

Land use changes result in increased phylogenetic clustering and preferential loss of species-rich sites for Michigan floral assemblages.

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Abstract

Distribution models are widely used to understand landscape biodiversity patterns, facilitate evolutionary and ecological studies, and for making informed conservation decisions. While it is common to examine consequences of climate change, impacts of land use on distributions, a major factor in limiting ranges and corridors between populations, are less well understood. Here, we use distribution models to quantify changes in biodiversity due to land use for Michigan floral assemblages. We leveraged a distribution model dataset (1930 species) integrated with dated phylogenetic information and USGS land use maps to parse Michigan areas with unsuitable habitat. Additionally, we quantify the degree of high-quality habitat lost for each species, identifying those most strongly impacted by land use changes. Approx. 39% of Michigan terrestrial habitat fell within "unsuitable" land use categories. Sites predicted to harbor the most species based on climatic variables were those sites that lost the greatest proportion due to land use changes. Further, excluded sites were preferentially those composed of more phylogenetically even communities. Overall, the impact of land use changes on community species richness was the preferential loss of sites with the predicted highest biodiversity. For phylodiversity metrics, land use changes increased the degree of community phylogenetic clustering. This results in overall decreased phylodiversity, leading to assemblages less equipped to respond to rapid climatic changes. Our results confirm land use to be a major, but somewhat overlooked, factor impacting local diversity dynamics and illustrate how local-scale land use impacts regional-scale richness and phylodiversity patterns, likely leading to increased community fragility.

Introduction

Species distribution models (SDMs), sometimes also called niche models, are important tools used for biodiversity mapping and conservation planning. These models can provide insight into patterns of biodiversity across multiple spatial scales, such as highlighting regions of exceptional species richness (Soltis and Soltis 2016), quantifying different facets of phylogenetic endemism and diversity (Kling et al. 2018), or parsing lineage-specific contributions to different community assembly mechanisms (Figueroa et al. 2022). SDMs are typically built using occurrence records, climatic, and topographic data (Zimmerman et al. 2010) and therefore demonstrate predictions of species ranges based on known occurrences and abiotic factors. Climate is known to substantially influence species distributions (Chen et al. 2011; Parmesan and Yohe 2003; Root et al. 2003), and it is this tight link between climatic conditions and species distributions that allows SDMs to be built primarily from climatically based predictor variables (reviewed in Zimmerman et al. 2010).

Researchers typically obtain occurrence records obtained from one of many aggregators (e.g., GBIF, iDigBio, iNaturalist, RAINBIO, SpeciesLink) and generate species distribution models based on several high-resolution climate data layers (e.g., WorldClim or ENVIREM). Coupled with the relative ease of access to software capable of predicting species distributions, there is ample opportunity for researchers to build predictive models of species ranges based on specimen data and climate maps. Such climate-informed models can provide key insights into species' potential responses to climate change and can be used to

predict specific range-shifts that might accompany changing climate conditions (Soltis and Soltis 2016). However, climate is not the sole factor determining species ranges. For example, biotic interactions, such as competition and facilitation, predator-prey, and plant-pollinator dynamics, can leave detectable traces on species distributions (Wisz et al. 2013). Additionally, the occurrence records used to build SDMs, often obtained from herbaria specimen collections for plant species, may account for historic occurrences and might not reflect present-day habitat availability.

One factor that could limit the utility of historic occurrence records when building SDMs is land use changes that have occurred since a species was last observed at a particular location, such as through habitat losses and alterations. While using land use data as part of the SDM construction process is not necessary, accommodating for the potential impact of unsuitable areas due to land use by incorporating land use data into the process of SDM analysis can provide information on habitat/ sites that may not be realistically accessible, highlight where corridors are inaccessible, or note areas that no longer exist (e.g., Zhang et al. 2012; Franklin 2010). Furthermore, land use changes can impact species distributions on much smaller time scales than climate dynamics and therefore incorporating land use data may be essential for creating a more complete picture of species distribution changes. Land use data can also highlight locations in which an occurrence record might be valid, but which do not represent a biological population from an ecological or conservation-centered approach (e.g., a backyard, small park, or some university campuses). Some of these issues might be dealt with by data-cleaning strategies (Figueroa et al. 2022; Soltis and Soltis 2016; Grady et al. *in prep*), however many of these procedures are not standardized, can vary considerably with the study's goals and area of interest (Zurell et al. 2020), and data cleaning still does not explicitly address the issue of land use changes on predictions of biodiversity.

Incorporating land use into SDM predictions of biodiversity is also critical for obtaining better conservation-focused recommendations. Anthropogenic activities falling under the scope of land use practices have significant impacts on species distributions. For example, land use changes such as for highways, agricultural plantations, or dams can fragment the landscape, impairing connectivity for migration and dispersal (Leonard et al. 2017; McGuire et al. 2016; Nuñez et al. 2013), and destroying habitat, especially for range-limited species (Schaffer-Smith et al. 2016). While an SDM may predict a broad distribution of a particular species, this distribution may be significantly altered (e.g., reduced, or fragmented) due to urban and suburban areas, and the failure to accommodate for those factors leaves researchers and conservation biologists with data that does not reflect the reality experienced by the lineages in question. Despite the clear and fundamental connections between land use practices, species distributions, and climate changes, biodiversity mapping studies employing SDMs often fail to account for land use in their modeling approaches (Zimmerman et al. 2010), and conservation-focused studies employ SDM approaches sparingly (Tulloch et al. 2016).

Often, a general goal of biodiversity mapping studies is to quantify metrics across large spatial scales. In doing so, areas of exceptional species richness (Soltis and Soltis 2016) or phylodiversity (Figueroa et al. 2022; De Souza et al. 2021) can be highlighted, and that information can be used subsequently to assist in biodiversity maintenance planning and assessment. And while some studies have incorporated land

use types to compare species richness (e.g., Schuster et al. 2019), and many studies have employed SDMs to identify biodiversity hotspots (e.g., Soltis and Soltis 2016), weaving together an SDM approach to compare biodiversity metrics with and without accounting for land use is less common, especially for phylodiversity metrics. Nevertheless, measures of evolutionary diversity are considered important for assessing conservation priorities in relation to land use changes (Zhang et al. 2017).

In this study, we sought to ask whether, and to what extent, accounting for land use changes altered predictions of biodiversity for a representative regional flora. To do this, we compared predictions of species richness and phylodiversity metrics for the Michigan (MI) flora before and after accounting for land use practices using an SDM approach. Michigan is an excellent state to examine the impact of land use because it contains a wide spectrum of land use types, ranging from metropolitan city centers, large agricultural plots, and numerous governmentally protected lands. It also encompasses a broad range of ecosystems, including deciduous and coniferous forests, grasslands, dunes, and freshwater coastal habitats. Further, Michigan harbors a substantial portion of the continent's available freshwater, accounting for 41% of the total area of the state, making the state's biodiversity condition relevant for the nation as a whole. Moreover, Michigan has a history of mismanagement of freshwater which has caused immense repercussions for the human and non-human populations in, for example, Flint (Szé 2020). Freshwater quality and availability are connected to land use management, reinforcing the importance of assessing the impact of land use for the sake of the state's biocultural diversity. For the present study, we assembled an SDM dataset of the MI flora and aimed to address the following questions: (1) how does land use impact sites predicted to host high or low species richness? (2) how does accounting for land use status change the distribution of phylogenetic diversity within MI assemblages? (3) which species are predicted to be most impacted by land use changes?

Methods

Species distribution model dataset.

We have previously published a species distribution model dataset for American seed plants (Figueroa et al. 2021), suitable for biogeographic studies of diversity at regional and continental scales (Figueroa et al. 2022). Briefly, this dataset was assembled by first aggregating occurrence records from GBIF, and iDigBio. Records were cleaned as described in (Figueroa et al. 2021, 2022), and species with at least 12 occurrence records after data cleaning were passed on to MaxEnt (version 3.1.4; www.github.com/mrmaxent/Maxent; Phillips et al. 2004, 2006) for distribution modeling. The following abiotic variables were used to build the models: from WorldClim (Fick and Hijmans 2017) we used Bioclim 1 (annual mean temperature), Bioclim 7 (temperature annual range), Bioclim 12 (annual precipitation) and Bioclim 17 (precipitation of driest quarter); from Soil Grids, we used sand content, soil organic carbon content, soil pH in water and coarse fragment volumetric percent, from GTOPO30 (https://doi.org/10.5066/F7DF6PQS), we used elevation. This dataset therefore represents climate/abiotic-based predictions of species richness for seed plants across the Americas and is available from Dryad at (Figueroa et al. 2021). Models were built at a grid cell resolution of 0.04° (2.5') per side. From

this full dataset, we subset those species listed as being present in the state of Michigan (MI), USA, based on GBIF and the University of Michigan Herbaria (https://michiganflora.net/home.aspx). Among the ~ 2700 vascular plant species listed by these aggregators, we modeled 1930 seed plant species as having ranges within MI. This dataset of species was used for all subsequent analyses presented here.

Land use maps and processing.

Through the United States Geological Survey (USGS) Gap Analysis Program (2016), high-resolution land use maps are available for each US state and ecoregion. These maps document contemporary (circa 2011) land use categories, providing a window into the current state of US occupied land. The history of such land use in the US is intimately tied to the history of settler colonialism, violent imperial expansion across the landscape, and extractive industries (Hernandez 2022; Whyte 2018; Dunbar-Ortiz 2015), each of which has contributed greatly to current climate change conditions (IPCC 2022; Reibold 2022; Addison and Roe 2018; McGregor 2016). It must be acknowledged at the outset, therefore, that the USGS land use maps also serve as a map of the history of how the biological landscape has been impacted by European settler colonization. Keeping in mind the explicit connections between the legacies of settler colonial landscape alterations, as well as the ways in which data sources and the researchers who use them continue to benefit from such legacies is necessary to situate research findings in their proper sociocultural and temporal context. Such explicit considerations of researcher positionality are an important component of ongoing decolonial scientific practices (Gemmel et al. 2020; de Leeuw and Hunt 2017). For the present study, it is impossible to separate the utilization of government data on land use changes, the historical context of settler colonial violence giving rise to the availability of such data, and the landscape changes themselves as products of settler colonialism.

The land use map for Michigan (MI) was obtained from the USGS LANDFIRE project (Gap Analysis Program 2016). These maps are described fully at (https://www.usgs.gov/programs/gap-analysis-project) and delimit 526 unique land use categories assessed across the United States at a 30 m² grid cell resolution (~ 0.0003°), downloadable by individual state or ecoregion. The land use categories represent data from 2011. To assess map accuracy in the present, we visually compared land use categories with current satellite imagery for MI occurrence records of three widespread species, *Quercus alba, Acer saccharum, Betula papyrifera*, and one rarer species, *Lonicera diocia*, randomly sampling ~ 50 records per species across the state.

Because the land use map contained more data than we required for this study and presented a much higher resolution than we were able to develop for our species distribution models, we processed the USGS map as follows. First, we excluded sites representing highly developed area or water by converting all sites with the following categories to zero-value: Open Water (5 sub-categories; 41% of total MI area); Agriculture and Developed Vegetation (4 sub-categories; 28% MI terrestrial area); and Developed and Other Human Use (5 sub-categories; 11% MI terrestrial area). Next, all remaining sites (which comprise 61% of total MI terrestrial area) were given a value of 1, indicating those sites are not excluded from downstream biodiversity analyses. This high-resolution binary land use map was then resampled to

match the resolution and projection of our SDMs (0.04°, Lat-Long projection with WGS84 coordinate system, respectively). Multiplication of this binary map with each SDM resulted in removal of SDM sites that fell within the excluded land use categories and produced distribution maps accounting for land use. These modified SDMs were then used to compare biodiversity predictions against those based solely on climate. A tabular summary of all Michigan land use types is available on the LANDFIRE USGS website. A figure showing the changes in land use map after processing is given in Supplemental Figure S1.

Biodiversity metrics and caveats.

We compared biodiversity predictions between climate-only models and those that also accounted for land use to evaluate the impact of heterogeneous contemporary land use practices for biodiversity assessment. We used species richness, and three phylogenetic diversity metrics for our analyses (based on Faith et al. 2004 and Webb 2000): the phylogenetic diversity index (PDI), which measures the total evolutionary history circumscribed by species in an assemblage; mean nearest taxon distance (MNTD), which quantifies the average evolutionary distance to the closest relative in an assemblage; and mean pairwise distance (MPD), which measures the average evolutionary distance between all pairs of species in an assemblage. We used the 'PHYLOMEASURES' package (Tsirogiannis and Sandel 2016) in the R statistical computing environment (R Core Team 2020) for phylodiversity measures because this package provides forms of these metrics that account for the correlation between phylodiversity and species richness (Tsirogiannis and Sandel 2016; but see Sandel 2018).

The phylogenetic diversity metrics reported here are standardized effect sizes, based on comparisons to a randomized null (Webb 2000). In principle, ecological communities can be composed of species that are less related than expected by chance, termed phylogenetically over-dispersed (PDI > 0), as might be expected under a competition-driven assembly process (Webb et al. 2002). Communities might also be composed of more closely related species than expected by chance, termed phylogenetic clustering (PDI < 0), as might be predicted if abiotic filtering dominates the assembly process. We have previously found the American flora to trend toward phylogenetic clustering (Figueroa et al. 2022) based on the species in this dataset, and results here are interpreted within that greater continental-scale trend.

To determine biodiversity metrics within sites (i.e., grid cells), we first gridded MI into 0.04°x0.04° resolution cells, then determined species' presence within each site (defined as at least 25% site coverage with a minimum SDM score of 10/100). Richness was then obtained by summing the number of species marked as present within each site, and phylodiversity metrics were obtained based on the community composition predicted within each site using the 'PHYLOMEASURES' package (Tsirogiannis and Sandel 2017). Dated phylogenetic relationships were obtained from the seed plant phylogeny of (Smith and Brown 2018; ALLMB phylogeny).

For county-level analyses, all sites within a county were aggregated. Shapefiles for individual MI counties were obtained from (https://gis-michigan.opendata.arcgis.com/datasets/counties-v17a/explore). To facilitate interpretation of these results, we aggregated diversity stats for each of Michigan's 83 counties and then visualize the aggregated county-level results using a novel comparative biodiversity metric. This

County Fragility Score measures the proportion of each county's species richness that is retained after accounting for contemporary land use changes and divides that expected species richness by the number of sites within that county not excluded due to land use type. This metric thus quantifies the fraction of biodiversity each site within a county is effectively responsible for maintaining. Higher fragility scores indicate counties in which each site is harboring a larger percentage of that county's total biodiversity, because the biodiversity is concentrated within fewer sites in that county.

Species response curves.

We assessed whether sites lost to land use changes were predicted to be high- or low-quality sites for individual species concurrent with community-level analyses. To do this, we generated species response curves that track the fraction of sites lost to land use changes in each of the one hundred value categories provided by the SDMs. Species whose high-scoring sites (defined here as all sites with a score of at least 70/100) averaged losses of at least 65% were flagged as species whose distribution modeling was critically impacted by land use.

Results

Impact of land use on community species richness.

Before accounting for land use changes, our SDMs predicted strong spatial heterogeneity to species richness across Michigan (Fig. 1a). The Upper Peninsula (UP) landform was predicted to harbor fewer species per site than the Lower Peninsula (LP). Southeast and Southwest MI coastal sites were predicted to harbor the greatest species richness. However, sites impacted by land use changes were geographically concentrated in the southern half of the Lower Peninsula (Figs. 1b), particularly in the Southeast, Southwest, and center of the LP, whereas in comparison the UP was relatively unaffected. The result of the combined geographic heterogeneity of both species richness predictions and land use practices was to preferentially lose sites with the greatest predicted species diversity (Fig. 1c). In particular, those sites predicted to harbor the top 20th percentile of species richness experienced near total loss of climatically predicted habitat availability. Some potential reasons for this pattern, in relation to the development of urban and metropolitan areas, are offered in the Discussion. Nevertheless, this indicates that predictions of species richness that fail to account for land use and rely solely on abiotic predictor variables, are likely to significantly overestimate biodiversity metrics for the MI flora.

Phylogenetic diversity and community composition.

We compared predicted phylogenetic diversity using three phylodiversity measures: PDI (Fig. 2), MPD (Fig. 3), and MNTD (Figure S2; see Methods for details). The most phylogenetically clustered sites (lowest PDI) were concentrated along coastal regions of the UP and the northern LP (Fig. 2a). Communities generally became progressively more phylogenetically even (PDI increased) moving south and west along the LP. MNTD patterns (Figure S2) generally mirrored those of PDI. MPD values (Fig. 3a) tended to be significantly high in the UP (MPD > 0), then gradually decreased in value moving south through MI into

the LP. Significantly negative MPD values were concentrated in the Southwest and Southeast of the LP. When land use changes were considered, the effect on phylodiversity was to lose sites with more positive PDI and MNTD values, and MPD values closer to zero. The combined effect of these changes was to increase phylogenetic clustering and push each distribution of community phylodiversity metrics towards the extremes. These results indicate that a failure to account for land use changes will overpredict the breadth of the distribution of phylodiversity in MI floral assemblages, as accounting for land use substantially narrows the distribution of phylodiversity values observed across communities.

Species response curves and county analyses.

At the community scale, the impact of accounting for land use was a general reduction in predicted biodiversity values. However, individual species varied substantially in how land use impacted our predictions of their distribution. In general, we observed three types of species response curves to land use changes (Fig. 4): greatest loss of high-scoring (SDM score > 70/100) habitat; greatest loss of low-scoring (SDM score < 30/100) habitat; and greatest loss of intermediate-scoring habitat (SDM score between 30–70). We aggregated these species level data to produce a list of 306 species, representing almost 200 genera, predicted to be most impacted by land use (Table S1), defined here as those species for which at least 65% of all high-scoring sites was lost due to land use (see Methods).

To facilitate application of our results, we aggregated and tabulated diversity stats by county for each of Michigan's 83 counties. Figure 5a presents a comparative biodiversity metric that visualizes these biodiversity results within each county, termed the *County Fragility Score* here (see Methods). This metric quantifies the spread of biodiversity across sites unaffected by land use changes within each county. Counties in the UP had low fragility scores because biodiversity in those counties was spread across numerous sites. In contrast, Southeast MI counties tended toward higher fragility scores because those counties harbored few sites unaffected by land use changes, and thus each site was effectively responsible for maintaining a higher proportion of that county's total biodiversity.

Two additional trends that emerged from county-level analyses are illustrated in Fig. 5. Within each county, regardless of county location or extent of land use changes, sites impacted by land use tended to be ones predicted to harbor a large fraction of the county's total species diversity (Fig. 5b). Thus, the impact of land use practices is to impact predicted species distributions across the entire state, even in counties with relatively less area impact by land use changes. Second, sites retained within each county tended to harbor a substantial portion of the species that would be predicted to occur in that county before accounting for land use (Fig. 5c). This was true even for counties predicted to lose the vast majority of sites. In other words, species richness and phylodiversity could appear unaffected by land use changes at the county level because retained sites are well representative of the total species diversity otherwise predicted for that county.

Discussion

Species distribution modeling integrates climate/ abiotic variables and occurrence record data to form predictive models of species' ranges. There are several advantages of using models over relying on point occurrence records include overcoming sampling limitations (Bartholett et al. 2007) and providing macroscale correlates of climatic predictors of species distributions. However, while using only point occurrence records may underestimate the true extent of possible habitat for a species, using only climate-based predictors in modeling species ranges can overestimate distributions by failing to account for land use practices that limit or otherwise eliminate climatically suitable sites (e.g., Alamgir et al. 2015; Zhang et al. 2012; Silva et al. 2006). Additional factors, such as habitat connectivity and freshwater availability, are also often impacted by land use changes and can affect species distributions, particularly in relation to climate change (McGuire et al. 2016).

Impacts of land use on Michigan diversity estimates.

Our analyses found that climatically suitable sites predicted to harbor the greatest species richness were preferentially those sites most impacted by land use changes (Fig. 1). Quantitatively, the effect of land use changes on species richness was to lose at least 50% of all sites within those containing the highest 20th percentile of predicted species richness (Fig. 1c). In application, this means that failure to account for land use changes will likely significantly overestimate the distribution of species diversity in MI. Further studies are needed to determine if this is a national/ continental trend, but if so, it would indicate a strong need for accurate land use maps in biodiversity mapping studies. Our results emphasize that the creation and maintenance of publicly accessible, high-resolution, land use maps of the kind used for this study could be vitally important for comprehensive mapping of global biodiversity patterns.

The underlying reasons for losing such high-diversity sites in MI could stem from a tendency for urban and metropolitan areas to occur on sites historically chosen for high productivity and/ or access to water/ trade routes. The area of the modern-day city of Detroit highlights the extreme impact of land use on biodiversity, with climatic predictors generally ranking the city's area as highly suitable, whereas contemporary land use clearly precludes such habitat availability. The area currently occupied by Detroit has housed Europeans since the 1600s, but Indigenous peoples have lived there for considerably longer, with current archeological sites in the area dating *at least* as far back as 11 Kya. Therefore, the area encompassing the modern-day city of Detroit has sustained human beings for millennia. Different societies and ways of life have shaped this area in very different manners, but societies based on highly extractive economies, such as those which have grown out of settler colonialism, have likely impacted the ecosystem properties and ecology of this area more intensely (McGregor et al. 2020; Davis and Todd 2017; Whyte 2017).

Species richness is only one metric of community-level biodiversity, with phylogenetic diversity being another (Swenson 2011). Despite this, the impact of land use on phylodiversity metrics is often less studied in published works. In our analyses, we found that accounting for land use led to a preferential loss of sites with more even phylogenetic structure (Fig. 2, 3, S2). We use the phrase "more even" because previous results with this SDM dataset indicate a general pattern of phylogenetic clustering to the

American flora (Figueroa et al. 2022), so results should be interpreted within that larger, continental-scale pattern.

Our phylodiversity results predict that overall land use practices in MI should increase the degree of phylogenetic clustering among floral assemblages. We suggest that this could result in decreased total evolutionary diversity, and therefore communities that are less equipped to adapt to rapid climatic changes. Increased community fragility, resulting from increased phylogenetic clustering, might exacerbate further the impacts of climate change on the MI flora. These results illustrate the potential links between local-scale patterns and regional community-scale properties that can be assessed with an integrative approach like we have used here.

Methodological considerations

The results we present here will be influenced by definitions of land use categories and how those are applied within the study context. We applied a conservative estimate of where land use changes have impacted biodiversity by only removing sites used for farming or with explicit human development and settlement. This likely underestimates the extent to which human activities have altered biodiversity patterns across the landscape for several reasons. First, ecosystems are strongly connected and landscape connectivity itself is an important aspect by which anthropogenic activities alter biodiversity dynamics (McGuire et al. 2016). Landscape fragmentation is not incorporated through simple land use categories. Second, activities which impact things like water or air quality are not captured explicitly by these land use categories but can nevertheless have impacts throughout a landscape. Further, the land use categories employed here represent the current state of land use practices and do not necessarily capture areas which might have been altered previously but are no longer being used for development, such as those recovering from developmental disturbances. Our results, therefore, provide a low estimate of some of the ways in which land use changes have reduced biodiversity in Michigan.

Another methodological consideration is grid cell size, or the resolution used for analyses. Scale-dependence is a ubiquitous feature of ecological studies, and the implications of our results could be interpreted to vary with scale of the analyses. To illustrate this, we quantified how much of each county's biodiversity was held within each site in that county (Fig. 5). This metric, the *County Fragility Score*, indicates what fraction of that county's biodiversity would be lost, on average, per site. Counties with higher fragility scores are therefore excellent candidates for increased restorative ecological efforts or conservation approaches aimed at safeguarding remaining biodiversity. County-level analyses are a coarser description of the biodiversity impacts of land use changes compared to the finer grid cell size of our SDMs.

An important consideration arising from the results of our county-scale analyses is that within most counties, the sites that remained after accounting for land use tended to harbor most, if not all, of the species predicted to be present within that county. Therefore, this could make it difficult to "see" the effects of land use when on the ground, because diversity would appear to be maintained at the county

level despite extensive loss of habitat. This is a scale-dependent issue that can arise from aggregating diversity for an entire county, rather than looking at the geographic distribution of that diversity within the county, and because retained sites were well representative of the total species diversity otherwise predicted for that county.

Although our community-level analyses provide key insights into the impacts of land use on many diversity metrics, we are also aware that land use changes have impacted species heterogeneously, even among species at the same trophic level. We quantified the impact of land use on each species' SDM to assess whether each species preferentially lost high or low scoring sites (Fig. 4). Compiling these results provided a list of 306 species predicted to be most negatively impacted by land use practices in MI (Table S1).

Conservation considerations

These results underscore the species-specific heterogeneity of potential responses to land use practices and highlight the need to be especially aware of which species are most critically affected by human-landscape interactions. This advocates strongly for local-scale knowledge in restorative ecological efforts, and highlights some of the potential pitfalls of national, continental, and global conservation mapping studies, which often focus on global-scale, top-down approaches that can have little utility at smaller spatial-scales (Wyborn and Evans 2021). Further, such broad-scale mapping studies tend to adhere to a one-size-fits-all model for safeguarding biodiversity that can result in significant harm to local communities (Gómez-Baggethun et al. 2013; Berkes 2007; Berkes 2004). Community-based conservation and ecological restoration efforts, on the other hand, employ bottom-up approaches that are more likely to elevate the importance of local knowledge and center the specific, and heterogeneous, needs of the areas in which they are applied (e.g., Hessami et al. 2021, Godden and Cowell 2016). Land management practices to safeguard biodiversity are more successful when local communities are centered and involved in policy planning (Nepal 2002).

An important policy consideration concerning our results on species diversity is that although MI has numerous governmentally protected and otherwise non-urbanized areas in the Upper Peninsula (UP), these regions are predicted to house less biodiversity overall than would be obtained in sites farther south, where land use has already provoked a bigger impact. This has important implications for where future restorative ecological efforts might be most useful in MI, as the climatic favorability is much higher in the southern and coastal regions of the state than in the UP. This by no means decreases the importance of the UP or the importance of conservation efforts there, however. The peninsula is vital for sustaining a large and relatively contiguous forest ecosystem, home to much of the state's remaining biodiversity. Rather, we interpret these results as suggestive that proper conservation policies in the Lower Peninsula (based on community-based conservation) could potentially have large impacts for safeguarding floristic diversity in MI.

Land use practices

Land use practices are inescapably tied to regional and global drivers of climate change because how humans interact with the landscape strongly influences, for example, the extent of greenhouse gas emissions, the degree of habitat connectivity, availability of habitat, and a myriad of other factors. Where humans carry out these land use practices helps determine the species-specific and ecosystem-specific impacts of land use at more local scales. Negative anthropogenic activities, such as industrial-scale mining, high levels of pollutant emissions, and large-scale crop monoculture and livestock farming practices, among others, are examples of land use practices that have become major drivers of climate changes (IPBES 2019). Although all land use practices have the potential to impact species distribution modeling approaches, not all land use is inherently detrimental to biodiversity maintenance. Indigenous land management systems, for example, have been and continue to be demonstrably capable of safeguarding high levels of biodiversity, equal and beyond those of governmentally allocated protected areas (Schuster et al. 2019). In many ways, this is due to Indigenous land stewardship methods that, compared to Western land use practices, do not rely on extensive deforestation, incorporate detailed localscale place-based knowledge, degrade soil and landscapes to far lesser extents, and emphasize the reciprocally dynamic ecological relationships present in biotic systems (Hessami et al. 2021; Fa et al. 2020; Schuster et al. 2019; Anderson 2013).

Conclusion

In this study, we leveraged an SDM dataset of Michigan seed plants (Figueroa et al. 2021) suitable for biogeographic and regional-scale diversity studies (Figueroa et al. 2022) to quantify how accounting for land use practices alters biodiversity predictions. Our results illustrate how local-scale land use changes can impact regional-scale diversity patterns, and lead to increased community-scale fragility. The impacts of land use changes on diversity metrics form only one component demonstrating how human alterations to landscapes affect ecosystem properties, nevertheless studies quantifying land use impacts on measures of diversity, especially phylogenetic diversity, are relatively uncommon (but see Kusuma et al. 2018; Turley and Brudvig 2016; Egorov et al. 2014; and van Meerbeek et al. 2014 for some exceptions), as is the integration of an SDM approach like the one we employed here. Nevertheless, recent research has suggested that land use changes may result in widespread loss of evolutionary diversity for North American floral assemblages (Zhang et al. 2017), consistent with our findings here for the Michigan flora.

Overall, we have leveraged detailed knowledge from the occurrence records of MI floral assemblage, climate data, and land use practices to quantify how accounting for land use is necessary to obtain more biologically relevant estimates of contemporary biodiversity patterns. These results also show how restorative ecological efforts and anti-settler colonial conservation practices would be greatly enhanced by knowledge of contemporary land use practices. The creation and maintenance of such land use maps should be a high priority for academic biologists and applied conservation practitioners alike.

The assessment of how land use and phylodiversity intersect is especially understudied, and our results showed how local scale clustering patterns might interact to increase regional-scale community fragility in the face of rapid climatic changes. We also assessed community fragility at the county level and

species-specific responses to land use practices. Together, these showed a high degree of heterogeneity that strongly advocates for prioritizing local-scale knowledge in any and all restorative efforts. Future studies will assess the generalizability of these results and provide a chance to see whether land use practices in the US always tend toward increased phylogenetic clustering of floral assemblages, and whether city centers tend to be situated in areas otherwise predicted to have high species and phylodiversity.

Declarations

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[COMPETING INTERESTS]

The authors have no competing interests to declare that are relevant to the content of this article.

[AUTHOR'S CONTRIBUTIONS]

H.F. and S.A.S conceived of the study. C.J.G., and A.S. wrote the code to assemble the dataset, C.J.G. implemented data aggregation and niche modelling methods, and J.B. coordinated computational activities. H.F. and S.A.S. developed methods to analyze the dataset and characterize elevational niches. H.F. and S.A.S. wrote the first draft of the manuscript. All authors contributed to developing methods to aggregate data records and analyze niche models as well as final edits and revisions to the manuscript.

[DATA AVAILABILITY]

Species distribution models, land use maps, and relevant code used for this study are deposited with and accessible from Dryad (<URL>). Original land use maps used for this study are publicly available from the USGS Gap Analysis Program at (https://www.usgs.gov/programs/gap-analysis-project). County maps for Michigan are publicly available at (https://gis-michigan.opendata.arcgis.com/datasets/counties-v17a/explore).

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Figures

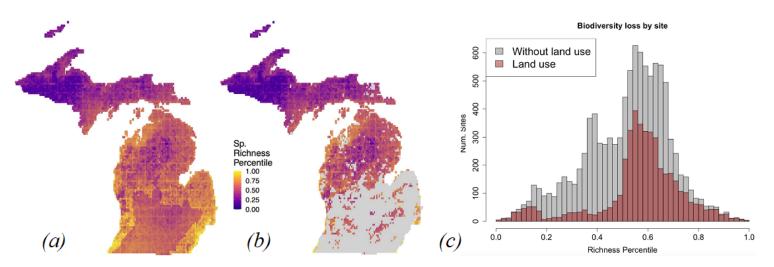


Figure 1

Predictions of richness for the Michigan seed plant flora based on species distribution models before (*a*), and after (*b*) accounting for contemporary (circa 2011) land use changes. Site richness is presented as percentile of maximum richness to ease interpretability of results. Areas most impacted by land use changes cover most of southern Michigan, including western and eastern coastal sites otherwise predicted to harbor the greatest diversity in the state. (*c*) Distribution of predicted richness among all sites (*grey bars*) and those lost due to land use changes (*red bars*). Sites in upper half of predicted richness (50th percentile and above) are preferentially those which experience the greatest loses. Additionally, sites in the top 20th percentile of predicted richness lose virtually all sites due to land use changes

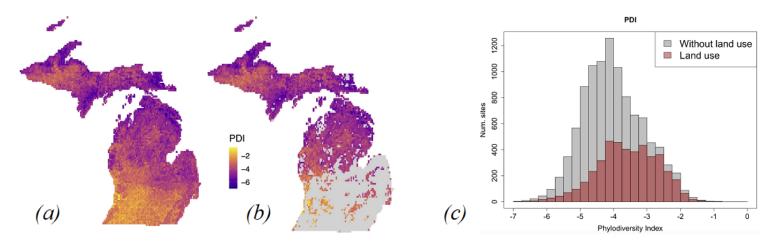


Figure 2

Predictions of phylogenetic diversity (PDI) for the Michigan seed plant flora based on species distribution models before (a), and after (b) accounting for contemporary (circa 2011) land use changes. PDI values were more even (less negative PDI values) for southwestern areas in Michigan and the western area of the Upper Peninsula landform. (c) Distribution of predicted PDI among all sites (grey bars) and those lost

due to land use changes (*red bars*). Sites lost to land use changes were preferentially from more phylogenetically even assemblages (less negative PDI values), suggesting that land use practices increase the degree of phylogenetic clustering in Michigan floral communities

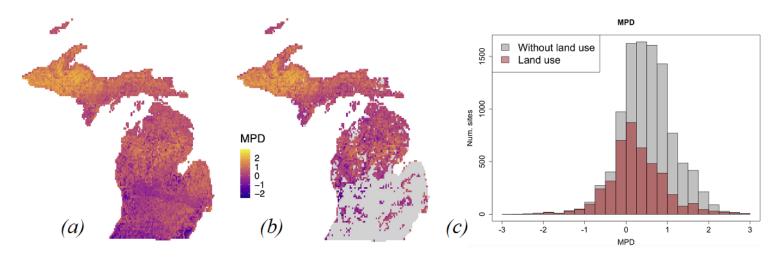


Figure 3

Predictions of mean pairwise distance (MPD) for the Michigan seed plant flora based on species distribution models before (*a*), and after (*b*) accounting for contemporary (circa 2011) land use changes. MPD values were overdispersed (MPD>0) for northwestern sites in the Upper Peninsula landform and clustered (MPD<0) for sites in the southern part of the state. (*c*) Distribution of predicted MPD among all sites (*grey bars*) and those lost due to land use changes (*red bars*). Sites lost to land use changes were preferentially from more phylogenetically even assemblages (MPD values closer to zero)

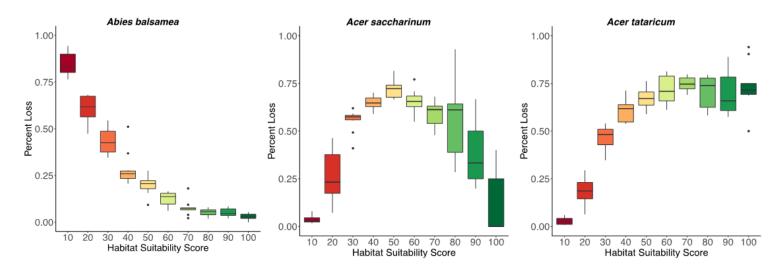


Figure 4

Representative species response curves illustrating the three forms commonly observed in our dataset. Plots illustrate the fraction of sites with a particular score (x-axis: Habitat Suitability Score) that are lost due to land use changes. (*Left*) Low scoring (SDM <30) sites are preferentially lost, whereas high-scoring sites (SDM >70) are relatively unaffected. (*Center*) Sites with the greatest proportion of loss are those of

intermediate quality (SDM between 30-70), with more extreme-scoring sites being progressively less impacted. (*Right*) High-quality sites (SDM >70) are preferentially those experiencing the greatest proportion of losses

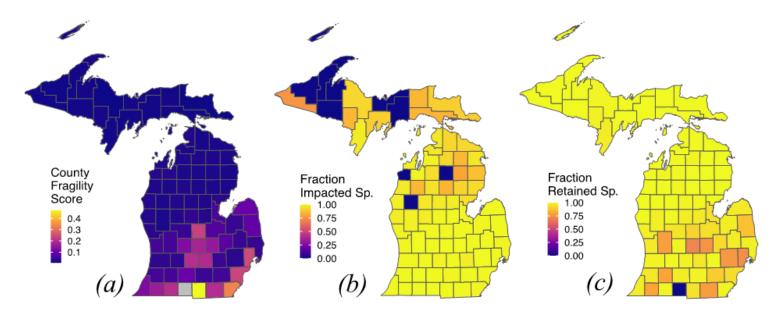


Figure 5

County level analyses aggregating community stats among all sites within a county. (a) The County Fragility Score reports the average fraction of a county's floral diversity maintained per site not excluded due to land use changes. Counties with large urban centers, such as Detroit and Flint, have higher Fragility Scores because their biodiversity is concentrated within fewer sites. Counties in more northern regions have lower scores because fewer sites in these counties are excluded due to land use changes so their biodiversity is spread out across more sites. (b) The Fraction of Impacted Species shows the proportion of a county's species present in sites lost due to land use changes within that county. Even for counties with relatively few excluded sites, those sites which are excluded harbor a large fraction of the species present in that county. (c) The Fraction of Retained Species shows the proportion of a county's species which remain in sites not excluded due to land use changes. Even for counties with a majority of sites lost to land use changes, the remaining sites are well representative of the total county composition, potentially obscuring the ability to see biodiversity losses at the county level

Supplementary Files

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