present across the plots and the most common deciduous tree species was yellow birch (*Betula alleghaniensis* Britt.). Future studies could determine whether yellow birch and other deciduous tree species increased significantly over time to determine whether their leaf litter could be a driving change in bryophyte community composition, which has been shown in other studies (Jean et al., 2017; Schmalholz & Granath, 2014).

CONCLUSION

Our study adds to the understanding of how key constituent communities of high elevation ecosystems change over time. However, there are other potential drivers that could influence the communities and explain why certain species are declining while others are not. Changes to temperature and humidity at the bryophyte habitat (e.g., microclimatic) scale could contribute to bryophyte decline and thus should be investigated further. Work continuing to monitor bryophyte communities in the future is also required to detect further shifts, especially for species of concern such as those which the spruce-fir moss spider inhabits. We should also utilize the rich history of specimens housed in herbaria to examine community changes through time, especially to compare pre versus post BWA community composition to determine how this invasive pest has impacted the bryophyte communities. Such temporal studies are crucial to understanding the drivers of community changes and allowing for the protection of critical species in an ecosystem.

AUTHOR CONTRIBUTIONS

Eric Shershen was the main contributor for data collection in 2020/2021, data analysis, and manuscript preparation. Sarah Stehn was the spruce-fir zone bryophyte community study investigator and data collector in 2007/2008 and provided discussion and editing feedback. Jessica M. Budke was involved in project conception, execution, interpretation, and major editing feedback.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Shershen, 2024) are available from the Open Science Framework (OSF): <https://doi.org/10.17605/OSF.IO/KPM7X>.

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