

A large phylo-floristic study on the present and future assembly of the Wisconsin flora – An area unique in North America

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With 1.4 million specimens the Wisconsin State Herbarium (WIS) is one of the largest in the Americas and Wisconsin offers botanists a unique opportunity to study species representing a confluence of global biomes. The state harbors >2640 species of vascular plants which have been sequenced for the two-gene plant DNA barcode to reconstruct a community phylogeny. At the same time >300 000 georeferenced specimens were used with bioclimatic and soil data to produce species distribution models for the flora, then subsequently aggregated to determine current and future patterns of species richness and phylogenetic diversity. Among the many surprising results uncovered are predictions that whereas species richness will increase as c. 850 taxa move into the state, c. 242 species will become extirpated by 2070. These most vulnerable species will not be affected at random. Furthermore, models suggest that Wisconsin's projected climate will be unsuitable for most species to be able to retain their present distributions; only 65 % will be able to retain more than half of their current distributions. However, the state's well known unglaciated Driftless Area may be able to serve as an Anthropocene refugium better than anywhere else in the region and should be targeted for increased land conservation.

Keywords

Climate, Community, Discovery, Niche, Phylogeny, Spatial, Taxonomy

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Accepted

27. 6. 2023

DOI

<https://doi.org/10.12685/bauhinia.1354>

The 2019 United Nation's Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES 2019) Global Assessment Report states that „around 1 million animal and plant species are now threatened with extinction, many within decades, more than ever before in human history [and] ... the average abundance of native species in most major land-based habitats has fallen by at least 20 %, mostly since 1900.” With these sobering statistics in mind a team of researchers within the Department of Botany at the University of Wisconsin-Madison, including this author, initiated a multi-year project funded by the US National Science Foundation entitled „Roles of functional, phylogenetic, and genetic diversity in structuring and sustaining plant communities through environmental change”. Our subject was the flora of the state of Wisconsin located in the Upper Midwest Great Lakes Region of North America. Why Wisconsin? One reason is access to the large repository of herbarium specimens within the Wisconsin State Herbarium (WIS), a collection of c. 1.4 million specimens housed at the University of Wisconsin-Madison and among the ca. 12 largest herbaria in the Western Hemisphere (Thiers 2022). For decades regional specimens collected since the mid-19th century (WIS was only established in 1854) have been actively used to document changes in the flora of the state.

Unfortunately, Wisconsin's unique landscape has been greatly altered by human activity. Today it is home to 11 federally recognized Native American tribes, more than any other state east of the Mississippi River, but their ancestors who first came to the state >10 000 years ago had minimal impact on

the biota compared to the transformation that occurred during colonization in the 19th century. This was especially pronounced during the waves of massive immigration from Europe that occurred between the years 1850–1900 when the state's human population increased from a mere 305 000 to a staggering 2 060 000. The current population is c. 5.9 million centered in a few rapidly expanding urban areas (e.g., the cities of Milwaukee and Madison) but also is scattered widely across the state where logging and agriculture continue to impact biodiversity across ecosystems. Human population growth, industrialization, farming, and other factors have led also to noticeable changes in local climate. In fact, Wisconsin recently was considered to be tied for first place among the 48 contiguous states of the USA for having experienced the largest annual average temperature increase (+0.67F/+0.37C per decade) since the first Earth Day was held on the campus of UW-Madison in 1970 (data from February 21, 2013 at <https://www.climatecentral.org/news/winters-are-warming-all-across-the-us-15590>).

Another reason to target Wisconsin is that although it is small in area, the state offers botanists an unparalleled opportunity to study terrestrial species representing a unique confluence of global biomes: boreal conifer forests, eastern deciduous forest, savannas, mixed hardwood forests, and grasslands, as well as various Great Lakes freshwater communities distributed across both a historically glaciated and unglaciated landscape. In total it is estimated that the state harbors at least 2640 species of vascular plants, of which 1873 are native and 767 are introduced; there are at least 158 families and 779 genera represented (Wetter et al. 2001).

The primary purpose of the study was to use Wisconsin as a model system in order to contrast patterns of vascular plant species richness with phylogenetic diversity by employing a comprehensive spatial phylogenetic (i.e., phylofloristic) approach. Much of this study, including more details of methodology and results than summarized below, was published by Spalink et al. (2018) with related papers published subsequently by Beck et al. (2022), Givnish et al. (2020), and others.

Methods

An ambitious specimen digitization effort by students and curators at WIS in recent years has resulted in >490 000 in-state records being databased of which >75 % have been precisely georeferenced (see <https://www.herbarium.wisc.edu>). Furthermore, in order to provide phylogenetic information to ecologists and others interested in studying changes in floristic composition through time (past, present, and future), we sequenced the two-gene universal plant DNA barcode (plastid *rbcl*+*matK*) and reconstructed a complete community phylogeny for the Wisconsin flora with genomic DNA extracted almost exclusively from historical herbarium specimens. To our knowledge no

other state in the USA has achieved this level of data completeness. At the same time >300 000 georeferenced specimens collected in the state were used together with bioclimatic and soil data to produce species distribution models for the entire native flora, which were subsequently aggregated in order to determine patterns of potential species richness and phylogenetic diversity across the state.

Result and discussion

Curiously, the pattern of species richness we revealed closely resembles the plant hardiness zone maps that are published and updated regularly by the US Department of Agriculture. These show a gradient from the SE corner of the state (updated recently to hardiness zone 5b) toward the NW (currently hardiness zone 3b). Likewise potential species richness is greatest in the southeastern and central regions of Wisconsin as shown in Fig 1. Some of these areas are precisely those that were rapidly cleared for agriculture in just one generation's time during the mid-1800s. Relatively few herbarium specimens exist from some of these human-altered areas, but we can hypothesize based on our models that they once supported high levels of vascular plant diversity, now lost forever.

In contrast, our estimation of phylogenetic diversity (a metric that not only considers numbers of species / richness, but also lineages or branches of the tree of life) shows a strikingly different pattern. Wisconsin is most phylogenetically diverse in the northern half of the state. The southern areas are species rich, but most of that diversity is attributable to many species from just a few families such as Asteraceae, Cyperaceae, and Poaceae. Thus, Southern Wisconsin is species rich, but phylogenetically poor. Even without sophisticated models or access to advanced computing, plant ecologists such as J. Curtis (1959) were able to document that the flora of the northern tier of the state is qualitatively different from the southern tier. For example, he documented Wisconsin's well known „tension zone“ – an imaginary diagonal line that divides the vegetation of the state between the northeast and the southwest – a pattern that closely resembles our map of statewide phylogenetic diversity (see Spalink et al. 2018).

Of course, we not only wish to look back in time or to document patterns of species richness and phylogenetic diversity today, but also to use our data to inform conservation biologists interested in what effects climate change may have on this region of North America in the next century. In order to predict future phylo-floristic change, a much larger supermatrix of c. 2300 Eastern North American vascular plants (i.e., not only those documented from Wisconsin) also was analyzed under models that account for 50 years of predicted climate change.

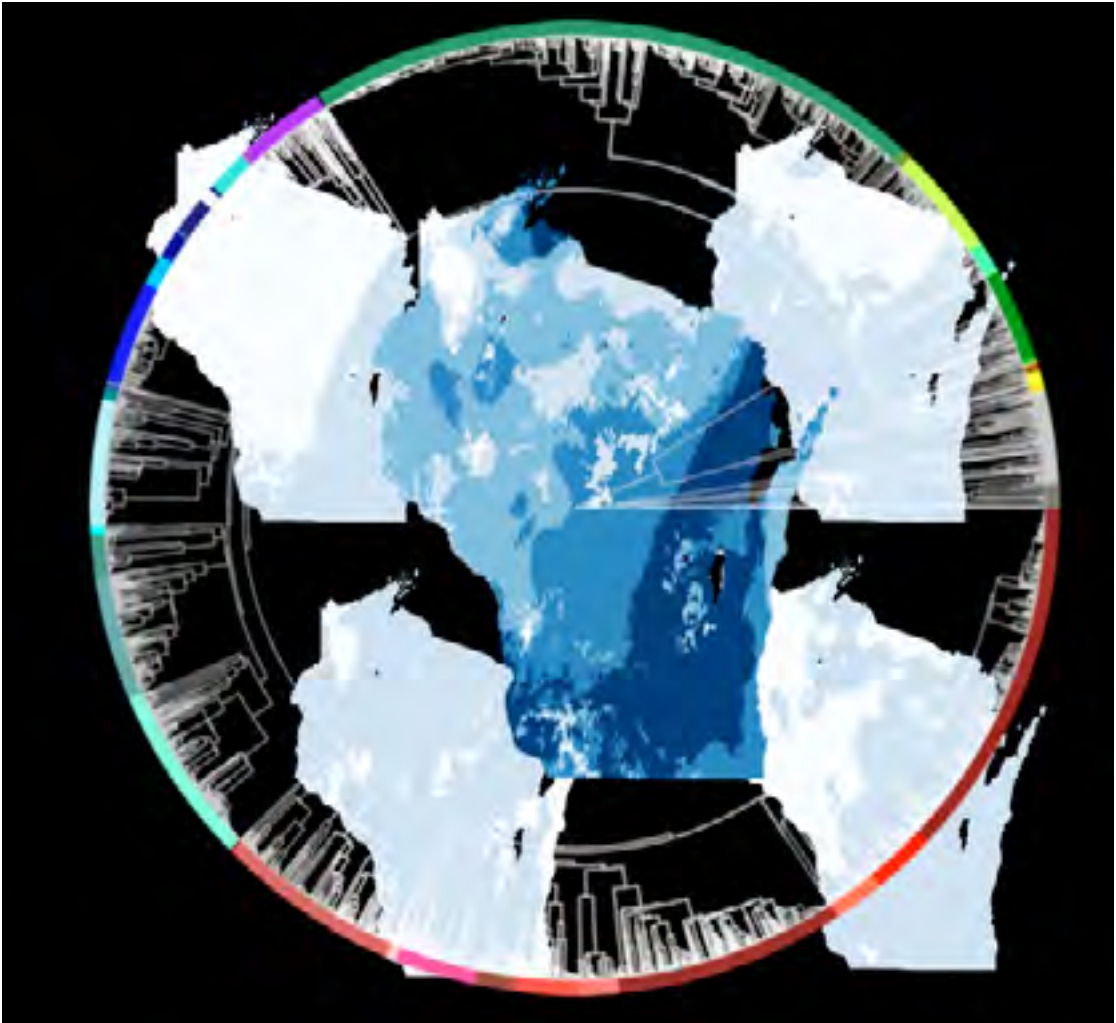


Fig. 1. Phylo-floristic summary figure.

More than 300 000 specimen occurrence records were employed to generate individual species distribution models such as the four inset maps (where the shade of blue scales with habitat suitability) for every native vascular plant species found in Wisconsin and then to aggregate them in order to document potential species richness across the entire state (central map, where darker blue indicates higher potential species richness). In addition, a time-calibrated community phylogeny of the state's entire vascular flora (circle tree, where colors indicate plant orders) was used with distribution maps to identify areas with high phylogenetic diversity (not shown). See Spalink et al. (2018) for further information regarding this phylo-floristic approach.

This approach was necessary because each year we document new occurrence records for species that were originally non-indigenous, but are now migrating into Wisconsin, especially from the south, as the climate becomes more mild. Among the many surprising results we uncovered are predictions that whereas overall species richness will actually increase as c. 850 southern taxa move northward into the state, some 242 species may become extirpated by 2070. Unfortunately, these most vulnerable species will not be lost at random from our flora, but instead represent 15 % of monocots, 28 % of ferns / lycopods, and 30 % of orchids, for example. In fact, we can predict exactly which species may be most at risk by using Schoener's D statistic

that measures the overlap in species' ranges comparing their present to future predicted distributions in Wisconsin. Sadly, our models suggest that Wisconsin's projected climate will be unsuitable for most species to be able to retain their present distributions; only 65 % will be able to retain more than half of their current distributions in the state. If these future predictions hold true, then attempting to restore past or maintain present floristic communities may need to be reconsidered. Already there is documented evidence that many vascular plants have shifted their center of distribution significantly to the northwest from comparisons of vegetation plots conducted in the 1950s then again in the 2000s (Ash et al. 2017). Of course it is important to consider also that these models and predictions based on climate do not take into account the role of various biotic factors on vegetation, such as overgrazing by herbivores including white tailed deer, death by pathogens, competition with or harm by invasive species including insects such as emerald ash borer, or effects of acid rain and nitrogen deposition on the soil mycobiome. Without human assistance (e.g., assisted migration) the fate of many threatened species may be even more grim than our models of future distribution suggest.

Conclusion

The same UN report cited earlier (IPBES 2019) also tells us that „it is not too late to make a difference, but only if we start now at every level from local to global. Through ‚transformative change‘, nature can still be conserved, restored and used sustainably.“ One bit of optimism revealed by our study is that our model of future phylogenetic diversity indicates that although Wisconsin's „Driftless Area“ is not a hotspot of species richness or phylogenetic diversity today, this region located in the SW corner of the state will become one of the few areas that is likely to maintain a relatively high percentage of phylogenetic diversity, even while it is lost elsewhere. This is an intriguing prediction because the Driftless Area is so named on account of the fact that it has never been glaciated, even while surrounded on all sides by ice sheet lobes at one time or another. It is a rugged landscape of forested hills, mesic valleys, spring fed trout streams, limestone caverns, and sandstone ridges. There is growing evidence that it once served as a Pleistocene glacial refugium for organisms including mollusks, small mammals, amphibians, and herbaceous vascular plants during the Last Glacial Maximum (see Li et al. 2013 for a review). What was once a refugial sink, later became a source as these plants and animals migrated northward behind with the retreating ice sheets. Could it someday become an important refugial sink again? This time for biodiversity under threat from a warming planet? If so, then land stewards are encouraged to focus their conservation efforts in this most unique region of the Upper Midwest and Western Great Lakes of North America.

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