


Spatial phylogenetics reveals evolutionary constraints on the assembly of a large regional flora

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PREMISE OF THE STUDY: We used spatial phylogenetics to analyze the assembly of the Wisconsin flora, linking processes of dispersal and niche evolution to spatial patterns of floristic and phylogenetic diversity and testing whether phylogenetic niche conservatism can account for these patterns.

METHODS: We used digitized records and a new molecular phylogeny for 93% of vascular plants in Wisconsin to estimate spatial variation in species richness and phylogenetic α and β diversity in a native flora shaped mainly by postglacial dispersal and response to environmental gradients. We developed distribution models for all species and used these to infer fine-scale variation in potential diversity, phylogenetic distance, and interspecific range overlaps. We identified 11 bioregions based on floristic composition, mapped areas of neo- and paleo-endemism to establish new conservation priorities and predict how community-assembly patterns should shift with climatic change.

KEY RESULTS: Spatial phylogenetic turnover most strongly reflects differences in temperature and spatial distance. For all vascular plants, assemblages shift from phylogenetically clustered to overdispersed northward, contrary to most other studies. This pattern is lost for angiosperms alone, illustrating the importance of phylogenetic scale.

CONCLUSIONS: Species ranges and assemblage composition appear driven primarily by phylogenetic niche conservatism. Closely related species are ecologically similar and occupy similar territories. The average level and geographic structure of plant phylogenetic diversity within Wisconsin are expected to greatly decline over the next half century, while potential species richness will increase throughout the state. Our methods can be applied to allochthonous communities throughout the world.

KEY WORDS climate change; community assembly; niche modeling; phylogenetic diversity; phylogenetic niche conservatism; Wisconsin.

Spatial phylogenetics—the geographic distribution of individual lineages and lineage diversity—is an important aspect of biodiversity that only recently has begun to receive scientific study. It reflects spatial variation in present and past environmental conditions, together with ecological and evolutionary processes, including dispersal, physiological tolerance, and biotic interactions, as well as in situ speciation, local extinction, adaptive divergence, and niche conservatism. Analyzing spatial variation in the presence and diversity of individual lineages can help us understand these processes (Rosauer et al., 2009; González-Caro et al., 2014; Mishler et al., 2014; Qian et al., 2014a; González-Orozco et al., 2016; Thornhill et al.,

2016). It can also help predict how future changes are likely to affect biodiversity and how it might be best conserved.

We quantified spatial variation in the diversity of species and lineages across the entire vascular flora of Wisconsin, United States. Our aims were to describe these patterns for the first time, test several hypotheses regarding the drivers of such patterns, identify floristically distinct bioregions, and establish regional priorities for conservation. These analyses are based on our new molecular phylogeny of the Wisconsin flora and new databases for the distribution of vascular plant species in Wisconsin and nearby regions. In contrast to other large areas whose spatial phylogenetics have recently

been studied (e.g., Australia, Thornhill et al., 2016; Chile, Scherson et al., 2017; California, Thornhill et al., 2017), Wisconsin has a native flora that is allochthonous, having been assembled almost wholly via dispersal following deglaciation only 1–9 kya. Of the 1873 vascular plant species native to Wisconsin, only one species and two interspecific taxa are endemic to the state. In situ speciation and adaptive divergence thus play trivial roles in the assembly of the flora. The general lack of relief (elevations vary only from 177 to 595 m a.s.l.) imposed by recent glaciation and a long absence of tectonic activity has resulted in gentle ecological gradients and absence of substantial geographic barriers to dispersal. Hence, the distributions of species and lineages that migrated to Wisconsin after the Last Glacial Maximum are likely based more on pre-existing levels of physiological tolerance than on dispersal ability or the evolution of localized species or adaptive innovations. Wisconsin is likely similar in these regards to other recently glaciated areas of northern North America and Eurasia.

We first used floristic data to document geographic trends in α diversity, the species richness of spatial cells, and β diversity, the compositional differences between spatial cells, throughout Wisconsin. Globally, species richness in most lineages declines with increasing latitude, presumably as a result of reduced speciation rates, productivity, time since catastrophic disturbance (e.g., glaciation), and increased extinction rates (Chown and Gaston, 2000; Mittelbach et al., 2007). We expect this pattern to be evident in Wisconsin. We also tested the hypothesis that β diversity among cells should increase with geographic distance (based on limited establishment and spatial autocorrelation of environmental conditions) and environmental differences (based on distributional limitations related to physiological tolerances).

We then used phylogenetic and spatial data for 93% of the vascular flora to test three hypotheses regarding spatial phylogenetics. First, phylogenetic clustering should increase with latitude within Wisconsin, in accordance with a frequent prediction of the tropical niche conservatism hypothesis—the idea that adaptation to low-latitude conditions is ancestral and that relatively few lineages have evolved the traits needed to survive under harsh conditions at higher latitudes (e.g., Qian et al., 2014b). In our context, this hypothesis implies a shift in phylogenetic clustering near the Tension Zone (see Fig. 1; Appendix S1, see the Supplemental Data with this article), an S-shaped band running northwest to southeast across the middle of Wisconsin that corresponds to a concentration of species limits within the state among the 182 taxa surveyed by Curtis (1959). North of the Tension Zone, temperatures are colder, humidity higher, snow deeper, and soils less fertile (Ash et al., 2017). Thus, the mean phylogenetic distance (MPD; Webb et al., 2002; Tucker and Cadotte, 2013; Tucker et al., 2017) among co-occurring species should be lower in these higher latitude areas.

Second, across broad taxonomic scales, closely related species and clades should have more similar spatial distributions than more distant relatives. This idea follows from descent with (limited)

modification, and has been previously confirmed in a number of contexts (e.g., Losos, 2008; Algar et al., 2009; Miller et al., 2013).

Third, phylogenetic niche conservatism (PNC) should dominate the assembly of the Wisconsin flora, given that the evolution of adaptations to particular conditions in particular lineages happened elsewhere and the flora was assembled quite recently via dispersal. If this hypothesis is correct, then we expect that (1) clade age and distributional area within Wisconsin within recently derived clades (e.g., genera) should be unrelated to each other, as a result of strong constraints on niche evolution. That is, because divergence along ecological gradients is limited through evolutionary time, the total niche space (and by extension, geographical area) occupied by a clade should not be related to the age of the clade. (2) The mean phylogenetic distance within genera should also be unrelated to their collective range area, for the same reason. (3) Close relatives within genera should have strongly overlapping ranges, but the MPD among congeners should not be related to the extent of this overlap.

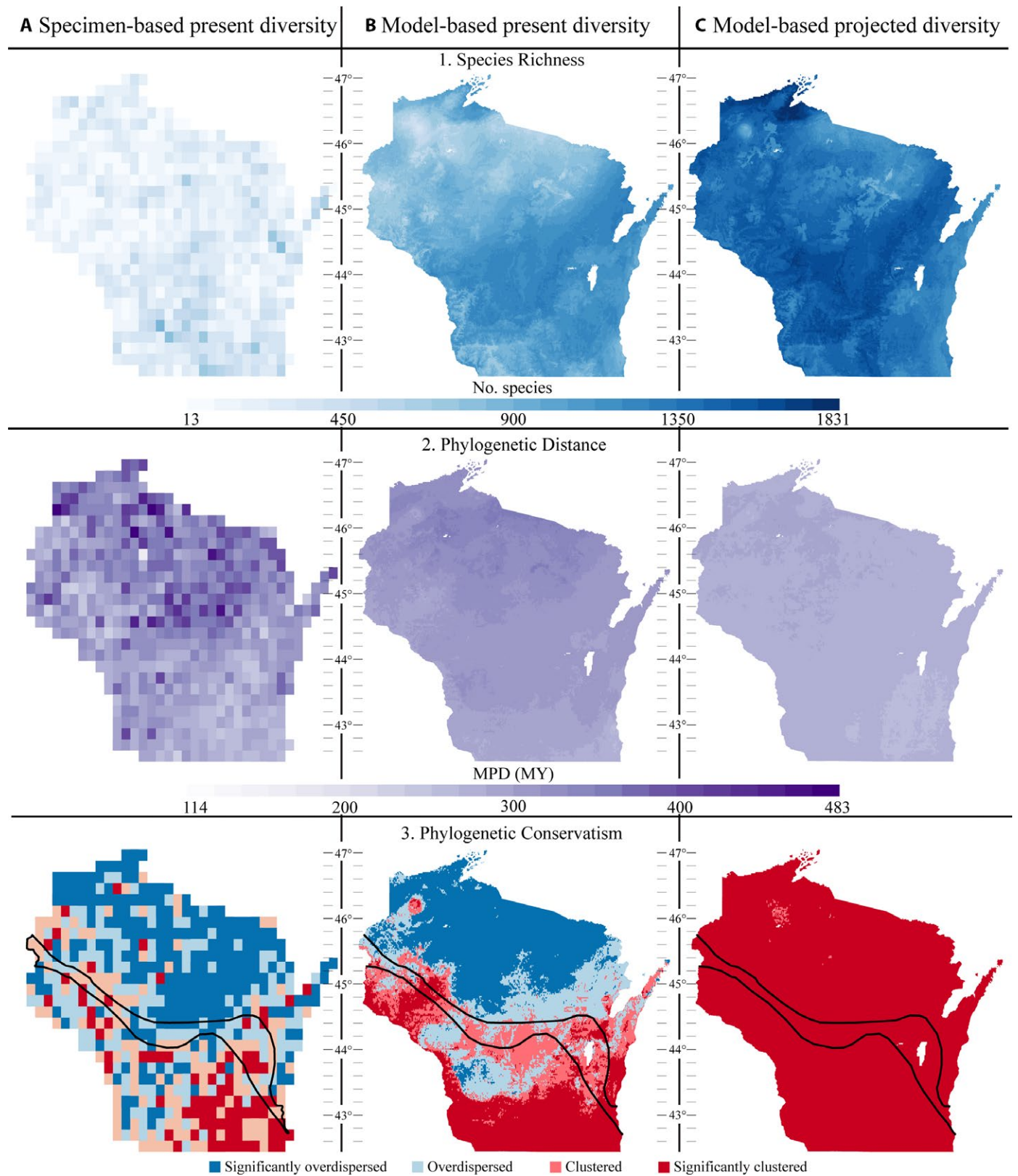
Finally, we used two methods to identify areas in Wisconsin that may be of conservation concern. First, we identified areas of paleo-endemism and neo-endemism, which have a concentration of the range-restricted long and short branches represented in Wisconsin, respectively, using the CANAPE method of Mishler et al. (2014). Second, we used projected species distribution models to identify which species may become extirpated, which species may begin to invade the state from nearby areas, and how spatial patterns of phylogenetic diversity may shift in the near future. In presenting results from both of these analyses, we aim to aid in the development of proactive conservation strategies to maximally preserve species and lineage diversity as well as assemblages with unique combinations of this diversity.

MATERIALS AND METHODS

Geographic context

Wisconsin has a land area of 140,673 km² and ranges from 42°3' to 47°2'N. Five floristic divisions are commonly recognized within Wisconsin and other states of the Great Lakes region: boreal forests, northern mixed forests with evergreen and deciduous trees, deciduous forests to the east and southeast, prairie elements from the Great Plains largely to the southwest, and temperate oak savannas that once dominated the south (Curtis, 1959). A marked transition occurs from the southern forests, prairies, and savannas to the northern forests and bogs across the so-called Tension Zone. Colder temperatures, lower evapotranspiration, greater moisture, and poorer soils prevail north of the Tension Zone. Wisconsin is further subdivided into 16 ecoregions (DNR of Wisconsin, 2014) defined by climatic, geological, and edaphic attributes affecting natural vegetation before

FIGURE 1. Present and projected diversity throughout Wisconsin. Column A: Patterns of diversity based on the specimen data set. Column B: Patterns of diversity based on the model data set. Column C: Future patterns of diversity based on the models projected to 2070. Row 1: Net species richness within assemblages. Row 2: Mean phylogenetic distance (millions of years, MY) among species present within each assemblage. Row 3: Phylogenetic conservatism and phylogenetic overdispersion within each assemblage based on comparison to a null model where tips are randomly shuffled across the phylogeny. Significantly overdispersed and conserved represent significant departure from the null model ($p < 0.025$ and $p > 0.975$, respectively). A shift from significant phylogenetic conservatism to significant phylogenetic overdispersion occurs over the floristic tension zone (black outline).



European settlement (Appendix S1). Outside the Driftless Area in southwestern Wisconsin and small areas in adjacent parts of Minnesota, Iowa, and Illinois, glaciers covered Wisconsin until 9–12 kya. Consequently, its flora and vegetation are essentially

allochthonous, largely reflecting Holocene dispersal of species that arose elsewhere, with subsequent sorting of these species across habitats based on their physiological tolerance and biotic interactions.

Phylogeny

We constructed a molecular phylogeny encompassing 93% of all native vascular plant species in Wisconsin flora and most native species of the flora of northeastern North America (Gleason and Cronquist, 1963; Cochrane et al., 1998). We used data from seven chloroplast DNA genes (*matK*, *rbcl*, *atpB*, *atpF-atpH*, *ndhF*, *rpl32*, and *trnH-psbA*), mostly obtained from GenBank. This data matrix was appended to the data set from Cameron et al. (2014), which includes *matK* and *rbcl* data for plant species of Wisconsin (see GenBank numbers at the Dryad Digital Repository: <https://doi.org/10.5061/dryad.kf6q10b> [Spalink et al., 2018]) to produce a data set including 15,117 aligned bases. Genes were independently aligned then concatenated. Phylogenetic analyses were conducted using maximum likelihood (ML) with bootstrapping with RAxML (Stamatakis, 2014) run in CIPRES v3.3 (Miller et al., 2010). LycopHYta rooted the analyses. We estimated a chronogram using the software treePL (Smith and O'Meara, 2012), using the same 59 ages obtained from the literature (Magallon et al., 2013; Rothfels et al., 2015) and employed by Cameron et al. (2014) as calibration points. Phylogenetic methods are detailed in Appendix S2.

Species distribution data

Measuring either α or β diversity across any large area is challenging. Species distribution records tend to be incomplete and suffer from regional, taxonomic, or temporal biases (Steege et al., 2010; Bystrakova et al., 2012; Maldonado et al., 2015; Spalink et al., 2016a; Stropp et al., 2016). Species distribution models can overcome some of these challenges, but are blind to issues such as habitat destruction, species interactions, shifts in disturbance regimes, limited environmental and edaphic variation within raster cells, and constraints imposed by species dispersal. Thus, analyses based on distribution records tend to underestimate actual diversity, whereas models will tend to overestimate diversity (Thornhill et al., 2017). We therefore used both approaches in our analyses to identify consistent patterns.

Species occurrence data for all native vascular plant species in the northeastern United States and adjacent Canada were downloaded from the Online Virtual Flora of Wisconsin (<http://wisflora.herbarium.wisc.edu/>; accessed 9 February 2016), the Consortium of Northeastern Herbaria (<http://portal.neherbaria.org/portal/>; accessed 11 February 2016), Harvard University Herbarium (HUH; <https://huh.harvard.edu/>; accessed 12 February 2016), Global Biodiversity Information Facility (<https://www.gbif.org/>; accessed 8 February 2016), and iDigBio (<https://www.idigbio.org/>; accessed 16 February 2016). We then filtered these data to eliminate erroneous records by removing duplicate records, then individually plotting the distributions of each species and manually eliminating records outside of the species' known ranges as documented by the Biota of North America Project (BONAP; <https://bonap.org/>; accessed February–May 2016).

Among states, Wisconsin ranks second after California for the number of publicly available, databased, georeferenced herbarium records, third after California and the small New England states for the number of specimens collected per unit area, and second after the New England states for number of collected specimens per species per unit area (Appendix S3). Despite having some of the best primary data on plant species distributions in the United States, the specimen-based database remains subject to collection bias, with many more specimens per unit area near the University of Wisconsin-Madison and in areas of unusual climate or substrate

known to harbor many unusual species (e.g., Apostle Islands, Door County Peninsula; Appendix S4).

To compensate for collection bias, we also developed a model-based database, using distributional records to generate species distribution models for all native northeastern North American species (SDMs) via MAXENT v3.3.3k (Phillips et al., 2005). We downloaded 19 bioclimatic rasters from WorldClim (<https://worldclim.org/>; Hijmans et al., 2005) and six edaphic variables from the Harmonized World Soil Database (www.fao.org/; Fao and Isric, 2009). To reduce model overfitting, we eliminated strongly cross-correlated variables ($r > 0.80$; Braunisch et al., 2013). We retained altitude, nine bioclimatic variables (mean annual temperature and precipitation, temperature and precipitation seasonality, annual temperature range, temperature of wettest quarter, and precipitation of driest quarter and warmest quarter), and five edaphic variables (soil bulk density, and soil % silt, loam, clay, and sand). We only considered species with a minimum of 10 unique occurrence records, which removed about 20 species from our analyses. Models were evaluated using the area under the receiver operating curve (AUC). We translated the logistic probabilities of species occurrence for each model to a binary presence–absence for each raster cell (Jiménez-Valverde and Lobo, 2007). See Appendix 2 for additional details.

Species richness, compositional turnover, and bioregions

We estimated spatial variation in species richness and composition using both specimen- and model-based data sets. For the specimen-based data set, we quantified species richness in 614 cells, each $0.2^\circ \times 0.2^\circ$ (hereafter, assemblages), by summing the number of unique species with specimens collected in those assemblages. We explored the use of both larger and smaller cell sizes, but ultimately used 0.2° cells, a coarse resolution considering the size of Wisconsin but fine enough to depict meaningful spatial patterns of diversity.

To examine the effects of collection biases and potential missing data in the specimen-based data set at this resolution, we generated rarefaction curves to determine the extent of sampling necessary to capture expected diversity, assuming that species are randomly sampled (Yang et al., 2013; Baldwin et al., 2017).

For the model-based data set, we measured potential species richness in 49,040 cells, each $0.017^\circ \times 0.017^\circ$ (hereafter, assemblages), which is the resolution of the bioclimatic and edaphic rasters used to develop the models. Potential species richness was defined as the number of species projected to be present in each assemblage.

We tested the hypothesis that β diversity should increase significantly with geographic distance throughout the state using Mantel tests. We used the Sørensen dissimilarity index (Sørensen, 1948) to measure β diversity, calculated as two times the number of species shared between two assemblages divided by two times the number of shared species plus the total number of unique species in both. We also tested the hypothesis that β diversity should increase with ecological distance between cells. We measured ecological distance as the Euclidean distance between pairs of assemblages based on the scaled bioclimatic values at each assemblage centroid. To avoid the circularity of measuring ecological distances among species distributions based on models developed using the ecological parameters themselves, we conducted these tests using only the specimen-based data set.

To determine whether species in Wisconsin are spatially grouped to form coherent bioregions (Bloomfield et al., 2017), we used the network theory approach of Edler et al. (2016) as implemented in the online interactive program Infomap Bioregions (<http://bioregions.org/>).

mapequation.org/). This program identifies the geographic structure of user-input species occurrences with an information-theoretic clustering algorithm (Rosvall and Bergstrom, 2008), with no predefined number or location of clusters. For this exercise, we used the model-based data set and selected species that were restricted to a maximum of 25% of the assemblages. We treated all identified bioregions that consisted only of single cells as noise. We calculated the ecological niche space maintained within each bioregion using the range of values of bioclimatic and edaphic traits from the centroids of the assemblages contained within the bioregions.

Phylogenetic diversity

We conducted spatial phylogenetic analyses that complement the floristic metrics to determine the extent and structure of phylogenetic diversity throughout Wisconsin. For both data sets, we calculated the mean pairwise phylogenetic distance (MPD) among species within each assemblage (Webb et al., 2002). This metric was chosen over Faith's phylogenetic diversity (Faith, 1994) because we are interested in how the evolutionary relatedness of species, as opposed to the total branch length connecting species, changes among assemblages. We also measured the standardized effect size (SES) of the MPD to test whether the observed values departed from what would be expected if lineages were randomly distributed or if there were no spatial structure associated with phylogenetic diversity (Kembel, 2009; Miller et al., 2016). To develop a null model, we performed 1000 randomizations, where species distributions were shuffled while retaining species richness within each assemblage and the range sizes of species. Measures of MPD and randomization tests were conducted using the picante package (Kembel et al., 2010) in R (R Core Team, 2017). Assemblages that departed significantly from null expectations were classified as either phylogenetically clustered ($p < 0.025$) or overdispersed ($p > 0.975$).

Testing for evolutionary constraints on species distributions

We calculated phylogenetic β diversity between cells and determined whether turnover increases with ecological and geographical distance. To provide further nuance to these analyses, we also calculated genus-specific phylogenetic β diversity to determine whether congeners become more distantly related to each other along these gradients. As with phylogenetic diversity, many metrics exist for describing patterns of phylogenetic turnover. Here, we calculated the mean phylogenetic distance between the species in one assemblage and their closest relatives in the second, using the comdistnt function in Picante (Kembel et al., 2010). If lineages are restricted in their ranges, then this phylogenetic distance should increase with the ecological distance among assemblages. Following the same methods as with floristic β diversity, we tested for significant correlations between phylogenetic β diversity geographic distance, and ecological distance using Mantel tests.

Under a model of phylogenetic niche conservatism (PNC), the niche breadth (and, by extension, range size) of a genus should not increase with the age of the genus, nor should the niche difference among congeners be determined by the phylogenetic distance between them. We tested whether the structure of biodiversity is consistent with what would be expected if PNC were a constraint on community assembly in Wisconsin. To test for PNC, we first measured the average phylogenetic distance among congeners within every genus present within Wisconsin. We then measured the range size (number of assemblages) occupied by each species and

genus. We tested whether the age of a clade is related to its range size. If niches are conserved, clade age would be a poor predictor of clade range. We then tested whether the average phylogenetic distance among congeners was related to their collective range sizes. If niches are not constrained, evolutionary divergence among two species should result in larger collective range sizes. Finally, we measured the average range overlap of congeners, under the expectation that congener ranges should overlap and that phylogenetic distance should poorly predict the extent of range overlap if niche evolution is constrained. For all genera with at least four species in Wisconsin, range overlap was measured using Schoener's D statistic, which ranges from 0 (no overlap) to 1 (identical ranges; Warren et al., 2008). For each genus, we tested whether the overlap among congeners is significantly related to their phylogenetic distances. For all tests of PNC, we used Pearson's correlation coefficient.

Identifying conservation priorities

We used CANAPE to identify regions containing an overabundance of geographically rare short branches (termed centers of neo-endemism), of geographically rare long branches (centers of paleo-endemism), or of both (centers of mixed endemism) (Mishler et al., 2014). CANAPE was conducted with both specimen and model-based data sets using Biodiverse v1.99 (Laffan et al., 2010). Areas of significant endemism were overlaid onto a map of areas currently protected by federal, state, local, and private agencies to help identify future conservation priorities (U.S. Geological Survey, Gap Analysis Program, 2016).

We also explored the possible implications of climate change on the extent and structure of diversity in Wisconsin. We projected all species distribution models to 2070 using the MIROC-ESM global climate model (Watanabe et al., 2011), which conservatively assumes greenhouse gas emissions will peak by 2040. This particular model was selected due to its demonstrated utility in producing meaningful hindcast and forecast predictions of species distributions in mid to high temperate latitudes, and particularly in northeastern North America (Allstadt et al., 2015; Ouyang et al., 2016; Pellissier et al., 2016; Peterson and Graves, 2016). Included in these projections were models for the native, vascular flora of northeastern North America. Using this expanded data set (described above), we estimated how diversity in Wisconsin may change if some species enter the state while others become extirpated. Based on projected models, we measured species richness, MPD, and SES-MPD in each assemblage. We then compared measures of diversity based on present-day and projected species distribution models. To determine which assemblages may exhibit the greatest phylogenetic turnover, we calculated assemblage-specific phylogenetic β diversity by measuring the percent of branch-lengths shared within each assemblage (Phylsorenson; phylsorenson function in Picante) after projected climate change. In addition to examining how assemblage composition may change, we investigated how the ranges of individual species and clades may change. We calculated species-specific overlap of ranges as predicted by the present and projected SDMs using Schoener's D statistic.

RESULTS

Phylogenetic analysis

Our phylogenetic analysis produced a well-resolved ML tree, including 93% of the vascular plant species found in Wisconsin

and over 80% of those in northeastern USA and adjacent Canada (Appendix 5). Missing species were not phylogenetically clustered. Most major taxonomic groups sensu APG IV (2016) were recovered as monophyletic, and estimated clade ages were consistent with previous estimates (Magallon et al., 2013).

Species distributions

We compiled a database of nearly 330,000 georeferenced herbarium records of specimens occurring within Wisconsin and a total of over 1.9 million records representing the North American distributions for all species in our data set. Rarefaction curves suggest that effective sampling was achieved in most assemblages at the $0.2^\circ \times 0.2^\circ$ resolution (Appendix S6), though missing data is an issue in assemblages where diversity is exceedingly low.

We developed species distribution models (SDMs) for 1850 of Wisconsin's 1873 native vascular species, omitting 23 species with insufficient distribution data. We developed an additional 777 models for species from throughout the northeastern United States and adjacent Canada. On average, models were constructed using 228 records per species and fit the training data with an AUC of 0.97. All but 60 species had more than 20 records each, and most of these were either narrowly distributed or of conservation concern.

Species richness

In the specimen-based data set, species richness in $0.2^\circ \times 0.2^\circ$ cells throughout Wisconsin varied from 3 to 851 species (Fig. 1A). The most diverse cells in this analysis overlapped Green Bay and Madison, urban centers with major universities and active herbaria. The least diverse cell, with only three species in the herbarium databases, was in rural Barron County, remote from such centers. Measures of potential species richness were generally higher in the model-based data set, ranging from 246 to 1316 potential species (Fig. 1B). There was no instance in which the SDM failed to capture the presence of a species as determined by the specimen data set. The least diverse cell in the model-based data set was also the one from Barron County having the fewest species collected. In both data sets, the southeastern quadrant of the state supported the highest levels of plant species richness; the northwestern quadrant, the lowest. Gymnosperms, ferns and lycophytes are proportionally more diverse north of the Tension Zone in both data sets, where they comprise as much as 24% of assemblage diversity in the specimen data set and 12% in the model data set (Appendix S7).

Floristic β diversity

Floristic dissimilarity between cells (β diversity) increased significantly with geographic distance, with the difference being especially strong in model-based analyses ($r = 0.81$, $df = 49038$, $P < 0.01$) compared with specimen-based ones ($r = 0.28$, $df = 613$, $P < 0.01$; Appendix S8). The correlations between β diversity and

ecological distance, calculated using only the specimen data set, were also significant for all climatic predictors ($r = 0.09$ – 0.25 , $df = 613$, $P < 0.01$). Mean annual temperature best explained β diversity, and temperature parameters overall explain turnover better than precipitation ($r = 0.14$ – 0.25 for temperature, $r = 0.09$ – 0.14 for precipitation).

Phylogenetic diversity

The mean phylogenetic distance among species in cells exhibited qualitatively similar patterns in the specimen- and model-based data sets, with MPD increasing with latitude (Fig. 1B). Tests for significant departures from the null model were also consistent between data sets. Most cells north of the Tension Zone (Fig. 1C) are significantly overdispersed (species are more distantly related to each other than expected by chance), while many in the south are phylogenetically clustered. Most assemblages overlaying the Tension Zone are neither significantly overdispersed nor clustered.

Phylogenetic β diversity

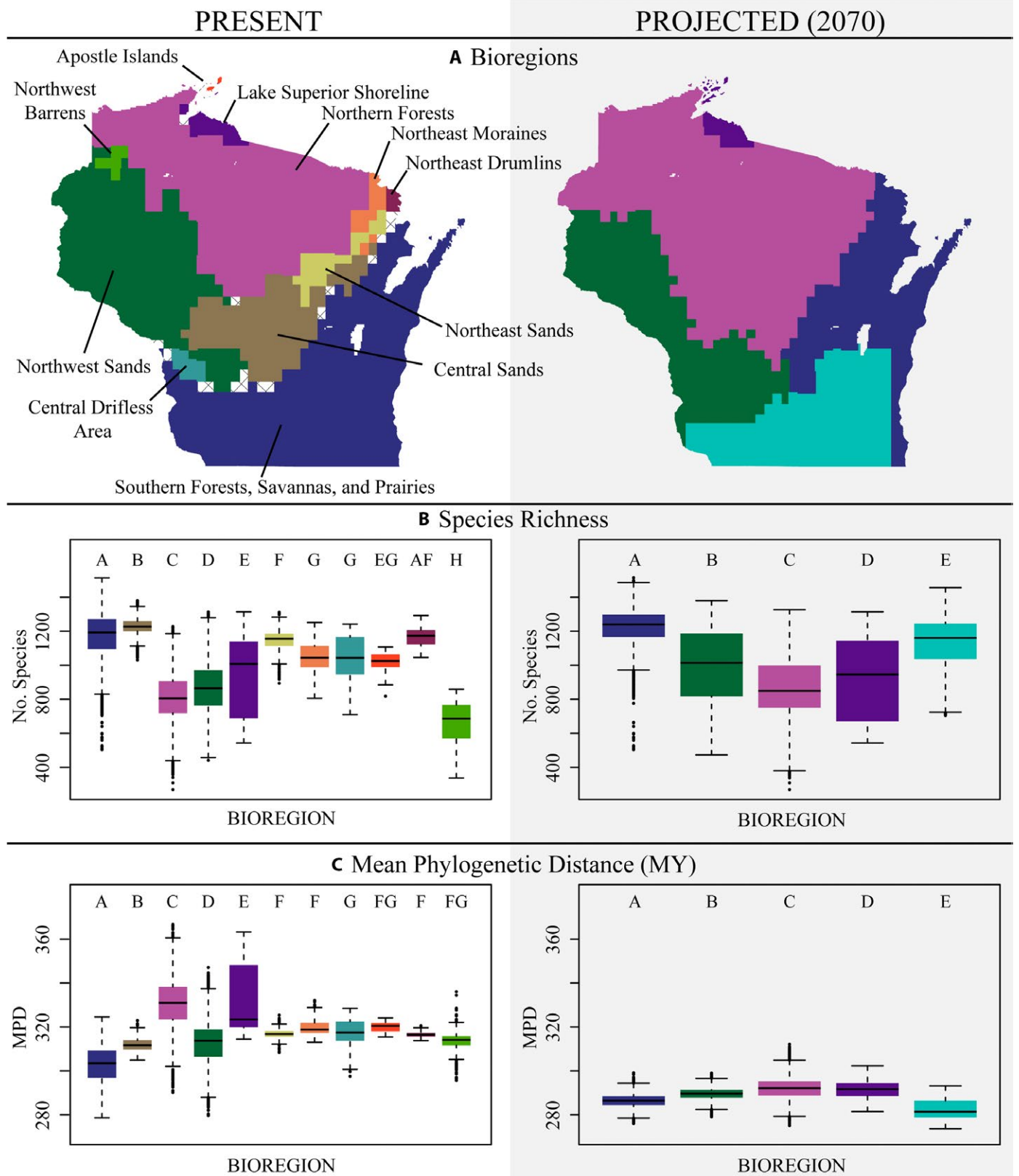
Phylogenetic β diversity between cells increased with geographical distance (specimen based: 0.09 , $df = 613$, $p < 0.01$; model based: $r = 0.59$, $df = 49038$, $p < 0.01$). In the specimen-based data set, changes in mean annual temperature, temperature seasonality, temperature during the wettest quarter, and precipitation during the warmest quarter were the climatic variables most strongly related to phylogenetic β diversity ($r = 0.11$, 0.12 , 0.13 , and 0.10 , respectively; $df = 613$, $p < 0.01$ in all cases). Notably, the correlations of phylogenetic β diversity to ecological distance were slightly stronger than those of phylogenetic β diversity to geographical distance. Ecological distances along temperature gradients strongly predicted phylogenetic β diversity at the generic level, with mean annual temperature being the strongest predictor for 45 genera and all temperature-related variables collectively being the strongest predictor for 102 variables. In contrast, geographic distance served as the best predictor for just 24 genera.

Floristic analyses revealed ecologically and phylogenetically distinct bioregions

On the basis of the Infomap Bioregions analysis, the postglacial assembly of Wisconsin's flora can be delineated into 11 distinct bioregions (Fig. 2A). The bioregions differ in several ways, including species richness (Fig. 2B), phylogenetic structure (Fig. 2C), climate, and soil (Appendix S9).

The Southern Forests, Savannas, and Prairies bioregion comprises a broad J-shaped swath from the northeast to the southwest (Fig. 2A). This bioregion is the largest and most southerly and contains assemblages with the least phylogenetic distance among vascular species, the smallest temperature range, the highest annual minimum temperature, and the warmest mean annual temperature (Appendix S9).

FIGURE 2. Present and projected bioregions as constructed using the online interactive program Infomap Bioregions (Edler et al., 2016) based on congruent distributions of species. (A) Bioregions. White areas with hash marks represent areas that were identified as floristically distinct, but here treated as noise due to their occurrence along the margins of larger bioregions and small spatial extents. (B) Box plot depicting the distribution of species richness among the assemblages that comprise each of the bioregions, with box plot colors corresponding to the map. (C) Box plot depicting the distribution of mean phylogenetic distance (millions of years) among species within each of the cell-level assemblages comprising the bioregions. Letters above box plots represent the significant differences among the bioregion based on ANOVA and Tukey–Kramer tests.



Substantial areas of this bioregion lie over dolomite. This bioregion has the highest aggregate number of species (1697, 99.0% of the total vascular flora, based on species models). Furthermore, all 27 species

found in a single bioregion occur only here, as do all but two of 32 species found in only two bioregions. Both patterns suggest a strong filtering effect across the flora based on temperature.

The Central Sands, Northeast Sands, Northeast Moraines, and Northeast Drumlins bioregions occur on sandy soils over a substantial portion of the belt of Cambrian sandstone and adjoining belts of Precambrian rocks and support assemblages that are species-rich, but show intermediate levels of phylogenetic distance (Fig. 2). The Central Sands has the second largest aggregate modeled flora (93.2% of the total); by contrast, only 76.8% of the flora is expected to occur in the Northeast Drumlins. The sandy, flat, wetland-rich bed of Glacial Lake Wisconsin occupies the heart of the Central Sands.

The Northern Forests bioregion is mostly underlain by Precambrian schists, granites, and sandstones, all of which tend to produce nutrient-poor soils, especially on glacial outwash plains; more fertile soils occur locally on moraines. The Northern Forests bioregion has the highest average elevation (Appendix S9), the coldest annual temperatures, and assemblages with the highest mean phylogenetic distance (Fig. 3C). Nearly all assemblages in this bioregion are phylogenetically overdispersed (Fig. 1).

The Northwest Sands bioregion in northwestern Wisconsin is species-poor at the assemblage level but in aggregate accounts for 91.9% of the total flora. It is marked by low winter snow, high summer rain, and the greatest seasonal variation in precipitation among all bioregions (Appendix S9). It is mostly underlain by outwash plains derived from Precambrian sandstones overrun by the Superior lobe of the Laurentide glaciers. The three “sands” bioregions have highly similar floras, with the overlap in species composition ranging from 95.2% to 96.4% (Fig. 2).

The Lake Superior Shoreline and Apostle Islands bioregions are the most diverse regions at the assemblage scale north of the

Tension Zone. Average annual temperatures in these bioregions are low, but annual minimum temperatures are significantly higher than those in the Northern Forests bioregion, moderated by the proximity of Lake Superior, which may account for their higher potential species richness (Appendix S9, Fig. 2). The Apostle Islands bioregion has the highest proportion of narrowly distributed species (here defined as occurring in one or two bioregions), many of which reach their southern limits here (Fig. 2). Its soils contain the highest proportion of clay, reflecting deposits on the bed of glacial Lake Superior (Appendix S9). Its aggregate flora is the second smallest, accounting for only 68.2% of the total flora, perhaps reflecting filtering due to low temperatures as well as the small geographic area involved.

The Central Driftless Area bioregion has warm summers, the lowest rainfall, the highest elevation in southern Wisconsin, and soils with a high proportion of silt (Appendix S9, Fig. 2). The Northwest Barrens bioregion, overlapping the southern half of the Superior glacial outwash plain and an extensive lake district in northwestern Wisconsin, is the most species depauperate at local and global scales, with only 62.8% of the total flora (Fig. 2). Interestingly, it is the only region north of the Tension Zone whose assemblages show phylogenetic conservatism (Fig. 1). Ecologically, this region is unique in its high seasonality in temperature and precipitation. It is coolest and has soils with the most sand and least silt (Appendix S9).

Tests of phylogenetic niche conservatism

There was no significant correlation between total range size and clade age in the Wisconsin vascular flora ($r^2 = -0.015$, $p = 0.85$; Appendix S10). The average phylogenetic distances between species within genera were similarly unrelated to their collective range sizes ($r^2 = -0.088$, $p > 0.27$). We found that all congener ranges overlap in Wisconsin at least partly, with the average overlap among all congeners of 54%. There was no significant relationship in any genus between the extent of range overlap and the average phylogenetic distance among congeners.

Categorical analysis of phylogenetic endemism

The specimen-based data set identified areas of neo- and mixed endemism along the northwestern, southwestern, and eastern edges of the state as well as in the Central Sand Hill and Forest Transition ecoregions (Fig. 3; Appendices S1, S11). Several cells in the Northern Forests bioregion were identified as areas of paleo-endemism. The model-based data set identified more areas of endemism than the specimen data set, with large sections of southern and eastern Wisconsin recovered as centers of mixed endemism and larger portions of the Northern Forest recovered as a center of paleo-endemism (Fig. 3; Appendix S11). Centers of neo-endemism were identified in the Northeast Sands ecoregion and along the southwestern edge of Wisconsin. The consensus between the two data sets highlights a conservative representation of the areas in Wisconsin that harbor significantly high proportions of the state's geographically rare lineages (Fig. 3). Several of these areas overlap entirely with lands already protected by federal, state, local, and private agencies. Other areas, however, remain unprotected. These include significant portions of the Southwest Savanna, Western Coulees and Ridges, coastal Lake Michigan, and the Central Sand Hill ecoregions (Fig. 3; Appendix S1).

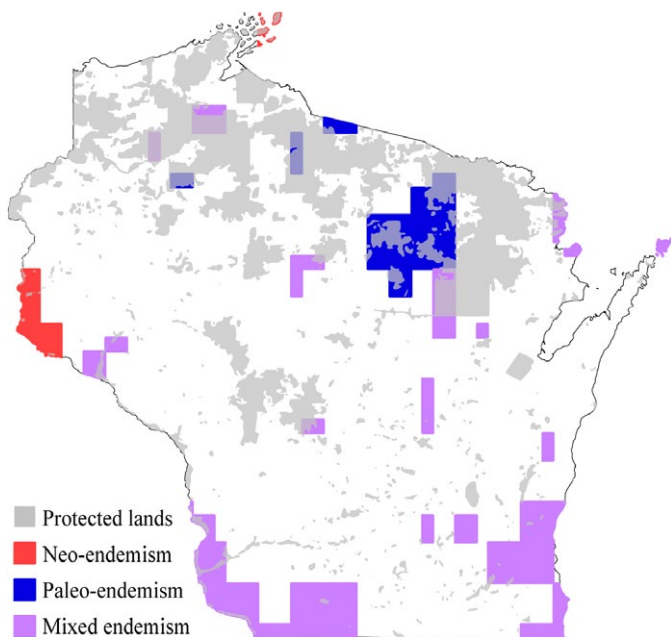


FIGURE 3. Centers of neo-endemism, paleo-endemism, and mixed endemism throughout Wisconsin, representing the consensus of the specimen and model-based analyses (Appendix S11). Areas of endemism represent regions harboring geographically rare lineages and could be used as a basis for targeted conservation efforts. Regions that are currently protected by federal, state, local, or private agencies are indicated in green.

Potential implications of climate change

Projected species distribution models predict that 242 of Wisconsin's species are expected to become extirpated from the state by 2070. These include 15% of Wisconsin's monocots, 26% of its orchids, 28% of its ferns and lycopods, and 30% of its gymnosperms. We also project that only 65% of species will retain more than half of their present distributions (Appendix S12). However, our models project that under climate change many new species may find suitable niche space somewhere in the state, resulting in a net increase in potential richness in assemblages throughout Wisconsin (Figs. 1, 4). Potential species richness in assemblages is projected to range from 520 to 1831 species, a 41% increase, on average, compared to potential richness as measured using models based on present-day conditions. The MPD in assemblages is expected to decrease, to the point that no assemblages are projected to exhibit phylogenetic overdispersion (Fig. 1). Assemblages in northern Wisconsin, which presently contain the majority of ferns, lycopods, and gymnosperms, are expected to increase greatly in floristic richness but will lose appreciable phylogenetic diversity (Fig. 4).

The models also predict that the geographic structure of floristic richness will simplify. Only four of Wisconsin's 11 current bioregions will persist to 2070 (Fig. 2A), while a new bioregion should form in southern Wisconsin as southerly species invade the state. Although the floristic richness of these bioregions remains comparable to those today (Fig. 2B), phylogenetic distances among species within bioregions are projected to decline (Fig. 2C).

DISCUSSION

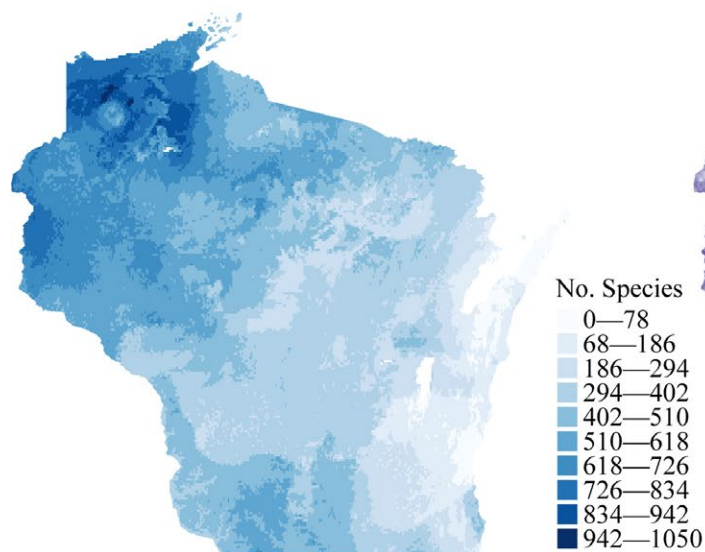
Species richness exhibits distinct geographic and ecological structure

Both the specimen- and model-based data sets confirmed a latitudinal decline in species richness, with relatively low α diversity observed north of the Tension Zone (Fig. 1) and bioregional floras

declining in size with latitude, from 99.0% of the total flora in the Southern Forests, Savannas, and Prairies bioregion to 62.8% and 68.2% of the total flora in the coldest bioregions, the Northwest Barrens and the Apostle Islands, respectively (see Results). The filtering effect of decreasing temperature with latitude is suggested by the fact that all 27 vascular plant species restricted to a single bioregion are found in the most southerly, warmest region (Southern Forests, Savannas, and Prairies), and all but two of the 32 species restricted to two bioregions are found there as well. The next two warmest bioregions (excluding the tiny Central Driftless Area), the Central Sands and Northwest Sands, have the next largest numbers of species (9 and 13, respectively) among those restricted to two bioregions. The taxonomic composition of assemblages shifts along this gradient as well, as evidenced by the relative increase in diversity of gymnosperms, ferns, and lycopods in the northern half of the state (Appendix S7). An exception to the latitudinal drop in species richness occurs near the coast of Lake Superior. The rise in assemblage-scale diversity there may reflect the decrease in elevation from the Northern Highlands in north-central Wisconsin (Appendix S1), the moderation of thermal extremes near Lake Superior, and/or the presence of both boreal forests on flat surfaces and species-rich deciduous forests on incised surfaces on the clay substrates deposited by Glacial Lake Superior.

Floristic β diversity increases with both geographic and ecological distance, with turnover occurring most rapidly along temperature gradients (Appendix S8). The correlation between β diversity and geographic distance is, however, much stronger for model-based than specimen-based analyses. Similar differences between model- and specimen-based analyses of phylogenetic diversity and endemism were also identified by Thornhill et al. (2017) for the California flora; almost surely such differences reflect the great underestimation of species occurrences by the inherently patchy collection of specimens. Other studies have documented temperature as the climatic variable most strongly correlated with species' range limits, e.g., for angiosperms in the British Isles (Woodward and Fogg, 1990) and trees throughout North America (Morin et al.,

A Projected change in species richness



B Percentage of phylogenetic diversity retained

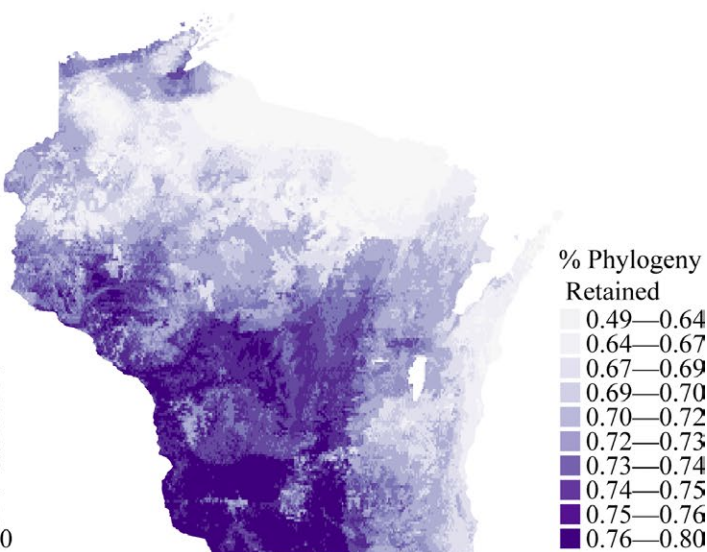


FIGURE 4. Projected change in diversity. (A) Projected increase in species richness in assemblages throughout the state. (B) Projected change in phylogenetic diversity throughout Wisconsin, calculated as the percentage of total branch lengths shared between present and projected diversity.

2007) and northern South America (González-Caro et al., 2014). The importance of temperature for setting range limits in Wisconsin does not reflect freezing per se, as the entire state frosts in the winter. Rather, it likely reflects the length of the growing season, temperature (and thus evapotranspiration) during that season, soil leaching (reflecting an excess of precipitation relative to evapotranspiration), and the intensity of winter freezing. The 406 species that reach northern limits and 223 that reach southern limits in Wisconsin (Appendix S5) may be limited by physiological tolerance (e.g., limits on photosynthesis, flowering, and/or fruiting). However, context-dependent biotic interactions (e.g., relative ability to compete, avoid predators, find mutualists under a given set of abiotic conditions) could also play a role. Thus, while the relationship between temperature and diversity is significant throughout the state, the importance of additional climatic and edaphic variables merit further study.

Phylogenetic structure of diversity exhibits geographic signal

Species distributional limits shape spatial patterns of phylogenetic structure in Wisconsin (Fig. 1B, C). In both the specimen- and model-based data sets, MPD within assemblages increases sharply north of 42.25°N, and peaks between 45.5° and 46.5°N. Nearly all assemblages north of 44.5° are phylogenetically overdispersed, whereas those south of 42.25° are phylogenetically clustered. This pattern is stronger in the model data set than in the specimen data set, where fewer assemblages in the southwest are significantly clustered. This region of the state—the Driftless Area (Appendix S1)—remained unglaciated during the LGM. As a result, it exhibits heterogeneity in topography and slope aspect that is largely absent from the rest of the state. Many northern species, including gymnosperms, ferns, and lycopods, occur disjunctly in this region, particularly on north-facing slopes and deeply incised valleys. The occurrence of lycopods, ferns, and gymnosperms in turn, is really what drives phylogenetic overdispersion in the Wisconsin flora. In both data sets, the floristic Tension Zone described by Curtis (1959), based on the highest concentration of range limits for 182 species, overlaps a swath of assemblages that are neither significantly clustered nor overdispersed. Our analyses, incorporating the distributions of nearly 2000 species, suggest that this zone is also a phylogenetic phenomenon, albeit more diffuse than the Tension Zone. That distinction, however, may be more apparent than real, given that Curtis' criteria for determining the width of the Tension Zone were undocumented.

The observed phylogenetic structure directly contradicted our hypothesis that phylogenetic clustering should occur in the north. Classic papers on the subject of phylogenetic community assembly suggest that communities in abiotically “harsh” regions should exhibit phylogenetic clustering, as only select clades would have evolved the necessary adaptations to survive in such regions (Losos, 2008; Ackerly, 2009; Cavender-Bares et al., 2009; Qian and Jiang, 2014). These analyses, however, focused almost exclusively on tree species or angiosperms. We found the opposite to be true: assemblages in the colder regions of northern Wisconsin are phylogenetically overdispersed, whereas those in the more temperate south are phylogenetically clustered (Fig. 1).

This discrepancy highlights the importance of phylogenetic scale (Cavender-Bares et al., 2009; Qian and Jiang, 2014). Regions in southern Wisconsin exhibit phylogenetic clustering largely because they support a high proportion of eudicots, whereas those in the north contain higher proportions of Wisconsin's ~100 species

of gymnosperms, ferns, and lycopods (Appendix S7). Indeed, 26% of Wisconsin's native eudicots have northern range limits in the state versus 9% with southern range limits. Given that range limits are concentrated in the Tension Zone, species with northern range limits are, in essence, southern species in Wisconsin. In contrast, 33% of Wisconsin's ferns and lycopods reach southern range limits in the state versus 13% with northern range limits; thus, these groups are mostly northern species. Thus, phylogenetic distances within northern communities include many long branches connecting gymnosperms, ferns and lycopods to the angiosperms, strongly increasing mean distances. Repeating these analyses with angiosperms alone reveals that only 6% of the assemblages originally classified as overdispersed remained once these distantly related lineages were removed (Appendix S13), while the number of conserved assemblages increased by 63%. Analyzing angiosperms alone thus resulted in patterns consistent with previous studies showing conservatism in “harsh” environments (Losos, 2008; Ackerly, 2009; Qian and Jiang, 2014). Phylogenetic scale therefore strongly affects the evolutionary and ecological dynamics of community phylogenetics. Whether gymnosperms, ferns, and lycopods should be included in such analyses likely depends on the study system. In the case of Wisconsin, the geographical variation in richness in these clades adds nuance to our understanding of how phylogenetic diversity is distributed throughout the state. In other systems where these clades are more evenly spread, their inclusion may be less important.

Niche limits range and phylogeny limits niche

We tested whether PNC explains patterns of diversity in Wisconsin using several lines of evidence. We found support for the hypothesis that closely related species would have overlapping ranges in Wisconsin. Indeed, congeneric species ranges overlap by 54% on average. We also found a significant phylogenetic signal associated with β diversity with both ecological and geographical distance. Within most genera (102 of 126), this turnover was most closely related to changes along temperature gradients, indicating that close relatives have similar physiological tolerances to climate that influence their distributions in Wisconsin. Thus, the evolutionary history of these clades does appear to leave a predictable imprint on the distributions of species in the state.

A model of PNC suggests that divergence along ecological gradients should be limited (Vamosi and Vamosi, 2011; Spalink et al., 2016b), such that congeners should be more ecologically similar than expected if niche evolved in a Brownian manner (Losos, 2008). Our results are consistent with this model. First, we found no correlation between range size and clade age among Wisconsin genera ($r^2 = 0.015$, $p = 0.85$), indicating that older genera do not have broader physiological tolerances than younger genera, at least among those species present in the Wisconsin flora. Second, average phylogenetic distances among congeners (Appendix S10) are similarly unrelated to their range size ($r^2 = 0.088$, $p > 0.27$), contrary to expectations if niches were evolving continuously by a random drift process. Third, the relationships between niche overlap and phylogenetic distance among congeners are nonsignificant in all cases.

These multiple lines of evidence consistently support PNC as playing a role in acting to shape the realized distributions of species in Wisconsin. Such conservatism has important implications in this era of climate change. For example, if the climatic niche space of Wisconsin changes to the point where it falls outside a species'

niche envelope, it will likely do so for its congeners as well. We thus expect the phylogenetic structure of Wisconsin's flora to shift as clades migrate and/or decline in abundance as climates change.

Establishing conservation priorities

Wisconsin exhibits a remarkable heterogeneity in the species richness and phylogenetic structure of assemblages. As both floristic and phylogenetic turnover increase with spatial distance, a conservation strategy aimed at protecting the greatest number of species and lineages in the state would ideally exhibit some geographical evenness. At present, most of the area of Wisconsin's protected lands is concentrated in the northern half of the state (Fig. 2), which includes several million acres of federal, state, and private forests, parks, and preserves. Our analyses highlight that these regions host only a small portion of Wisconsin's diversity. By contrast, most urban and agricultural development is spread throughout the portions of the state with the highest species richness, particularly in the south and east. We suggest that new priorities for conservation should include those centers of mixed and neo-endemism that occur in these areas; they are both species rich and contain an abundance of regionally rare lineages (Fig. 2). It should be recognized, however, that the extensive areas of "endemism" detected within Wisconsin near its southern borders are almost certainly the result of large numbers of species from warmer climates entering the state in the southwest (the area of warmest temperatures) and in the southeast (the area of least thermal seasonality, due to proximity to Lake Michigan and relatively low latitude). These are therefore not areas of endemism created by the traditional causes of local speciation or local refuge from extinction, but instead caused by limited invasion by species from other climatic regions nearby.

Climate change has already had far-reaching impacts around the world: species distributions are changing (Perry, 2005; Wolf et al., 2016; Ash et al., 2017), and some species are going extinct while others are increasing in abundance (Condit et al., 2009; Germino et al., 2016). The floristic composition of communities is also changing in ways that reflect both phylogenetic and geophysical structure (Willis et al., 2008; Tveiten et al., 2015). We have developed models to predict how these changes could manifest in Wisconsin. First, our models predict that projected climates in Wisconsin will displace the distributions of most species. Only 65% are modeled to retain more than half of their present distributions based on climatic suitability (Appendix S12). This massive turnover in floristic composition may eventually result in a net increase in diversity in the state (Fig. 1), despite more than 242 species becoming extirpated (including over 25% of the state's orchids, ferns, lycophytes, and gymnosperms). Our models also predict that, despite the expected increase in species number, the expected addition and extirpation of native plant lineages could eliminate nearly all phylogenetic heterogeneity across the state in the near future (Fig. 1). Indeed, no assemblage is projected to remain phylogenetically overdispersed by 2070 (Fig. 1). Changes in phylogenetic β diversity within assemblages (Fig. 3B) explain approximately 42% of the changes in expected species richness, reflecting a phylogenetic unevenness in species gains and losses. For example, assemblages in northern Wisconsin are expected to increase greatly in floristic richness but will lose appreciable phylogenetic structure.

These predictions hinge on the unrealistic assumption that plant species can extend their ranges as fast as climates change.

This rapid dispersal is unlikely. In fact, analyzed shifts in the distributions of 78 Wisconsin plant species over the last 50 years reveal that although species have generally shifted their distributions in ways that track climate change, most species lag behind these climate changes by about two-thirds of expectations (Ash et al., 2017), probably reflecting that species can often persist at sites (suggesting that their potential ranges generally exceed their realized ranges), slowing extirpations, and that many species are limited in their ability to colonize new sites, particularly when habitats are fragmented (Rogers et al., 2009). A second caveat to these predictions is that the resolution of the models is too crude to capture the local microhabitats where some species may be able to persist as relicts. Whereas our models predict extirpation, in these instances species ranges would instead become reduced, localized, or fragmented.

Nevertheless, we expect comparable patterns to emerge in climatically similar, recently glaciated regions with allochthonous floras throughout North America. The projected loss of the boreal element from the Midwest is noteworthy because it includes the many ferns, lycophytes, orchids, sedges, and gymnosperms that reach their southern limits here. The essentially allochthonous flora of the midwestern United States means that although many species may be regionally extirpated, they will likely persist elsewhere, softening the conservation consequences of climate change, making global losses unlikely. Although regional climate change presents a major challenge for conservation, our models suggest that attempting to maintain the present distributions of species throughout Wisconsin, and the Great Lakes region generally, is both futile and probably unnecessary. By contrast, regions in North America with largely autochthonous floras such as California, the Gulf Coast, and Hawaii are vulnerable to high rates of global species extinction. Such regions would benefit far more from efforts to conserve local populations and assist their migration to newly suitable habitats.

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AUTHOR CONTRIBUTIONS

K.J.S., T.J.G., D.M.W., K.M.C., and D.S. conceived the study. D.S., R.K., M.C.P., B.T.D., P.L., J.G.Z., J.R., C.P.D., M.A.F., and W.S.A. gathered the data. D.S. and R.K. analyzed the data. D.S. wrote the manuscript with contributions from all authors.

DATA ACCESSIBILITY

All DNA matrices, phylogenies, treePL control files, scripts, and GenBank numbers are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.kf6q10b> (Spalink et al., 2018).

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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