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RESEARCH ARTICLE

Spatial phylogenetic patterns in the North American moss flora are shaped by history and climate

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Abstract

Aim: We documented patterns of phylogenetic diversity (PD) and phylogenetic endemism (PE) in the moss flora of North America, determined how environmental variables explain these patterns, compared the patterns in mosses to known patterns in angiosperms and explored how patterns driven by sub-clades might conflict with patterns driven by other sub-clades.

Location: North America north of Mexico.

Taxon: Mosses (Bryophyta).

Methods: A maximum-likelihood tree inferred from publicly available sequence data and locality data from ca. 7.5×10^5 herbarium specimens were combined to build a dataset of 935 species (representing ca. 67% of the known moss flora). Spatial randomization procedures were used to find significance levels of PD and relative phylogenetic diversity (RPD) for the full dataset and three major sub-clades, as well as to carry out a categorical analysis of Neo- and Paleo-endemism (CANAPE). Range weighted turnover in both species and PE was used to identify phytogeographic regions across the continent. Ordinations of environmental data were used to determine the distribution of PD, RPD, and phytogeographic regions within environmental space. Results of this study were compared to known patterns of phylodiversity in angiosperms.

Results: Phylodiversity is distributed non-randomly. Some patterns, for example, long branches in the southeastern US, are consistent with angiosperms; however, there are strong contrasts as well. Overall patterns of PD and RPD are strongly influenced by different phylogenetic scales within mosses, indicating that signal from one clade can obscure patterns in others. Three primary phytogeographic zones are defined by both differing geological histories and differing current abiotic conditions. Phytogeographic regions, PD, and RPD are all aligned with environmental variables.

Main conclusions: There is evidence for both ecological and historical factors in shaping the moss flora of North America, and biogeographic differences between angiosperms and mosses appear to align with important life-history differences between the two groups.

KEYWORDS
biogeography, bryophyte, CANAPE, phylogenetic diversity, refugia, species assembly, species richness

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Understanding the role of evolution in driving patterns of richness and endemism has long been at the heart of biogeographic studies. Only recently, however, have methods been developed to address these questions at broad spatial scales and across large segments of the tree of life (Faith, 1992; Mishler et al., 2020; Rosauer et al., 2009). Spatial phylogenetic methods, which focus on the distribution of phylogenetic branches rather than species richness, explicitly address the fact that species are not equally closely related. As such, they are proving to be powerful tools in efforts to develop meaningful conservation strategies (Kling et al., 2018) as well as elucidating the influences of geological history and current abiotic conditions on patterns of richness and endemism (Allen et al., 2019; Mienna et al., 2019; Mishler et al., 2020; Thornhill et al., 2017). Importantly, these approaches also provide context for management of biodiversity in the face of ongoing climate change and other anthropogenic disturbances (González-Orozco et al., 2014; Kling et al., 2018).

Studies of vascular plant phylogenetic diversity (PD; a measure of how much of the phylogeny is contained in a location) and of relative phylogenetic diversity (RPD; a measure of the distribution of branch lengths) have both confirmed earlier biogeographic hypotheses and added novel insights into our understanding of plant distributions. In California, for example, Thornhill et al. (2017) found a positive association between aridity and phylogenetic endemism (PE; i.e., PD that is inversely weighted by the range size of branches), which appears to confirm the long-held but previously untested assertion that aridification can drive diversification in plants (Stebbins, 1952). Mishler et al. (2020) came to a similar conclusion in finding a striking division between signals of recent diversification in the western half of the North American angiosperm flora and a more ancient assemblage in the eastern half. In a study of the Floridian vascular flora, Allen et al. (2019) also found prominent differences in patterns of PD and RPD related to the transition from the temperate to tropical floristic elements combined with massive influences of Pleistocene sea level rise across the peninsula.

The emerging critical mass of these studies across North America informs plant biogeography and highlights the importance of patterns of PD. However, meta-analyses of earlier phylogeographic studies illustrate that co-occurring lineages have unique evolutionary histories, and generalizations from one branch of the tree of life cannot be projected onto other branches (Avise, 2000; Brunsfeld et al., 2001; Manos & Meireles, 2015; Soltis et al., 2006). Given that richness and endemism are markedly different for different groups of organisms across North America (Jenkins et al., 2015), comparisons of PD across lineages promise to provide novel insights into how constraints imposed by differing life histories and metabolisms lead to different biogeographic patterns (Earl et al., 2021).

To date, spatial phylogenetic studies of plants have focused primarily on angiosperms, and mosses are a group of plants distinctly different from angiosperms in ways that could be expected to lead to biogeographic differences. For example, mosses are typically two or more orders of magnitude smaller than angiosperms and have some degree of desiccation tolerance, which means their relationship to water is drastically different from that of seed plants (Proctor, 2000; Proctor et al., 2007). Additionally, mosses lack flowers, fruits, and roots, they employ spore dispersal rather than seed dispersal, and they rely on sperm swimming through a film of water from male gametangia to female gametangia in order to reproduce sexually (Mishler & Oliver, 2009). Therefore, many of the biotic and abiotic interactions that are important in seed plant lineages are absent or markedly different in mosses.

Several of the differences listed above have clear biogeographic implications. For example, spore dispersal likely explains the fact that absolute endemism (i.e., the proportion of taxa entirely restricted to a region) of named moss species at continental scales is very low (Carter et al., 2016; Frahm & Vitt, 1993). Differing abiotic and biotic interactions may also influence diversification rates, which would therefore impact patterns of PD. Diversification rates in mosses can be on par with rapid angiosperm radiations (Wall, 2005), but net diversification rates over the course of plant evolutionary history appear to be lower than the rate in angiosperms (Laenen et al., 2014).

In this study, we compared patterns of PD and RPD to better understand the roles of ecological and evolutionary drivers of biotic assembly. Patterns of significantly high or low PD could reflect a number of processes. For example, overdispersion (significantly higher PD than expected by chance) could be caused by competitive exclusion of ecologically similar species (Violle et al., 2011). This interpretation is often associated with stable, favourable environmental conditions in which competitive interactions rather than habitat preferences determine species coexistence. In contrast, ecological clustering (significantly lower PD than expected by chance) could be caused by evolutionary niche conservatism which results in closely related species co-occurring because shared traits allow them to inhabit similar environments (Webb et al., 2002). Clustering is thought to be more important when environmental conditions are relatively harsh or unpredictable (Huang et al., 2021).

Patterns of significantly high or low RPD may reflect different processes than patterns of PD, so it is useful to study PD and RPD in conjunction. Because RPD reflects the distribution of long or short branches, it is a useful potential indicator of biogeographic and evolutionary assembly processes. The concentration of more long branches than expected (significantly high RPD) could indicate a refugium, whereas the concentration of more short branches than expected (significantly low RPD) could indicate a region in which recent diversification has played a large role in community assembly.

We hypothesized that the biological differences outlined above should lead to different spatial phylogenetic patterns between mosses and angiosperms across North America. In addition to reporting patterns of richness and PD, we tested the following five specific hypotheses: (1) PD is non-randomly distributed across the continent. We predicted that, similar to the angiosperm flora (Mishler et al., 2020), moss PD is significantly lower than expected by chance throughout the continent due to environmental filtering. (2) RPD is non-randomly distributed across the continent. Angiosperm RPD is sharply divided, with long branches in the east and short branches in western North America (Mishler et al., 2020); we expected a similar pattern for the mosses. (3) Centers of endemism are located in the Pacific Northwest and the southern Appalachians. (4) Regions with significantly high PD and high RPD are concentrated in regions with wet, relatively aseasonal climates that were not glaciated during the Pleistocene, because dry or strongly seasonal climates and glacial activity might be expected to reduce PD and RPD. (5) Patterns of spatial turnover based on species and based on PD would differ. If environmental conditions filter lineages based on their conserved habitat preferences, this should be expressed as differences between the species-based and PD-based spatial turnover maps.

1 | MATERIALS AND METHODS

1.1 | Spatial and phylogenetic data

We constructed a molecular phylogram for 935 moss species, approximately (67%) of the species known from North America (Carter, 2021). We conducted a hierarchical analysis of the NCBI GenBank plant sequence database (compiled 5 November 2020) using PyPHLAWD (Smith & Walker, 2018) to create a molecular dataset for phylogenetic analysis. Default blastn settings were used to obtain sequences for known North American moss taxa. We then applied the PyPHLAWD script *find_good_clusters_for_concat.py* to identify the gene regions (clusters) for phylogenetic analysis and then removed loci missing in more than 15% of our taxa. The resultant dataset (see Supporting Information) includes nine gene regions: five plastid loci (RPL16, trnL-trnF, rbcL, RPS4, and trnG), three nuclear ribosomal loci (26S, 18S, and ITS) and one mitochondrial locus (nad5). Sequences for each locus were aligned with MAFFT 7 (Katoh & Standley, 2013) using the "-auto" flag after which nucleotide positions with more than 50% missing data were removed using TrimAl (Capella-Gutiérrez et al., 2009). Loci were concatenated with "pxcat" from the Phyx toolbox (Brown et al., 2017). A maximum likelihood phylogeny was constructed in RAxML v8.2.9 (Stamatakis, 2014) with the "-f a" option, GTRCAT rate heterogeneity model and 100 bootstrap replicates. Data were partitioned by locus. Alignment summary statistics were calculated using AMAS (Borowiec, 2016).

Spatial data were obtained from an earlier study (Carter, 2021) and were trimmed to include the 935 species for which sequence data were available. Nomenclature was standardized to the Flora of North America project (hereafter FNA; Flora of North America Editorial Committee, 2007, 2014), using a custom thesaurus with more than 4000 names (accepted names and synonyms) built from the online database TROPICOS (https://www.tropicos.org/home) and from major relevant regional floras (e.g., Crum & Anderson, 1981; Norris & Shevock, 2004). All intra-specific names were collapsed to species. Duplicate specimens were removed, as were records for which coordinates and political boundaries did not match. The initial cleaned dataset included a total of 746,648 occurrence records based on herbarium specimens, with a median of 300 (range 1 to 11,117) records per species. Spatial data were aggregated into grid cells of 100 × 100 km after transformation to an Albers equal area projection. This size balanced the need to use small grid cells to detect fine-scale spatial patterns while retaining a reasonable redundancy (Baldwin et al., 2017). Except where specified otherwise, all data management and analyses were performed in R (R Core Team, 2020) using custom scripts.

Sampling intensity varied widely across grid cells (1–9075 collections per grid cell, median = 65). To reduce impacts of uneven sampling, grid cells with fewer than 15 species were removed. This resulted in the exclusion of 714 of the 2089 grid cells (34.1%) and included most of central Canada and a portion of the south-central United States. The threshold of 15 species was chosen after computing both alpha and beta diversity metrics across the full dataset of 2089 grid cells. Grid cells below that threshold were unstable in alpha and beta diversity metrics.

1.2 | Alpha diversity metrics

Taxon richness (TR), PD, PE, RPD and relative phylogenetic endemism (RPE) were calculated in *Biodiverse 1.99_088* (Laffan et al., 2010) following Mishler et al. (2014) and Thornhill et al. (2016). Briefly, occurrence records were aggregated into grid cells to calculate TR. PD was quantified for each grid cell as the sum of branch lengths for a tree pruned to include only species in that grid cell. PE uses a similar approach to PD, but scales branch lengths based on the inverse of their range size. RPD is a ratio between PD on the observed tree and PD on a comparison tree that has equal branch lengths throughout, and RPE is a metric similar to RPD but using branch lengths scaled by range size (PE).

Phylogenetic diversity can be measuring using different facets of the phylogeny (Kling et al., 2018): phylograms (with branch lengths scaled to inferred genetic change), chronograms (branch lengths scaled to inferred time) or cladograms (all branch lengths scaled to the same length). Different facets can sometimes show different patterns on the landscape (Allen et al., 2019; Kling et al., 2018; Thornhill et al., 2017), because they emphasize different aspects of phylodiversity. We chose to use a phylogram here since we wanted to emphasize patterns of genetic diversity on the landscape in phylogenetic context.

Randomization tests, constrained so that each species retained the same range size and each grid cell retained the same richness, were implemented using the 'rand_structured' option in *Biodiverse* to determine significantly high and low values for each metric. CANAPE (categorical analysis of neo- and paleo-endemism; Mishler et al., 2014) was performed to identify grid cells with significantly high PE and then to identify which of these grid cells have significant concentrations of short, range-restricted branches (indicating neo-endemism), long, range-restricted branches (indicating paleo-endemism), or a mixture of the two following Mishler et al. (2014) and Thornhill et al. (2016).

1.3 | Beta diversity metrics

Spatial patterns of beta diversity were examined using two metrics: range-weighted turnover using species (range-weighted turnover: RWT) or using phylogenetic branch lengths (phylo-range-weighted turnover: PRWT). Both metrics place a higher weight on range-restricted species (or branches) in the turnover calculation than standard turnover metrics (Laffan et al., 2016). In both cases, *Biodiverse* was used to generate distances among grid cells and then a UPGMA tree to identify regions (i.e., clusters of grid cells) that had similar species composition or shared similar branches of the phylogeny, respectively.

1.4 | Range size differences

To determine whether differences in range size between species of mosses and angiosperms might be important in interpreting differences in results of randomization tests between the two groups, angiosperm occurrence data from Mishler et al. (2020) were downloaded and aggregated to the same grid cell size as the grid cells in the moss analyses. A Wilcoxon rank sum test was used to test the whether the range sizes differed between mosses and angiosperms.

1.5 | Environmental analyses

To visualize the distribution of TR, PD and RPD within environmental space, we selected five environmental variables that capture broad patterns but avoid collinearity. Four climate variables were obtained from WORLDCLIM (Fick & Hijmans, 2017): mean annual temperature, annual precipitation, temperature seasonality and precipitation seasonality. A fifth environmental variable, topographic position index (hereafter 'topography') was obtained from Amatulli et al. (2018). This index quantifies topographic heterogeneity and is a measure roughly equivalent to the standard deviation of elevation within each grid cell. Because environmental data and species data used different projections, climate data for each grid cell were obtained by using the midpoint of each grid cell to sample from the climate layers.

To test whether environmental variables were correlated with regions of significantly high or low PD and RPD while taking into account spatial autocorrelation, spatial generalized linear mixed models (GLMMs) were employed. Prior to running the GLMMs, standard logistic regressions (LRs) with no spatial term were conducted with the *glm* function in R using the five environmental variables after checking the predictors for normality. Thus, a total of eight analyses were conducted, one GLMM and one LR each for significantly high PD, significantly low PD, significantly high RPD and significantly low RPD. The GLMMs were implemented using the *fitme* function from the 'spaMM' package version 3.7.2 (Rousset & Ferdy, 2014) with a binomial response and employing the Matérn spatial model with the environmental variables as fixed effects and spatial position (using grid cell centers) as a random effect. Significance of individual fixed effects was assessed by re-running the GLMMs excluding each variable one at a time and then comparing the nested model to the full model using a likelihood ratio test.

In addition to the significance tests, we visualized the distribution of grid cells with high TR (grid cells in the highest 10% for TR), and regions with significantly high or low PD and RPD, across environmental variables using principal component analysis (PCA). Variables were scaled prior to running the PCA by setting scale = true within the *prcomp* R function.

To determine how phytogeographic regions from the beta diversity analyses were related to one another climatically, a linear discriminant analysis (LDA) was run using the same dataset as the PCA and using the six primary regions identified by the PRWT analysis.

1.6 | Sub-clade analyses

Patterns in alpha and beta diversity measured across the entire flora could be affected by patterns that are strong within some subclades but not others. For example, in mosses the pleurocarpous clade putatively has greater richness in cool, wet, forested regions and the haplolepidious clade has greater richness in drier regions. To test the extent to which these major clades contributed to (or differed from) the overall patterns, the alpha diversity metrics as described above were computed for three subsets of all mosses: the 'true mosses', i.e., all mosses except *Sphagnum*, which is the first branch to split from the rest of mosses in the phylogeny; haplolepidious mosses, which are a well-supported clade of acrocarpous mosses including many arid-adapted lineages, e.g., Pottiaceae and Grimmiaceae; and third, the pleurocarpous mosses, which are a well-supported clade within mosses that are typically associated ecologically with mesic, forested habitats. Of the 935 species in the full dataset, the true mosses comprised 817 species, the haplolepidious mosses comprised 313 species and the pleurocarpous mosses comprised 264 species.

2 | RESULTS

2.1 | Spatial and phylogenetic data

The final aligned and concatenated supermatrix contained 935 species and 9 loci, with each locus representation across an average of 38% of our taxa (range: 15%–61%). The final concatenated alignment had a total length of 8575 bp with 67% missing data. The proportion of parsimony-informative and variable sites were 45% and 58%, respectively. The phylogenetic reconstruction recovered a topology largely consistent with previous estimates of moss phylogeny (Liu et al., 2019).

The matrix of spatial data included 67.3% of the species recognized by FNA, and phylogenetic coverage was generally good, with the inclusion of 90.1% of genera and 95.0% of families recognized by FNA. After cleaning the spatial data, the 935 species occurred across 1375 100 × 100 km grid cells, with a median richness of 70 species per grid cell (range 15–352).

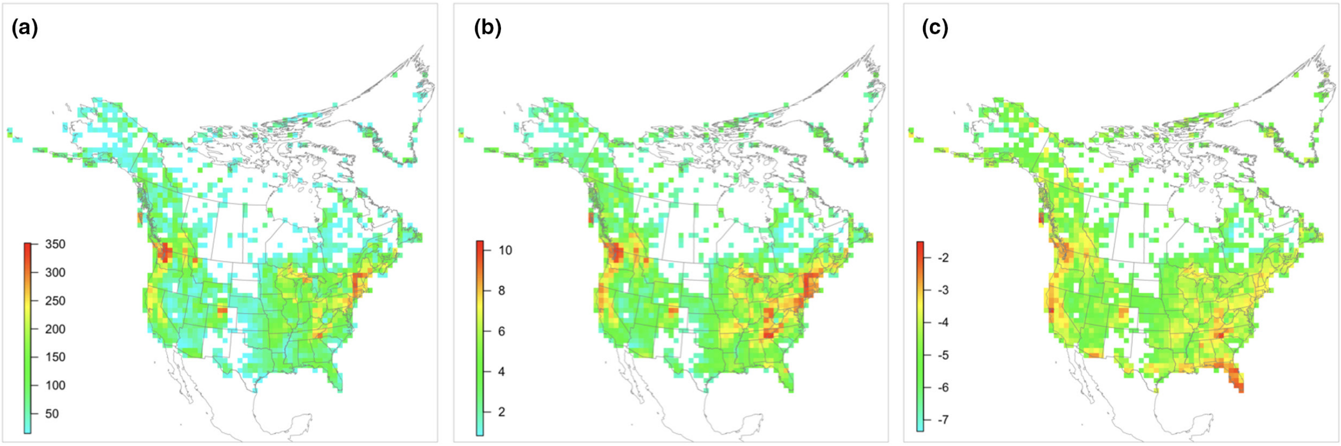

FIGURE 1 Heat maps of (a) taxon richness, (b) phylogenetic diversity and (c) phylogenetic endemism (PE) of the moss flora of North America (PE is presented as log PE). All maps are in Albers equal area projection

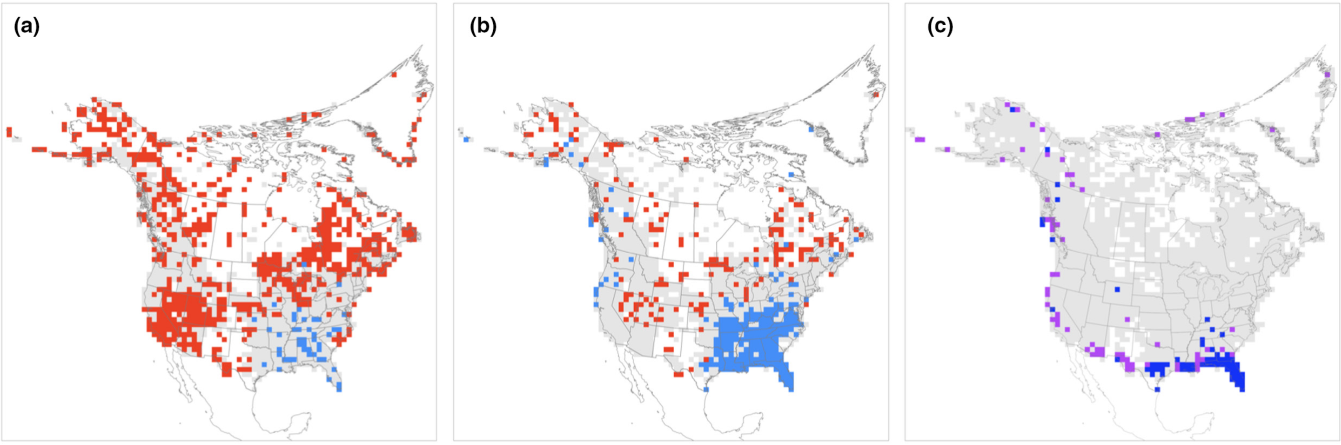

FIGURE 2 Significance of alpha diversity metrics: (a) phylogenetic diversity (PD)—red grid cells have significantly low PD and blue grid cells have significantly high PD; (b) relative phylogenetic diversity (RPD)—red grid cells have significantly low RPD and blue grid cells have significantly high RPD; and (c) regions of significant endemism, with centers of paleo-endemism in blue and centers of mixed endemism in purple. All maps are in Albers equal area projection

2.2 | Alpha diversity metrics

Taxon richness was generally high in two areas (Figure 1a). In the west, taxon-rich cells extended along the coastal mountain ranges from approximately Vancouver to San Francisco. In the east, richness was high in the northeastern US from Maine to the southern terminus of the Appalachians and extending west through the Great Lakes region. There were four concentrations of very high richness. These were, in order, northwestern Washington (with outlying grid cells in the Haida Gwaii islands and western Montana), New England (central Maine through Massachusetts), north-central Colorado, and the southern tip of the Appalachians at the boundary between North Carolina and Tennessee.

Patterns of raw PD were broadly similar to TR (Figure 1b), with high areas along the west coast and throughout the northeast and north-central US; however the peaks were different. Highest PD was in the southern Appalachians and northwestern Washington, followed by a similar New England region and a region in southern Ohio. In contrast, PE was concentrated in Florida and around Vancouver, with isolated grid cells near San Francisco, in southeastern Arizona and at the southern tip of the Appalachians (Figure 1c).

Areas with significantly high PD were concentrated in the southeastern US (Figure 2a). Much of the rest of the continent was found to have significantly low PD, with particularly dense clusters throughout Quebec and extending south through the Great Lakes, in the arid southwest, and throughout much of Northwestern Canada and Alaska.

Patterns of significantly high or low RPD were somewhat different from patterns of significant PD (Figure 2b). Significantly high RPD was found to be nearly ubiquitous across the southeastern US, with additional isolated cells throughout the Pacific Northwest and extending through mountainous regions of Canada and Alaska. Significantly low RPD cells were concentrated in southeastern Canada and the interior United States.

The CANAPE results indicated that Florida and the southern coast along the Gulf of Mexico is a hotspot of paleoendemism, with additional isolated grid cells in western mountainous regions (Figure 2c). Areas of mixed endemism were more widespread and extended along the Mexican border, throughout California, and in scattered grid cells in western Canada and Alaska and across the arctic. No grid cells were identified as hotspots of neoendemism or met the criteria for super endemism (PE significantly high with an alpha of 0.01).

2.3 | Beta diversity metrics

The RWT and PRWT clustering analyses were largely congruent in identifying three major regions (east, west and north) comprising six primary clusters of grid cells: north (including most of the taiga and Canadian Rockies), eastern US excluding Florida, Pacific coast, interior west, Florida, and a southwestern region along the Mexican-US border (Figures 3 and 4). Meaningful subsets of these six clusters were also defined within the six primary clusters. There were two important differences between the RWT and PRWT analyses (Figure S1). First, in the RWT analyses, two clear clusters were apparent in the north, whereas this split was not apparent in the PRWT analysis. Second, the relative similarities of the three geographic groups differed between the two analyses. In the PRWT analysis, the interior west region (including the Great Basin Desert and Rocky Mountains) clustered with the north rather than with the Pacific cluster as in the RWT analysis. Additionally, in the PRWT analysis, both Florida and the southwestern (Mexican border) cluster were deeply separated from the rest of the continent, while in the RWT analysis, the southwestern cluster aligned with the west and the Florida cluster aligned with the east (Figure S1).

2.4 | Range size differences among angiosperms and mosses

Species range sizes, measured as occupancy across 100 × 100 km grid cells, differed among angiosperms and mosses. Moss range sizes varied from one grid cell to 877 (mean 130.7, median 73), while angiosperm range size varied from one grid cell to 1274 (mean 52.9, median 8). Moss range sizes were found to be significantly larger based on a Wilcoxon rank sum test ($W = 3.85 \times 10^7$, $p < 0.0001$).

2.5 | Environmental analyses

Within the PCA of environmental variables, there is a clear separation among the high TR grid cells in the east and those found in the west, but both groups are in areas with relatively high precipitation (Figure 5). Eastern grid cells occur in warm, high precipitation areas and are relatively consistent with one another (i.e., have low

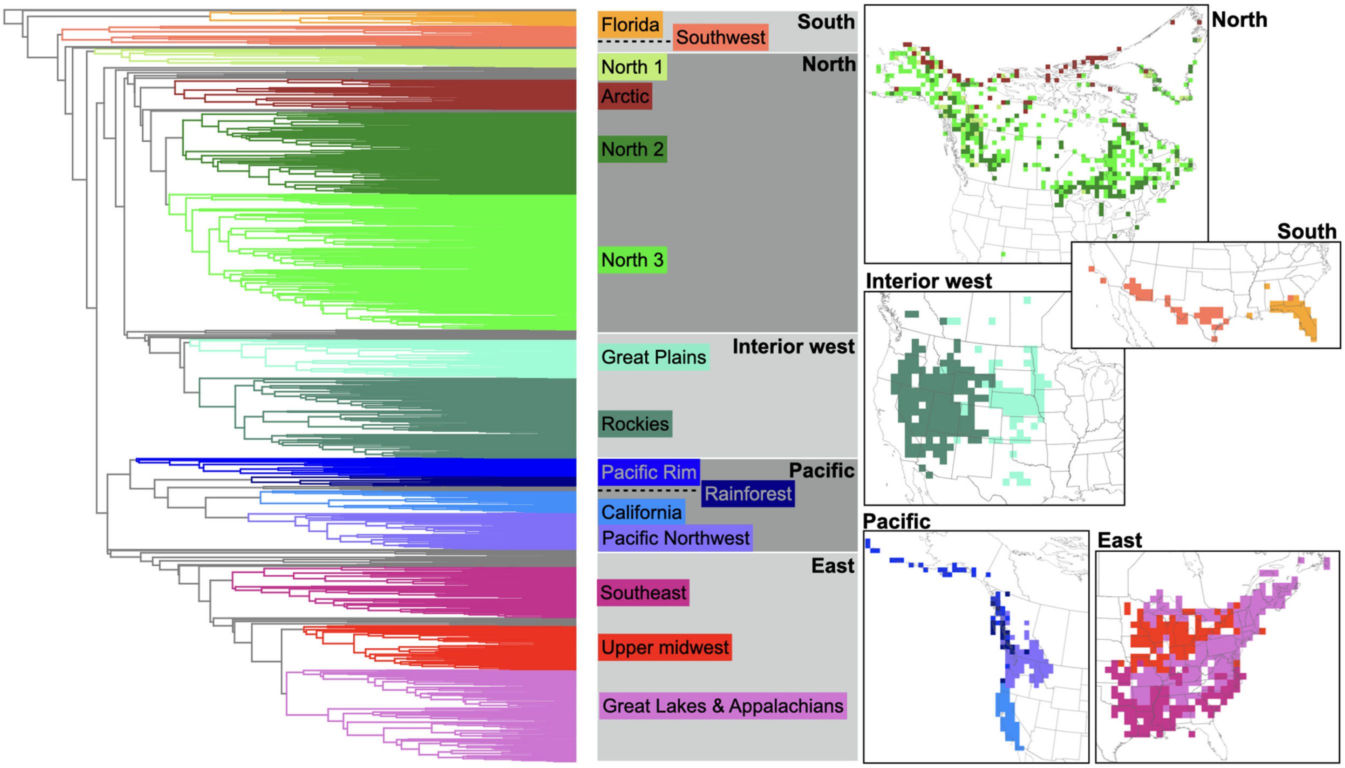

FIGURE 3 Geographic subregions of North America based of phylogenetic range weighted turnover. All maps are in Albers equal area projection

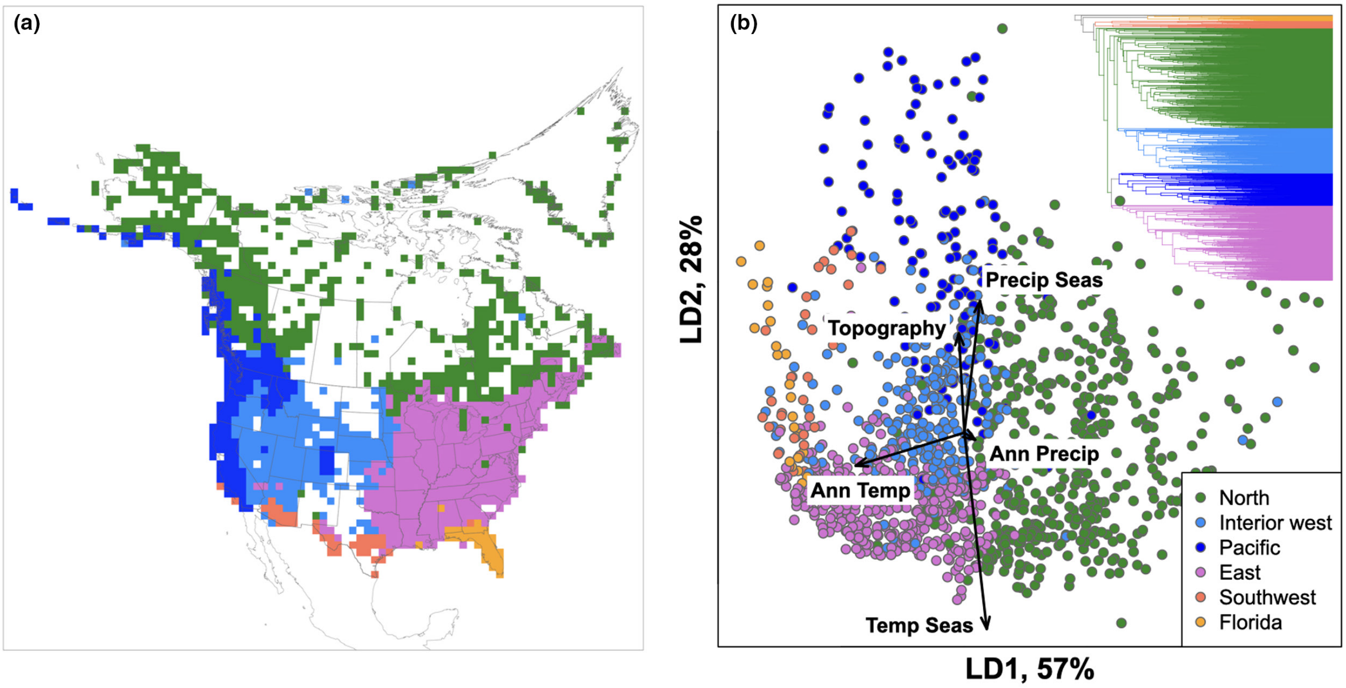

FIGURE 4 The six primary phytogeographic regions (a) identified by phylogenetic range weighted turnover, with linear discriminant analysis (b) of environmental variables across the regions. Inset dendrogram indicates phylogenetic similarity among the six geographic regions. Map is in Albers equal area projection

variance), whereas western grid cells with high richness tend to have high precipitation, have high topographic heterogeneity and have greater variance than the eastern areas. Grid cells with significantly high PD and RPD are predominantly high precipitation, warm areas with low seasonality in both temperature and precipitation, whereas grid cells with significantly low PD and RPD have centroids similar to non-significant grid cells.

Tests for the importance of spatial autocorrelation between environmental variables and regions with significantly high or low PD and RPD confirmed that spatial autocorrelation plays a strong role at this spatial scale (Table S1) and suggest that caution should be taken in interpreting the results of the ordinations. LRs predicting the presence of significantly high or low PD and RPD without a spatial term generally found that both temperature and precipitation were significant predictors of high and low PD and RPD, while temperature seasonality, precipitation seasonality and topography tended not to be significant. In contrast, in the GLMMs employing a spatial term there were only two instances where environmental predictors significantly improved model fit (temperature as a predictor for significantly low RPD and precipitation seasonality as a predictor for significantly high RPD; see Table S1).

Moss ecoregions also separated clearly using ordination (Figure 4). The northern cluster is distinct along the first LDA axis, which is weighted most heavily by temperature. The second LDA axis is driven primarily by seasonality but also topography, and effectively separates the eastern, Pacific and interior west clusters.

2.6 | Sub-clade analyses

Areas of significant PD and RPD were roughly congruent among the analyses of different sub-clades and between sub-clades and the full dataset, but there were several noteworthy differences (Figures S2 and S3). Pleurocarpous mosses had the greatest differences, with more clustering in the west and more overdispersion in the southeast than any of the other datasets. In the haplolepidious mosses, grid cells with overdispersion were limited to Florida and the gulf coast, in contrast with overdispersion throughout the southeast in the other datasets. In all the subsets, the strong signal of clustering in eastern Canada seen in the overall analysis was dampened, indicating that the presence of that pattern in the full dataset was driven almost exclusively by *Sphagnum* (the only group absent from all three subsets). *Sphagnum* similarly dominated the signal in the RPD results for the full dataset. Each of the three subsets contain large concentrations of significantly short branches in the western US, not seen in the full analysis. Concentration of long branches in the southeast are consistent across the subsets and full analysis.

3 | DISCUSSION

3.1 | General spatial patterns

Our results support the recognition of three primary phytogeographic regions for the mosses of North America (north, east and west). Not surprisingly, the three primary regions differ in current climate as well as in their histories across geologic time. As expected, patterns of TR and PD across the continent are very similar, with highest values in the Pacific Northwest and New England (and extending down the Appalachians). The Pacific Northwest has long been appreciated as a hotspot for bryophyte diversity (Geffert et al., 2013; Tan & Pócs, 2000), but the high richness and PD in the northeast has been less recognized. Both regions lie in zones that have current climates favourable to bryophytes (cool, high precipitation), which suggests an ecological component to the maintenance of PD. However, they also lie at the suture zones between the North and West phytogeographic regions (the Pacific Northwest) and between North and East phytogeographic regions (New England). The boundary between the North and the West + East approximates, in what is unlikely to be coincidence, the southern extent of the last glacial maximum. This clearly suggests that geological history is also important in explaining patterns of moss diversity across the continent.

Dispersal limitation is not likely to explain the floristic differences across regions. Despite the strong floristic differences among regions, approximately 81% of bryophyte species in North America are also native to another continent (Carter, 2021), and genetic studies often find evidence of intercontinental dispersal (Patiño & Vanderpoorten, 2018). The fact that there are distinct regional floristic differences, even though many species have the potential to disperse across long distances, suggests that abiotic filtering is important. This corroborates an earlier finding by Collart et al. (2021), who found that in liverworts across two large-scale datasets, phylogenetic turnover was much more closely tied to macroclimatic turnover than to geographic distance.

There are also abiotic differences between areas of highest raw PD and areas of significantly high PD and RPD. Raw PD peaks in areas with relatively cool and wet climates, with the two peaks (Pacific Northwest and New England/Appalachians) differentiated by warmer and wetter climates in the east and more heterogeneous topography in the west (Figure 5). Regions of significantly high PD and RPD were primarily located in the warm, wet climates of the southeast. This offset between areas with highest raw PD (cool and wet) versus significantly high PD (warm and wet) illustrates the importance of contrasting raw PD, which correlates with richness, with unexpectedly high PD, which does not. In this case, the pattern is driven by tropical lineages in warm, wet regions that are excluded from the rest of the continent. These relationships have a strong signal of spatial autocorrelation (Table S1); however, given the spatial and temporal scales in question, we do not regard this as being critical to their interpretation.

Processes at geological timescales are clearly important in North America as well, and Schofield (1980) and Carter (2021) argued for the importance of Pleistocene refugia in the development of current patterns of endemism in the flora. Northern North America was nearly completely glaciated at the last glacial maximum, and though both remained unglaciated through the Pleistocene, the east and west have distinctly different histories from each other. The west saw massive ecological shifts with the cooling and drying of the Miocene (Graham, 1999), while the east has maintained a relatively consistent warm and wet climate through the same period. The importance of the southeast as a refuge for more tropical floristic elements throughout the Tertiary has been well documented with plant fossils (Manchester, 1999; Tiffney, 1985a, 1985b; Wolfe, 1975) and has been largely supported by a meta-analysis of plant phylogenies (Manos & Meireles, 2015). Although relevant fossil data for bryophytes are largely lacking (reviewed by Carter, 2021), bryologists have long noted that the southeast bears a similar signal of tertiary relictualism for bryophytes (Anderson, 1971; Anderson & Zander, 1973; Crum, 1972; Frahm & Vitt, 1993; Schofield, 1980). In the following discussion of PD and RPD in the three primary moss phytoregions, it is important to keep in mind that we are currently unable to fully disentangle the relative importance of current climatic differences and different geological histories of the regions.

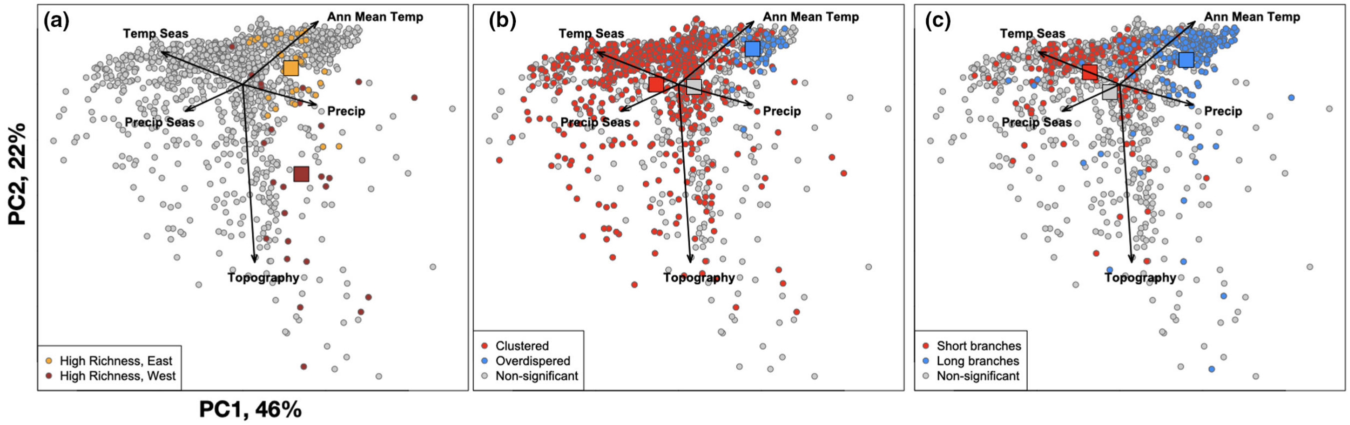

FIGURE 5 Principle components analysis of environmental variables in relation to patterns of phylogenetic diversity (PD). (a) Eastern and western grid cells with highest overall taxon richness. (b) Grid cells with significantly high and low PD. (c) Grid cells with significantly high and low relative phylogenetic diversity. Squares indicate group centroids

3.2 | Regional differences

3.2.1 | The North

Most of the north had lower than expected PD, suggesting strong ecological filtering. This is unsurprising given the harsh climate and a similar pattern seen in the angiosperms of the region (Mishler et al., 2020). RPD values tended toward significantly shorter branches than expected. Concentrations of low RPD around Quebec differed from the angiosperm pattern (Mishler et al., 2020), which had generally high RPD in eastern Canada. Species in the genus *Sphagnum* comprise a large proportion of the moss flora of the north, and especially the region around Quebec. *Sphagnum* diverged very early from the rest of the mosses yet comprises a clade of relatively recently diverged species (Shaw et al., 2016), and this likely plays a strong role in calculations of both PD and RPD for regions where *Sphagnum* richness is high. This at least partly explains the discrepancy between the distributions of branch lengths between angiosperms and mosses in Canada. It also, at least in part, explains the differences in the northern clusters derived from the species-based versus lineage-based turnover metrics.

Northern cells identified as centers of endemism in the CANAPE analysis were concentrated in western and northern Canada and Alaska. Cells were a mix of paleo- and mixed endemism, suggesting that northern glacial refugia, as discussed by Steere (1976), may have been important throughout the Pleistocene.

3.2.2 | The East

In the east, most cells had significantly high RPD and either non-significant or significantly high PD. Angiosperms in the same region, in contrast, had mostly significantly high RPD but significantly low PD (Mishler et al., 2020). In both floras, the high RPD is a strong confirmation that the southeastern US is an important refugium (Anderson, 1971; Manos & Meireles, 2015; Wolfe, 1975). The explanation for phylogenetic clustering in the angiosperm flora but overdispersion in the moss flora is less straightforward. The expected pattern at this spatial scale (as seen in angiosperms) is phylogenetic clustering because co-occurring species will tend to be more closely related than species drawn at random from across the continent. The lack of clustering in mosses might be because there are few major moss lineages in the east that do not also occur in the west or north; thus, few lineages are strongly over-represented in the east. In addition, lineages with high diversity in the north or west (e.g., Orthotrichaceae, Grimmiaceae) have at least a few species each that are widespread in the east; thus, increasing the evenness of sampling across the phylogeny in eastern grid cells. Another consideration is that in North America, angiosperms have far more recognized species, and species on average have ranges that are much smaller than moss species ranges. It is unclear the extent to which this is a biological difference or a difference in species ranking, but regardless, if lineages with small ranges are compared to those with larger ranges, spatial patterns could be expected to differ.

The eastern region contained the primary center of paleo-endemism in the CANAPE analyses and, contrary to expectation, these cells were concentrated in Florida and the Gulf Coast rather than the southern Appalachians. The Floridian center of paleo-endemism may only be an edge-effect but is nonetheless of interest. It is the only region in the North America that has a high density of tropical lineages, and those lineages all have small ranges within North America (though many are wide-ranging tropical species). This combination of evolutionarily unique (in the context of North America) lineages with small range sizes (again in the context of North America) is the information used by CANAPE to define centers of paleo-endemism.

3.2.3 | The West

In the west, most grid cells had significantly low PD and had non-significant RPD, though there were scattered grid cells in Washington, Oregon, California, and Arizona with higher than expected RPD and scattered grid cells in the Rocky Mountains with lower than expected RPD. This contrasts with patterns seen in the angiosperm flora, which had uniformly low PD in the west and mixed low and non-significant RPD. The presence of low PD cells coinciding with a lack of many low RPD cells in the west may suggest that ecological filtering of existing lineages has a more important role than in situ diversification (e.g., in response to Miocene aridification) for mosses. An important caveat to this interpretation is that moss lineages that have undergone recent divergence are likely to be undersampled due to morphological similarity and therefore the result here may be biased. In fact, most of the clear cases of recent divergence among North American mosses are from western clades, for example, *Homalothecium* (Huttunen et al., 2008), *Scleropodium* (Carter, 2012), *Orthotrichum* (Medina et al., 2012, 2013) and *Pulvigera* (Lara et al., 2020).

Another important insight comes from the examination of different phylogenetic subsets in the west. Unlike the analysis of the full dataset, each of the subsets that lacked *Sphagnum* indicated strong phylogenetic clustering in the west. This discrepancy illustrates how a strong pattern in one sub-clade can obscure the signal from other sub-clades in a high-level phylogenetic analysis, underscoring the necessity to look at spatial phylogenetic patterns at multiple nested levels in future studies.

Western grid cells identified as centers of endemism occurred primarily in the California Floristic Province and along the Mexican border and consisted primarily of regions with mixed endemism. The California Floristic Province is a well-known center of both neo- and paleo-endemism for angiosperms (Baldwin et al., 2017; Thornhill et al., 2017) and this result confirms the importance of this region for bryophytes as well. Mixed endemism in southeastern Arizona is likely an edge effect, as discussed above for Florida, driven by species from the uppermost reaches of the Madrean sky islands that extend northward from Mexico into Arizona.

Patterns of beta diversity in the western region differed between the PRWT and RWT analyses. In both cases, the west was clearly separated into two sub-regions: the Pacific coast region and the interior west region. In the lineage-based PRWT analysis, the interior west clustered with the northern clusters, while in the species-based RWT analysis, the interior west clustered with the pacific coast region. This discrepancy indicates that the evolutionary connection of the interior west to the north is greater than might be expected based on species turnover. This is largely consistent with an idea that has been alluded to though not explicitly stated (Carter, 2021; Carter et al., 2016; Schofield, 1980) that the flora of the interior represents an extension of more northern lineages despite high species similarity with the mountainous regions along the pacific coast. This illustrates the utility in comparing patterns of phylogenetic turnover with traditional species-based metrics to provide a more nuanced understanding of biogeographic patterns. In general, the differences between patterns of lineage-based and species-based results in this study highlights the potential for spatial phylogenetics to uncover biogeographic patterns that remain obscure in purely species-based analyses.

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CONFLICT OF INTEREST

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

The sequence alignment, ML tree and occurrence data used in this study are openly available from the Dryad Digital Repository (https://doi.org/10.5061/dryad.r7sqv9sd2).

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BIOSKETCH

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SUPPORTING INFORMATION

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