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Research Article

Detecting community changes in response to management practices using bryophyte herbarium specimens collected in the southern Appalachians

Eric Shershen[1,2], Jessica M. Budke[2]

1 *The Ohio State University, Columbus OH, USA*
2 *University of Tennessee, Knoxville TN, USA*
Corresponding author: Eric Shershen (ericdshershen@gmail.com)

Abstract

Aim: Monitoring plant communities in response to drivers of global change is essential for understanding ecosystem health and conservation over time. Natural history collections are underutilized, open-source data that can be leveraged to study how communities change over time. This informs how under surveyed organisms, like bryophytes, may be impacted by drivers of global change.

Location: We used herbarium specimen data to examine bryophyte community change in the southern Appalachians before and after the arrival of the balsam wooly adelgid (BWA).

Methods: We used herbarium collections to examine raw and rarefied alpha diversity, as well as rarefied dissimilarity, over time. We compared two timespans, pre-BWA invasion and initial canopy recovery from invasion, to determine if species were either lost from, persisted in, or were new to high elevation areas and if these species had any shared features.

Results: We found that mountains with greater disturbance resulted in lower levels of rarefied richness and that more extreme management practices may drive greater changes to the bryophyte community. However, this result cannot be decoupled from the disturbance with our data. Finally, we found that generalists significantly persisted through time compared to expected and compared to specialist species.

Main conclusions: This is a promising use of herbarium specimens as the results match those of field-based experiments. As such, herbarium collections may be used as a substitute for permanent plots for lands with limited resources or a lack of expertise to determine the impacts management practices or invasion events have on ecological communities.

Key words: Bryophytes, Community change, Invasion, Management practice, Natural history collections, southern Appalachians

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Introduction

Ecosystems face concurrent agents of global change, including invasive species and climate change, which make developing and implementing management plans challenging. Land managers often balance research alongside stakeholder and societal interests to effectively combat agents of global change to reduce biodiversity loss (Enquist et al. 2017; Hallett et al. 2017). One common method to evaluate the effectiveness of such research-informed decisions is establishing and monitoring permanent plots to study community changes over time. Permanent plots have been shown to be powerful tools, especially when monitoring communities following a disturbance event (Weber et al. 2006; Brice et al. 2019) or when management strategies are changed (Waring et al. 2016). While permanent plots are vital for a deeper understanding of community changes over time, they may not be feasible due to the prohibitive costs or person-power required to establish, maintain, and regularly survey them (de Bello et al. 2020). This manufactures a barrier for managed lands that have limited and or inconsistent funding, leading to a vacuum of knowledge regarding the flora of those lands and how they respond to agents of global change and management practices.

An alternative that avoids the increased level of resources permanent plots consume, is to use the abundant specimen data housed in plant natural history collections (herbaria; Thiers 2023). These data are freely available through online portals, such as the Global Biodiversity Information Facility (www.gbif.org), Southeast Regional Network of Expertise and Collections (www.sernec-portal.org), and The Consortium of Bryophyte Herbaria (www.bryophyteportal.org) and provide key information about location, date of collection, and habitat. These collections, while freely available, do present other costs (e.g. housing specimens, employing staff to maintain collections), but such expenses are not taxon specific, typically supported through institutions as opposed to individual researchers/managers, and enable a plethora of studies across fields of research to be conducted. These include studies that identify changes in plant phenology (Park et al. 2021; Faidiga et al. 2023), distribution (Bergamini et al. 2009; Auld et al. 2022), genetic diversity (Labouisse et al. 2020; Závada et al. 2022), and community composition over time (Dolan et al. 2011; Dodd et al. 2015; Ewers-Saucedo et al. 2021). In addition, using collected specimens enables researchers to validate species identification and update specimen information as taxonomy shifts or if less seasoned collectors had identified the specimen, an expert can validate them. It is important to note that specimens can only provide presence data and are predisposed to collection biases (Daru et al. 2018) such as increased sampling in easily accessible areas, where surveys focus on specific taxa, or areas where avid collectors frequent. However, in areas where longitudinal studies with permanent plots have not been established or where certain organisms, such as bryophytes, have not been included, herbarium data are a potential alternative for understanding how communities have changed through time in response to a disturbance event or management decision.

Many community change studies focus on vascular plants at the species level and exclude bryophytes (Franklin et al. 2004; Becker-Scarpitta et al.

2018). When bryophytes are included in long-term community change studies, they are often lumped together as “non-vascular plants”, as opposed to documenting these organisms at the species level, which is standard for vascular plants (Kopecký and Szabó 2013; Collins et al. 2022). This is likely due to the difficulty identifying bryophytes in the field, as the vast majority require microscopic examination to confirm species level identifications. However, lumping all bryophytes into a single category hinders studies from understanding how their communities change at the species level in response to management decisions and disturbances. This leads to species loss, and consequently the ecosystem functions they provide. Bryophytes increase soil stability (Gao et al. 2020), provide habitat to a plethora of taxa at the base of food webs (Bartels and Nelson 2007; Ziesche and Roth 2008; Coyle 2009), and sequester large amounts of carbon (Yu et al. 2011; Kasimir et al. 2021; Slate et al. 2024). Such losses in ecosystem function would be detrimental to their ecosystems. In addition, the Global Biodiversity Information Facility (GBIF) documents over 1.3 million preserved bryophyte specimens identified to the species level from the United States collected from the 1800’s to the present, with major collections in the west, northeast, and the southeast (GBIF 2023). Thus, bryophytes are a promising group to use herbarium specimen data to document species level community change through time, as is standard in vascular plant community change studies.

Here, we use the Great Smoky Mountains National Park (GSMNP) within the southern Appalachians as a case study to examine bryophyte community composition through time using herbarium specimens. The GSMNP has a rich history of bryophyte collections over the past century (Sharp 1939; Schofield 1960; Norris 1964; Studlar 1982; National Park Service 1995, 1999; Choberka 1998; Stehn et al. 2010a, 2010b; Shershen et al. 2024). The park also experienced a major invasion event by the balsam wooly adelgid (BWA). First documented in 1962, this pest caused roughly 90% mortality to the *Abies fraseri* (fraser fir), thus opening the canopy (Speers 1958; Jenkins 2003). These changes to canopy cover can dramatically alter the microclimate of the understory. Across the GSMNP different BWA management strategies were applied to the high elevation sites with varying degrees of effectiveness (Johnson 1980; pers. comm. Paul Super, Research Coordinator at the National Park Service 2023). There have been no studies examining the impact of the BWA on bryophyte community composition from pre-BWA invasion to initial canopy recovery (ICR) or how the different management strategies impacted the bryophyte communities. This is especially important since bryophytes make up the bulk of the ground cover and richness within high elevation areas of the GSMNP (Stehn et al. 2010a).

We aim to address the following questions using herbarium specimen data. 1) How has bryophyte community composition changed through time in the GSMNP? Specifically, how have the high elevation communities changed after the BWA invasion? 2) How have different BWA management strategies impacted bryophyte community composition? For these questions, we predict that mountain peaks with greater BWA impact and those with more extreme management strategies will have larger effects on the bryophyte communities. This is because such impacts opened the canopy and bryophytes have been shown to be especially vulnerable to canopy changes (Halpern et al. 2014). 3) If changes in the bryophyte community composition are detected, are there shared features, such as substrate specificity, growth form, or taxonomic order, that define the species present prior to the BWA invasion compared to the present day? We predict that substrate generalists will be better able to handle such stresses and persist through the disturbance. This is because another study examined spruce decline in response to an invasive pest noted substrate generalists having a broader niche, including increased light tolerance, and thus were more abundant in their diseased plots (Fudali 2008).

Methods

Extensive bryophyte collecting has been conducted within the GSMNP between 1913 and 2022 (Sharp 1939; Schofield 1960; Norris 1964; Studlar 1982; National Park Service 1995, 1999; Choeberka et al. 1998; Stehn et al. 2010a, 2010b; Shershen et al. 2024) in addition to species targeted and random collection events. Specimen data from this timespan was downloaded from the Consortium of Bryophyte Herbaria (CNBH) and Global Biodiversity Information Facility (GBIF) in August of 2023 (GBIF.org 2023; Consortium of Bryophyte Herbaria 2023). Specimens not yet available through these online portals were added to these data (Stehn et al. 2010a, 2010b; Shershen et al. 2024). Species names were synonymized using Tropicos to account for taxonomic changes over time (Tropicos.org 2023) and followed Goffinet and Buck (2024) for mosses or Söderström et al. (2016) for liverworts. Duplicate records and specimens possessing only genus-level identifications were removed. Remaining specimens were georeferenced as needed and coordinates for all the specimens were uploaded to ArcGIS Pro version 3.3 (ESRI 2023) wherein elevation was extracted to each specimen. Specimens were then grouped spatially by mountain peak [Kuwohi (formerly Clingmans Dome), Mt. Kephart, Mt. LeConte, and Mt. Sterling]. These peaks were selected due to the different management strategies applied following the BWA invasion. To prevent overlap of specimen data, we applied a buffer area of 15 km^2 around the center of each peak, ensuring each specimen was only counted for one mountain. Since the BWA impacts only high elevations above 1340 m (Whittaker 1956), an additional spatial group was created containing any specimen collected within the GSMNP above 1340 m, including those specimens collected on the aforementioned peaks.

Mt. LeConte and Mt. Kephart had little to no management for BWA due to limited access for strategy implementation (Johnson 1980; pers. comm. Paul Super, Research Coordinator at National Park Service 2023). Both chemical and biotic controls were used to manage the BWA on Kuwohi, which resulted in positive impact on the fir community. Mt. Sterling had the highest level of management, including clear-cutting strips of trees to create a buffer zone and biotic controls (Johnson 1980; pers. comm. Paul Super, Research Coordinator at National Park Service 2023). However, these management practices were found to have a minimal effect reducing the BWA invasion on Mt. Sterling (Johnson 1980; pers. comm. Paul Super, Research Coordinator at National Park Service 2023). The four mountain peaks, along with the high elevation group, will be called spatial groupings hereafter.

The specimen data from all spatial groupings was then divided into three timespans defined by ecologically relevant dates for the BWA invasion. The first timespan was 1934 through 1962. The GSMNP was established in 1934, which began a more intensive period of species documentation. Specimens collected prior to 1934 were excluded since there were not enough collected prior to 1934 to analyze as a standalone timespan. In 1962 the first documentation of BWA severely impacting areas within the park boundary was recorded (Johnson 1980; Jenkins 2003). The second timespan was 1963 through 1999, the period when BWA was dramatically impacting high elevation areas until the first study documenting fir canopy recovery in the park in 1999 (Smith and Nicholas 2000). The final timespan was 2000 through 2022, which is from initial canopy recovery to the time this study was conducted. We will refer to these timespans as pre-BWA (1934–1962), post-BWA (1963–1999), and initial canopy recovery (ICR; 2000–2022), respectively. A species list was generated for each spatial grouping and timespan. Using these species lists, an abundance matrix was generated.

Richness (number of unique species) was calculated using this matrix for each spatial grouping and for each timespan. Richness was standardized by sampling effort via rarefaction using the vegan package in R (Oksanen et al. 2016; R Core Team 2023). Rarefaction randomly samples community data with the level of rarefaction set to the lowest level of sampling effort being compared (Sanders 1968; Simberloff 1972; Heck et al. 1975). In our case, this is set to the timespan with the lowest number of specimens collected for each mountain peak. We ran 9,999 rarefaction iterations for each timespan for each of spatial groupings except the high elevation grouping. For each iteration we determined the direction of difference between each timespan's rarefied richness to each other. The percentage of times a timespan had a higher rarefied richness compared to another timespan is reported in Table 1. In addition, a rarefied dissimilarity was calculated to examine the differences in rarefied richness between timespans using the vegan package in R (Oksanen et al. 2016).

We also examined changes in individual species between the pre-BWA (1934–1962) and ICR (2000–2022) timespans for the high elevation spatial group using our matrices. For only this spatial group we determined which species were 1) present in the GSMNP before the arrival of the BWA (pre-BWA timespan) and then absent during initial canopy recovery (ICR timespan), 2) present during both the pre-BWA and ICR timespans, or 3) absent pre-BWA and then present during the ICR. Thus, we refer to these species as lost (present pre-BWA and absent during ICR), persisted (present pre-BWA and present during ICR), and new (absent pre-BWA and present during ICR). We acknowledge that the confirmation of true absences is impossible, however this is true of all surveying methods, including permanent plots and targeted sampling (GBIF.org 2023). The history of bryophyte surveys within the park at these high elevations was exhaustive for pre-BWA (Sharp 1939; Schofield 1960), and exhaustive within the confines of surveyed plots for the ICR (Stehn et al. 2010a, 2010b; Shershen et al. 2024), reducing the biases that arise from surveys targeting specific species. The high elevation spatial group encompasses all specimens collected on mountain peaks within the park, further reducing the chances of erroneous absences.

Table 1. Percentage of rarefaction iterations that had the same difference in direction for each timespan comparison. If a timespan has a higher rarefied richness value for a majority of the iterations (close to 100%), we can confidently infer the rarefied richnesses are different from one another.

Spatial Group	pre-BWA vs post-BWA		post-BWA vs ICR		pre-BWA vs ICR	
	pre-BWA higher	Post-BWA higher	Post-BWA higher	ICR higher	Pre-BWA higher	ICR higher
Kephart	0%	100%	100%	0%	100%	0%
Kuwohi	47.4%	52.6%	100%	0%	100%	0%
LeConte	46.8%	53.2%	100%	0%	100%	0%
Sterling	0.35%	99.7%	100%	0%	100%	0%

Substrate specificity, growth form, and taxonomic order were determined for each bryophyte species in the high elevation spatial group. Substrate specificity was scored by counting the number of substrates a species was known to inhabit as reported in the Flora of North America (FNA; Flora of North America Editorial Committee 1993) using a modified version of a bryophyte substrate scoring system (Hill et al. 2017; Suppl. material 1). The number of substrate types a species can potentially occupy was summed and each species was categorized as having the ability to occupy either one substrate type (specialist), two substrate types (flexible), or three or more substrate types (generalist). This division was to break up phylogenetically similar species in the generalist category to avoid phylogenetic pseudo-replication. Species' growth form was scored as either an acrocarpous moss, pleurocarpous moss, or liverwort. The taxonomic order for each species was determined using the moss classification of Goffinet and Buck (2024) or the liverwort classification of Söderström et al. (2016). These data were then analyzed with Chi square tests to determine if any of these features were different between the lost, persisted, and new species for the high elevation spatial group. Comparisons are adjusted for multiple comparisons as needed using a sequential Holms-Bonferroni correction.

Results

Alpha diversity

Bryophyte sampling effort varies over time with higher numbers of specimens typically resulting from extensive surveys for monitoring reports or individual research studies (Sharp 1939; Schofield 1960; Norris 1964; Studlar 1982; National Park Service 1995, 1999; Choberka et al. 1998; Stehn et al. 2010a, 2010b; Shershen et al. 2024, Fig. 1). Examining uncorrected richness (total number of unique species) across all spatial groupings, we observed a decline from the pre-BWA to post-BWA timespan and an even more dramatic decrease in the ICR timespan (Fig. 2). However, when we standardized by sampling effort using rarefaction, we observed two distinct patterns. On Mt. Sterling and Mt. Kephart rarefied alpha diversity increased from pre-BWA to the post-BWA timespan, followed by a decline in the ICR timespan (Fig. 3A, C); whereas Kuwohi and Mt. LeConte had no difference between the pre and post-BWA timespans, but had a sharp decrease in rarefied alpha diversity during the ICR (Fig. 3B, D).

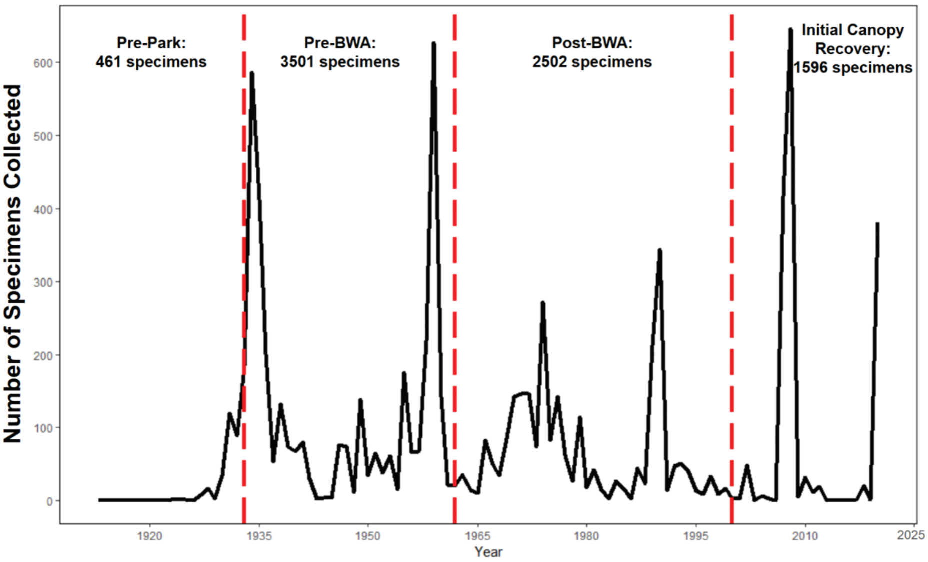

Figure 1. Number of specimens collected per year from 1913 to 2022. Red dashed lines represent the divisions between timespans. Total number of specimens collected during each timespan listed below timespan name.

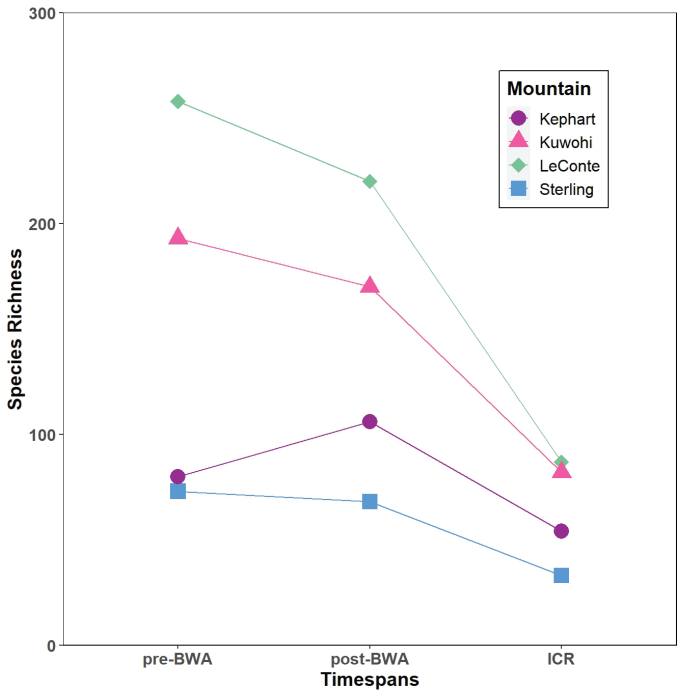

Figure 2. Species richness (number of unique species, not rarefied) across each spatial grouping for each timespan. These include pre-BWA (Balsam Wooly Adelgid, 1934–1962), post-BWA (1963–1999), and ICR (Initial Canopy Recovery, 2000–2022).

Dissimilarity

We examined rarefied dissimilarity to determine how different the communities were between pairs of timespans (pre-BWA and post-BWA, post-BWA and ICR, and pre-BWA and ICR). We observed dissimilarity levels above 0.5 for all comparisons across all four of the mountain peaks (Fig. 4). Mt. Sterling and Mt. Kephart consistently had higher dissimilarity levels compared to Mt. LeConte and Kuwohi for these comparisons (Fig. 4).

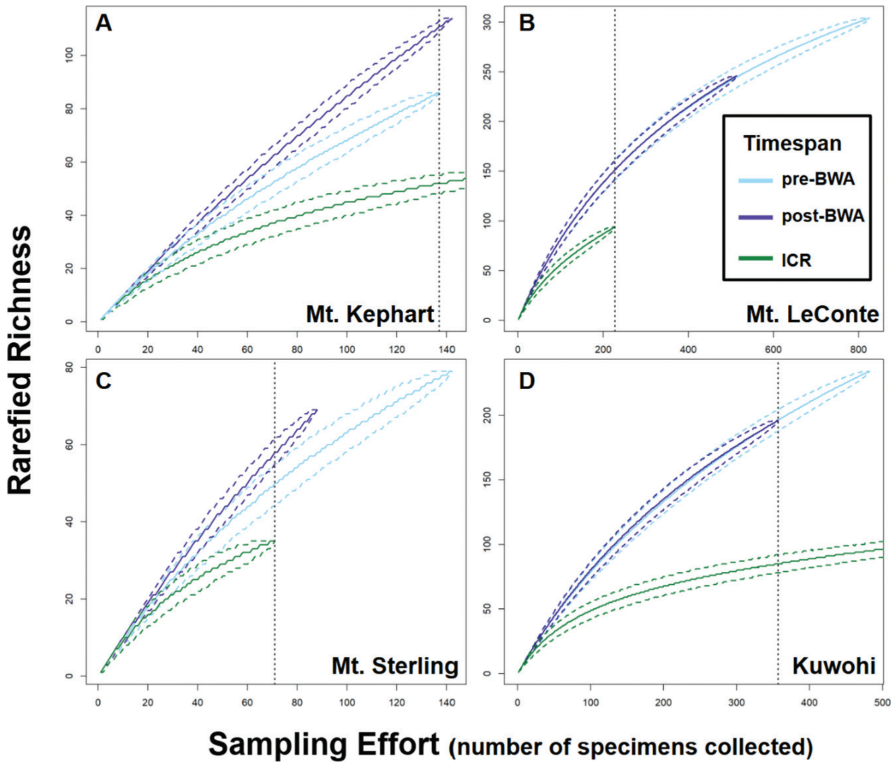

Figure 3. Rarefied species richness curves for mountain peaks managed and unmanaged for BWA (Balsam Wooly Adelgid). Unmanaged mountain peaks include **A.** Mt. Kephart, **B.** Mt. LeConte, whereas BWA managed mountains include **C.** Mt. Sterling, and **D.** Kuwohi. Median rarefied richness is represented by a solid line with the upper and lower quantiles as dashed lines on either side of the median. Each set of colored lines corresponds to a distinct timespan with pre-BWA in light blue, post-BWA in purple, and ICR (Initial Canopy Recovery) in green. Vertical dashed black lines indicate the lowest level of sampling effort (number of specimens collected) across the three timespans for each mountain.

Species change

We used Chi-square tests to examine how the high elevation spatial group differed between the pre-BWA and ICR timespans to determine if there were any shared characteristics between species that were lost, persisted, or new. We found that substrate specificity (whether a species is a specialist, flexible, or generalist) significantly differed between lost, persisted, and new species ($\chi^2 = 13.07$, df = 4, p-value = 0.011). Following this test, we determined if the standardized residuals were either greater or less than the absolute critical value (-2.77) to determine which observations were significantly different than expected. We found that between these two timespans (pre-BWA and ICR) fewer generalists were lost and more generalists persist compared to the expected values (Table 2). All other observed values were not significantly different from the expected values (Table 2).

When we compared substrate specificity groups, there were significantly more generalist species that persisted compared to specialist species ($\chi^2 = 10.56$, df = 1, corrected p-value = 0.009; Table 3). All other comparisons were not significantly different (Table 3). When grouping by growth form, there were no significant differences in any species change group following (Table 4). When we examined taxonomic order in relation to species change, there were a few orders where there were significant differences between the lost, new, and persisting species (Table 5). These included significantly more species lost

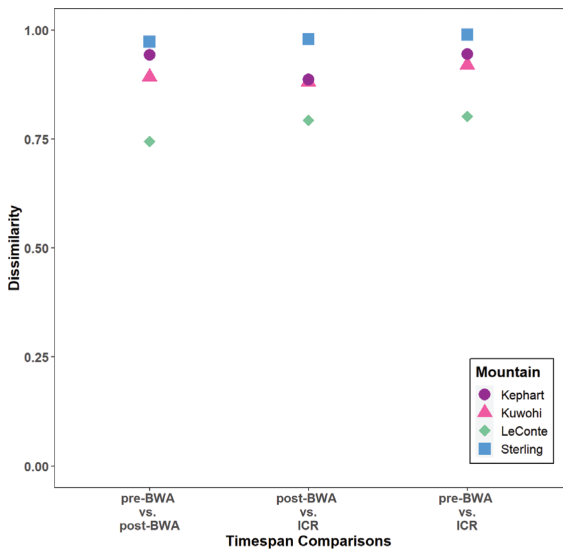

Figure 4. Rarefied dissimilarity of bryophyte communities through time. Rarefied dissimilarity was observed between pre-BWA (Balsam Wooly Adelgid) and post-BWA, post-BWA and ICR (Initial Canopy Recovery), and pre-BWA and ICR for each mountain peak at q = 0.

than new for Jungermanniales (χ^2 = 39.1, df = 1, corrected p-value = 2.7e-8), Porellales (χ^2 = 16,2 m df = 1, corrected p-value = 5.7e^{-5}), Hypnales (χ^2 = 26.1, df = 1, corrected p-value = 2.15e-5), Grimmiales (χ^2 = 13, df = 1, corrected p-value = 0.019), Bryales (χ^2 = 11.27, df = 1, corrected p-value = 0.046), Pottiales (χ^2 = 6, df = 1, correct p-value = 0.014), and Dicranales (χ^2 = 13, df = 1, corrected p-value = 0.019); significantly more species persisting than new for Jungermanniales (χ^2 = 20.17, df = 1, corrected p-value = 0.0044), Hypnales (χ^2 = 16, df = 1, corrected p-value = 0.004), Dicranales (χ^2 = 11, df = 1, corrected p-value = 0.0018), Sphagnales (χ^2 = 6, df = 1, corrected p-value = 0.014) and Porellales (χ^2 = 16.2, df = 1, corrected p-value = 0.0037); and significantly more species lost than persisted for Grimmiales (χ^2 = 13, df = 1, corrected p-value = 0.019) and Bryales (χ^2 = 7.12, df = 1, corrected p-value = 0.015).

Table 2. Substrate specialist differences between observed and expected results. High elevation spatial group differences between pre-BWA (Balsam Wooly Adelgid) and ICR (Initial Canopy Recovery) for substrate specificity groups focusing on the difference between the number of lost, new, and persisting species. Examining the full dataset, Chi-squared = 13.07, df = 4, p-value = 0.011. Significant differences between observed and expected are indicated with an asterisk.

Substrate Group	Species Change	Observed	Expected	Standardized Residuals
Specialist	Lost	58	51.6	1.7
Specialist	Persist	19	27.5	-2.3
Specialist	New	6	3.8	1.3
Flexible	Lost	66	62.9	1.4
Flexible	Persist	29	33.4	-0.82
Flexible	New	2	4.7	-1.48
Generalist	Lost	51	60.4	-3.0*
Generalist	Persist	45	32.1	3.0*
Generalist	New	5	4.5	0.1

Table 3. Substrate specificity group differences between species change groups. Observed change of substrate specificity groups from the high elevation spatial group compared between pre-BWA (Balsam Wooly Adelgid) and ICR (initial canopy recovery) timespans. Only two substrate groups were compared at a time using chi-square tests and the other not included in the test is marked with a dash. Significantly different groups are indicated with an asterisk.

Species Change	Specialist	Flexible	Generalist	Chi-squared	df	Corrected p-value
Lost	58	–	51	0.45	1	1
Lost	58	66	–	0.52	1	1
Lost	–	66	51	1.92	1	1
Persisted	19	–	45	10.56	1	0.009*
Persisted	19	29	–	2.08	1	1
Persisted	–	29	45	3.46	1	0.48
New	6	–	5	0.09	1	1
New	6	2	–	2.00	1	1
New	–	2	5	1.29	1	1

Table 4. Species change compared between growth forms. These include acrocarpous mosses, liverworts, and pleurocarpous mosses between pre-BWA (Balsam Wooly Adelgid) invasion and ICR (Initial Canopy Recovery) in the high elevation spatial grouping. Significant comparisons are indicated with an asterisk.

Species Change	Acrocarpous Moss	Liverwort	Pleurocarpous Moss	Chi-squared	df	Corrected p-value
Lost	62	–	46	2.74	1	0.84
Lost	62	67	–	0.19	1	1
Lost	–	67	46	3.9	1	0.43
Persisted	29	–	32	0.15	1	1
Persisted	29	32	–	0.15	1	1
Persisted	–	32	32	0	1	1
New	2	–	7	2.78	1	0.77
New	2	4	–	0.67	1	1
New	–	4	7	0.82	1	1

Discussion

The southeast is one of several regions which has been extensively surveyed for bryophytes, and this case study represents what could be achieved with natural history collections in other regions for not only bryophytes, but for other taxonomic groups in other regions as well. Overall, we detected two patterns of changes in rarefied richness that could be dependent on management strategy implementation. In the case of less successful management of BWA (Mt. Sterling), bryophyte rarefied richness increased post-disturbance, and decreased during recovery which aligns with other literature examining bryophyte community change following disturbance (Fudali 2008; Pedro et al. 2016). We also found that substrate generalists were significantly more likely to persist through a disturbance than specialists. We observed how differing management strategies can influence bryophyte communities, with more extreme canopy altering practices yielding greater change to the community, yet based on the available data, these cannot be decoupled from the effects of BWA in the GSMNP. Finally, we document the importance of rarefying richness when examining community change through time using natural history collections.

Table 5. Species change (new, lost, persisted) compared within taxonomic orders for liverworts, acrocarps, and pleurocarps. Comparisons are for changes between pre-BWA (Balsam Wooly Adelgid) invasion and Initial Canopy Recovery (ICR) for the high elevation spatial grouping using chi-square tests. Significant differences are indicated with an asterisk.

Growth Form	Order	Number of Species Lost	Number of Species Persisted	Number of Species New	Chi square	df	Corrected p-value
Liverworts	Jungermanniales	42	23	–	5.55	1	0.06
		42	–	1	39.1	1	<0.001*
		–	23	1	20.17	1	<0.001*
	Porellales	19	–	1	16.2	1	<0.001*
		19	5	–	8.17	1	0.008*
		–	5	1	2.67	1	0.3
	Marchantiales	1	–	0	1	1	0.64
		1	0	–	1	1	0.32
		–	0	0	–	0	–
	Metzgeriales	5	–	1	2.67	1	0.1
		–	4	1	1.8	1	0.36
		5	4	–	0.11	1	1
	Pallaviciniales	–	0	1	1	1	0.32
		0	–	1	1	1	0.64
		0	0	–	–	1	–
Acrocarpous Mosses	Andreaeales	–	2	0	2	1	0.16
		0	2	–	2	1	0.32
		0	–	0	–	1	–
	Bartramiales	–	1	0	0	1	1
		1	–	0	0	1	1
		1	1	–	0	1	1
	Bryales	14	–	1	11.27	1	<0.001*
		14	3	–	7.12	1	0.015*
		–	3	1	1	1	0.96
	Dicranales	13	–	0	13	1	<0.001*
		–	11	0	11	1	0.002*
		13	11	–	0.17	1	1
	Diphysciales	1	–	0	1	1	0.32
		1	0	–	1	1	0.64
		–	0	0	–	1	–
	Encalyptales	1	–	0	1	1	0.32
		1	0	–	1	1	0.64
		–	0	0	–	1	–
	Funariales	1	–	0	1	1	0.32
		1	0	–	1	1	0.64
		–	0	0	–	1	–
	Grimmiales	13	–	0	13	1	<0.001*
		13	0	–	13	1	<0.001*
		–	0	0	–	1	–
	Hedwigiales	1	–	0	1	1	0.32
		1	0	–	1	1	0.64
		–	0	0	–	1	–

Growth Form	Order	Number of Species Lost	Number of Species Persisted	Number of Species New	Chi square	df	Corrected p-value
Acrocarpous Mosses	Polytrichales	4	–	1	1.8	1	0.18
		–	3	1	1	1	0.64
		4	3	–	0.14	1	1
	Pottiales	6	–	0	6	1	0.014*
		–	2	0	2	1	0.48
		6	2	–	2	1	0.32
	Rhizogoniales	2	–	0	2	1	0.16
		2	0	–	2	1	0.32
		–	0	0	–	1	–
	Sphagnales	–	6	0	6	1	0.014*
		5	–	0	5	1	0.05
		5	6	–	0.091	1	1
	Tetraphidales	–	1	0	1	1	0.32
		0	1	–	1	1	0.64
		0	–	0	–	1	–
Pleurocarpous Mosses	Hookeriales	1	–	0	1	1	0.32
		1	0	–	1	1	0.64
		–	0	0	–	1	–
	Hypnales	41	–	6	26.1	1	<0.001*
		–	30	6	16	1	<0.001*
		41	30	–	1.7	1	0.57
	Orthotrichales	4	–	1	1.8	1	0.18
		4	2	–	0.67	1	0.82
		–	2	1	0.33	1	1

Rarefying richness

Our results add yet another example demonstrating the importance of rarefying richness when examining community change across unevenly sampled regions. In Fig. 2, we observed declines in richness through time across three of the mountain peaks. This pattern was likely driven disparities in sampling effort between time points, as seen in Fig. 1. When we rarefied our data to match the lowest number of specimens collected, and repeated this process across 9,999 iterations, we see starkly different patterns wherein rarefied richness either increases or stays the same from pre-BWA to post-BWA. This pattern illustrated by rarefaction more closely aligns to what we would expect would occur based on the literature surrounding canopy opening disturbances impact on the bryophyte community. Had we not corrected for sampling biases, our interpretations on management and disturbances may have led to inaccurate statements that could result in detrimental management decisions based on our findings.

Communities following disturbance

Changes in canopy cover can influence microclimate and the available niches resulting in community compositional changes over time (Gray et al. 2002). In this study, the BWA (Balsam Wooly Adelgid) invasion killed over 90% of the fir trees in the GSMNP, which opened the canopy and increased light levels in the understory (Jenkins 2003; Royo and Carson 2006). In studies leveraging permanent plots, bryophyte richness has been shown to initially increase following disturbances (Kimmerer et al. 1982; Jonsson and Esseen 1990), especially those which alter the canopy (Fudali 2008; Pedro et al. 2016). Our study corroborates these findings; for two of the spatial groupings, rarefied bryophyte richness increased during the post-BWA timespan when the canopy would be expected to be the most open followed by a decrease in richness during the initial canopy recovery period (ICR) when the canopy would be closing (Fig. 3). This was observed for Mt. Sterling which experienced clear-cutting and had the worst impact of BWA (Johnson 1980). The second peak was Mt. Kephart, which was too remote to implement management strategies. Mt. Kephart is the closest of the peaks in this study to Mt. Sterling, and so it may be that the proximity to an infested peak could have negatively impacted the canopy, resulting in this same pattern.

From a disturbed state such as the post-BWA, communities can either recover to pre-disturbance state, remain in limbo between community succession states, or shift to a new community (Beisner et al. 2003; Aguadé-Gorgorió et al. 2024). Bryophyte communities have been shown to recover more slowly following disturbances (Dynesius 2015) and have been predicted to lag behind other species with respect to climate change-driven range shifts (Zanatta et al. 2020). In our case, if the canopy recovered and fully closed, we would expect to see a decrease in available niches and as such a decline in richness. We did observe a decline in bryophyte richness from post-BWA to ICR across all spatial groups, supporting this prediction (Fig. 3). However, we observed greater dissimilarity between pre-BWA and ICR than we would expect if the pre-disturbance bryophyte community had fully recovered (Fig. 4). This could be due to species turnover, a lag in recovery in the understory as species re-colonize, or a new bryophyte community is forming following canopy recovery. It may also be that the timespans required for canopy recovery from BWA are not long enough for complete recovery (Dynesius 2015).

Management strategies and bryophyte communities

Mountains with varying management strategies for BWA had dramatic differences in bryophyte community composition. We compared the pre-BWA to ICR timespans rarefied richness and dissimilarity metrics to test for community changes. If communities returned to their pre-BWA compositions, we expected the dissimilarity between pre-BWA and ICR to be low. Instead, we observed dissimilarity above 50% between these timespans for all mountain peaks, with Mt. Sterling having the highest levels of dissimilarity (Fig. 4) indicating that these communities have different compositions. It is important to note that one of the mountains managed for BWA, Kuwohi, had lower dissimilarity (Fig. 4) with nearly identical rarefied richness between the pre-BWA and post-BWA timespans across the iterations (Table 1, Fig. 3). This could be due to Kuwohi having the most success managing for the BWA invasion (chemical and biotic controls) out of the mountains examined (Johnson 1980). While Mt. Sterling was managed for BWA with both clearcutting and biotic controls, reports state this combination of practices was not successful at reducing the BWA invasion (Johnson 1980). Dissimilarity was higher for Mt. Sterling compared to Kuwohi (Fig. 4), and Mt. Sterling had a stark increase in rarefied diversity from pre-BWA to post-BWA (Table 1, Fig. 3). In addition, dissimilarity for Mt. Sterling was higher than either of the unmanaged peaks (Fig. 4). Consequently, it is possible that an aggressive management approach like clearcutting strips of canopy was more harmful to the bryophyte community than leaving the peak unmanaged or using pesticides as on Kuwohi. However, we observed the same patterns of rarefied richness for Mt. Sterling and Mt. Kephart as well as similar levels of dissimilarity (Figs 3, 4). As Mt. Sterling was managed and Mt. Kephart was not, this shows that the effects of BWA and the effects of management cannot be strictly decoupled based on our data alone. This entanglement provides the basis of future work to explore how canopy altering disturbances and clearcutting may impact the herbaceous understory. Until then, this study may encourage land managers to opt for less extreme management strategies when managing for the entire community.

It may also be best to focus on the differences using rarefied richness metrics to evaluate species change through time when using herbarium specimens. This is because dissimilarity relies on the presence and absence of species, and as such sampling bias can skew the calculated value. As we increase the number of specimens pooled in a spatial grouping, we would expect lower levels of dissimilarity as we detect shared species between time points more frequently. Whereas at low efforts of sampling, randomly collecting a less common species could greatly increase the dissimilarity between groups. We can use rarefaction to balance this limitation of dissimilarity and herbarium data to detect trends in bryophyte community change following disturbances. Careful consideration is needed when interpreting such results, and greater emphasis should be placed on results from rarefied richness. To determine if this holds true on larger scales and for more prominent disturbances, more studies of similar management strategies could be examined to see if the same strategies yield similar trends in dissimilarity and richness with herbarium data. This would enable for more powerful statistical models to be incorporated to test for differences and to detangle the effects of disturbance and management.

Trends in substrate specificity

Being able to detect changes in substrate specificity using herbarium specimens could aid in determining the effects of management decisions in areas lacking permanent plots. When examining the relationship between substrate specificity and species change from pre-BWA to the ICR timespan, we observed that fewer generalists were lost and more persisted than expected (Table 2). There were also significantly more generalists than specialists that persisted from the pre-BWA to the ICR timespan (Table 3, Fig. 5). This aligns with the prediction that species capable of living on multiple substrates have a higher probability of surviving disturbances since they have a larger variety of habitats where they can persist or colonize (Almoussawi et al. 2019; Noualhaguet et al. 2023). It has been shown for vascular plants in the tropics that specialists require more time to re-establish following disturbance (Acebey et al. 2003). Thus, in our study, the generalists could have either persisted through the disturbance or recolonized more quickly than the specialists. Across taxa, specialists have been declining and replaced by generalist species in response to disturbances (Clavel et al. 2011; Tordoni et al. 2019; Rolls et al. 2023). Detecting these trends in substrate specificity with

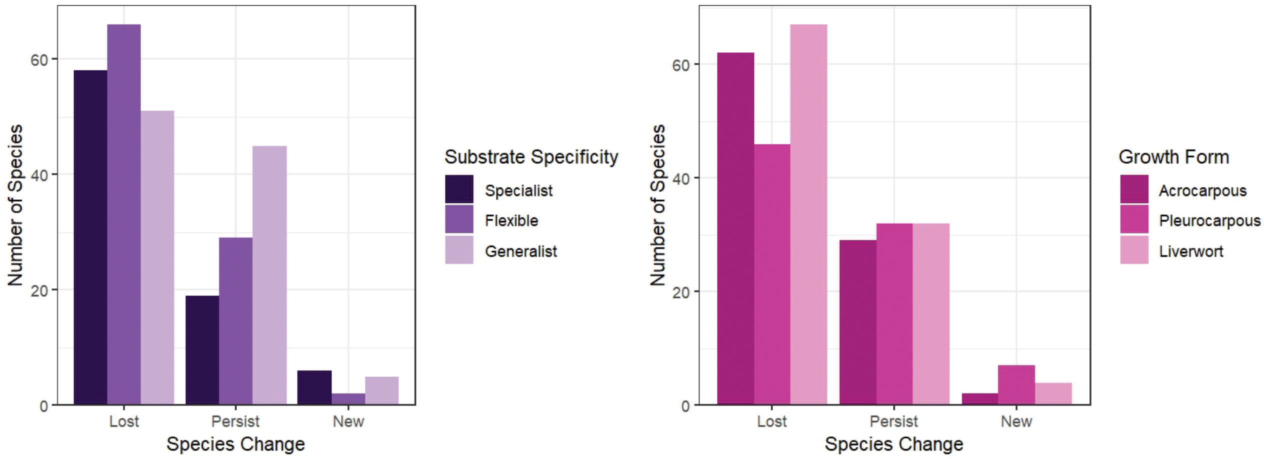

Figure 5. Species change through time for substrate specificity and growth form groups. Number of species lost, persisting, and new to the high elevation spatial grouping between pre-BWA invasion (Balsam Wooly Adelgid) and ICR (Initial Canopy Recovery) for specialist, flexible, and generalist species as well as between the different growth forms (acrocarps, pleurocarps, and liverwort). See Tables 3, 4 for results testing for significant differences between groups.

herbarium data is promising, as managed lands that lack permanent plots may be able to leverage natural history collections to assess how disturbances and management decisions alter the communities they aim to preserve, especially if such environmental changes are known to alter substrate availability.

The high fir tree mortality due to the BWA invasion as well as clearcutting as a management strategy resulted in an increase in logs on the forest floor (Johnson 1980). This increase in downed wood benefits species that require this substrate. However, they decay and inevitably disappear, thus reducing the substrate availability for bryophyte species requiring downed logs (Söderström 1988). For specialists who only inhabit downed logs, this loss would be highly detrimental, whereas generalists who can survive on other substrates would be able to persist through time, even as substrate availability changes (Halpern 2014). Increased substrate availability has been shown to positively benefit rare bryophytes (Ódor and Standovár 2002), as such, land managers should consider rare species substrates when designing and implementing conservation efforts. This is especially critical for downed wood substrate specialist species that are declining in abundance within the Great Smoky Mountains National Park (Shershen et al. 2024).

Trends in taxonomic order

When grouping bryophytes by growth form and examining species change from the pre-BWA to the ICR timespan, we observed more liverwort species were lost compared to pleurocarpous and acrocarpous mosses (Table 4, Fig. 5). While these were not statistically significant differences, this trend aligns with literature documenting liverworts being more sensitive to canopy opening compared to mosses (Fenton et al. 2003; Halpern et al. 2014). Liverworts are also more likely to exhibit substrate specificity than compared to pleurocarpous mosses, which are often generalists (Noualhaguet et al. 2023). This may be concerning since studies have shown that liverworts are more likely to remain locally extirpated following canopy disturbances (Fenton et al. 2003).

Bryophytes in different taxonomic orders had different trends in species change from the pre-BWA to the ICR timespan. However, a majority of the significant comparisons between species change groups were between new species and the lost or persisted groups. The orders with significantly different levels of species change, were driven by small numbers of new species entering the community compared to the large number that were lost or persisted (Table 5). There is no other shared trend among growth forms or characteristics of these orders likely driving these differences. This information is valuable in that it allows for targeted searches for “lost” species to determine if they are truly lost or if sampling efforts have not been sufficient to detect them. It also may be the case that these “new” species are from lower elevations, with climate change altering the available niches allowing them to invade the higher elevations. This use of herbarium specimens is an entire study, as seen by previous work (Bergamini et al. 2009).

Conservation implications and future directions

Resurveying and establishment of permanent plots remains a vital tool to preserve biodiversity, but in lands with limited funding or for taxa not included in surveys, herbaria may be a critical conservation tool to understanding how communities change in response to both agents of global change and changes to land management. In recent history natural history collections have been used for understanding natural and anthropogenic impacts on biological communities and will be vital in the future (Hedrick et al. 2020). They also aid with understanding distribution changes (Bergamini et al. 2009; Auld et al. 2022), shifts in phenology (Park et al. 2021; Faidiga et al. 2023), and improved understanding of threatened species (Nualart et al. 2017). They can also document extinctions and provide type specimens that can confirm a species has been extirpated (Nualart et al. 2017). These outcomes of natural history focused studies can then be used to design and implement management strategies to preserve the biodiversity of a landscape. Our study demonstrates that natural history collections can even be used to evaluate the effectiveness and consequences of such management decisions, adding novel ways in which conservation organizations can leverage herbaria.

Future research directions should compare costly permanent plot collections with herbarium records from the same area and timespans to determine how similar the results are from these two types of data. Another avenue could be examining a greater number of sites under the same management strategy to allow for more vigorous statistical analysis and help determine whether herbarium data can be more broadly utilized for evaluating community change following management changes. This would advance the field of conservation for lands without permanent plots, but requires continued surveying to ensure future work can benefit from robust collections. Such collections can be bolstered by forays that allocate time to identify and prepare herbarium grade specimens, leveraging undergraduate coursework (e.g. field botany courses or those with opportunities to collect) to increase sampling of common plants, and informal collection trips and bioblitz events that invite experts to identify and preserve specimens.

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

Use of AI

No use of AI was reported.

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Author contributions

All authors have contributed equally.

Author ORCIDs

Eric Shershen https://orcid.org/0009-0004-9362-9605
Jessica M. Budke https://orcid.org/0000-0003-1149-1522

Data availability

All data used for this work is available through open-access, online portals. Data is openly available at https://doi.org/10.17605/OSF.IO/PQNY4.

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Supplementary material 1

Original substrate classes and their descriptions from table 18 of Preston et al. (2017)

Authors: Eric Shershen, Jessica M. Budke

Data type: docx

Explanation note: Substrate classes used in this study were condensed for the rock and soil classes to match the more general substrate descriptions used in the FNA (Flora of North America Editorial Committee 1993).

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