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RESEARCH ARTICLE

Identifying candidate plants for climate-informed restoration

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Ecological adaptation to rapid climate change requires information about which species might establish, persist, or disappear from plant communities. While range shift projections are available for selected individual species, these analyses are rarely focused on the plant community. Here, we leverage plant community surveys across the United States to identify potential shifts in silver maple community assemblages across a temperature gradient (hardiness zones). We analyzed 1,052 vegetation survey plots using multivariate techniques and found marginally significant community-level differences in silver maple community assemblages across U.S. Department of Agriculture hardiness zones. We identified species associated with silver maple communities across both broad and narrow ranges of hardiness zones. We illustrate how this approach can be used for climate-informed management. Taxa associated with a narrow range of hardiness zones may be candidates for assisted migration, the relocation of species outside of their historical native range in anticipation of climate change. In contrast, taxa associated with a broad range of hardiness zones may be able to adapt to climate change, particularly if the population is genetically diverse or if restoration includes assisted gene flow, where seeds or individuals are sourced from populations in the direction of projected climate change within their native ranges. Our study demonstrates how macroscale community analysis can leverage existing datasets to identify taxa for future climate-informed conservation and restoration.

Key words: *Acer saccharinum*, assisted gene-flow, assisted migration, climate change, floodplain forest, indicator species

Implications for Practice

- Climate-informed restoration would benefit from information about how plant assemblages, not just individual species, are likely to shift with climate change.
- Plant species with broad climatic tolerances may be able to maintain populations with climate change, but could benefit from strategies that add individuals from populations in the direction of projected climate change (assisted gene flow).
- Plant species with narrow climatic tolerances may require the movement of individuals outside of their historic range to keep up with climate change (assisted migration).
- Candidate species lists presented here can inform the testing of seed sourcing for locally sourced versus warm-adapted provenance in silver maple communities.
- The approach illustrated here can be applied to other communities and ecosystems to help identify taxa to prioritize for management and research.

Introduction

Climate change poses an unprecedented threat to global biodiversity (Parmesan et al. 2022; IPCC 2023), in part because many species are unlikely to shift their ranges rapidly enough to keep up with climate change (Corlett & Westcott 2013; Bradley et al. 2024). Maintaining diverse, functional plant communities with the ability to adapt to future climate change is critical for building climate resilience. Under climate change, many species are projected to be locally extirpated, potentially disrupting ecosystem function (Harrison et al. 2014). Adding diversity and functional redundancy with native species adapted to projected future climate makes it more likely that if currently established species decline or become locally extinct under changing conditions, other species can fill their niche (Reich et al. 2012; Prober et al. 2015; Gann et al. 2019).

Conservation and restoration strategies aimed at enhancing the climate resilience of species and communities can include assisted migration, here defined as the relocation of species outside of their historical native range in anticipation of climate change (Hoegh-Guldberg et al. 2008; Hof et al. 2017). Strategies may also include assisted gene flow, or the introduction of seeds or individuals within a species' current range that are sourced from populations in the direction of projected climate change (e.g. Aitken & Whitlock 2013; Prober et al. 2015; Gann et al. 2019). Climate-informed adaptive management

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approaches may also include "prestoration" (maintaining warm-adapted species currently present at the site, Butterfield et al. 2017) as well as approaches aimed at increasing functional redundancy and genetic diversity (Richardson et al. 2009). While these are useful and intuitive concepts, they remain rarely implemented (e.g. Twardek et al. 2023), perhaps stemming from a lack of scientific guidance about which species are particularly vulnerable to climate change (and therefore would be candidates for assisted migration, Fig. 1A) versus which species have populations across climatic gradients (and therefore would be candidates for assisted gene flow, Fig. 1B).

Species distribution models are often used in climate-informed conservation practice to predict how suitable habitats for particular target species may change under climate change (e.g. Pearson & Dawson 2003; Forester et al. 2013; Willis et al. 2015). However, species distribution modeling studies often focus on a subset of taxa (e.g. trees, Iverson et al. 2008) and typically lack information about the surrounding community. While this approach can be effective for informing individual species management (e.g. by identifying current and future areas with suitable habitat for focal species, Iverson et al. 2008; Gray et al. 2011; Etterson et al. 2020), it is less applicable for community-level restoration, which would optimally consider all species within a focal community. As a result, there is an ongoing need for analyses that support climate-informed conservation and restoration efforts based on species associated with similar plant communities.

Development of climate-informed management strategies is especially urgent for ecological communities that are already threatened. An example is floodplain forest communities, which are among the most threatened ecosystem types in the eastern United States due to extensive habitat loss driven primarily by expanding agriculture, urbanization, and industrial development (Brown et al. 2005; Vogler & Vukomanovic 2021). Floodplain forests support high levels of plant biodiversity and act as key contributors to hydrologic and climate regulation (Havrdová et al. 2023), making their conservation a high priority. Floodplain forest communities typically experience periodic flooding along with temperature and humidity gradients that influence the vegetative community composition (Havrdová et al. 2023). Floodplain forests of the eastern United States are characterized by the presence of silver maple trees (*Acer saccharinum*), which are resilient to flooding events (Marks & Atia 2020). Recently, there has been growing concern about the potential effects of climate change on these fragile ecosystems (Marks et al. 2021; Havrdová et al. 2023). By mid-century, the eastern United States is projected to become wetter and to warm between 1.5 and 4.5°C (Karmalkar et al. 2019), which could affect plant community assembly. While the broad geographic distribution of silver maple trees, ranging from Mississippi to southern Quebec (Gabriel 1990), may confer climate resilience to this characteristic riparian species, less is known about the potential climate resilience of other plants that are part of floodplain forest communities.

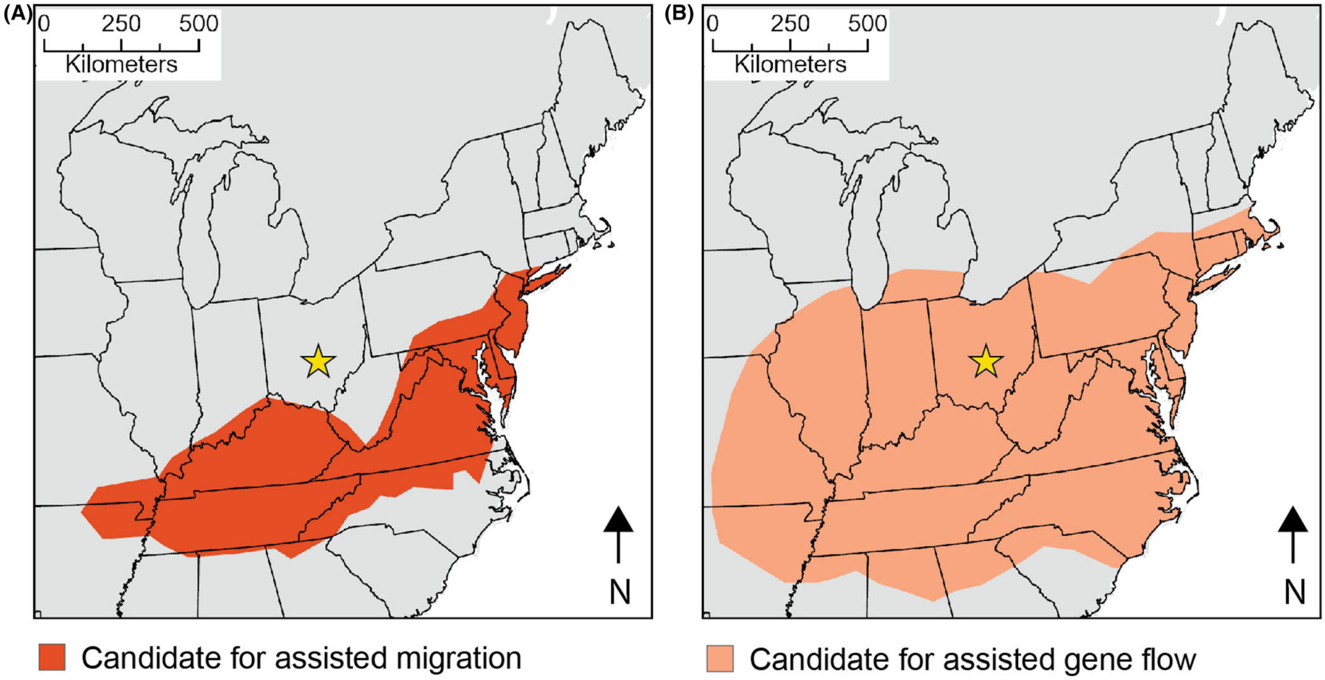

Figure 1. Conceptual comparison of restoration approaches for a hypothetical restoration site in Ohio (star). (A) Assisted migration, where a species is relocated outside of its historical native range in anticipation of climate change, could be a viable approach for this candidate species, which has a relatively narrow range (dark orange) and is not yet present at the restoration site. (B) Assisted gene flow, where seeds from warm-adapted populations are included in restoration plantings in anticipation of climate change, could be a viable approach for this candidate species, which has a broader range (light orange) and is present at or near the restoration site.

Here, we use silver maple communities as a case study to illustrate an approach for informing community conservation and restoration under climate change. Using a comprehensive dataset of vegetation surveys across the eastern United States, we evaluate silver maple communities across a large-scale temperature gradient. We hypothesize that species assemblages will differ across the temperature gradient, given that not all species are likely to have the same broad climatic tolerance as silver maple trees. Considering projected increases in temperature, we identify plant assemblages associated with broad climatic gradients that may be more resilient to climate change, serving as candidates for assisted gene flow. We also identify taxa with close ties to specific temperature regimes, which may require assisted migration to persist in silver maple communities under future climatic conditions.

Methods

We used the Standardized Plant Community with Introduced Status (SPCIS) database (Petri et al. 2023), which consists of standardized and georeferenced plant community survey data from across the United States (85,455 total plots) measuring plant presence and percent cover within plots or transects encompassing ~20 × 20 m. SPCIS data include multiple state and federal survey campaigns, such as the National Park Service's Inventory and Monitoring Dataset and state natural heritage surveys, largely collected between 2000 and 2020. To focus on silver maple communities in the eastern United States, we subset the data to plots containing any records of silver maple that were located east of 100°W longitude (Gabriel 1990), resulting in a total of 1,137 plots containing silver maple (hereafter, silver maple plots)We also restricted the dataset to records of species designated as native in the contiguous United States by the U.S. Department of Agriculture (USDA) Plants Database because native species support greater abundance and diversity of birds, insects, and other native animals, making them better candidates for conservation (Burghardt et al. 2010; Narango et al. 2018). To exclude rare species, which are generally not good candidates for restoration, we retained species that occurred in 3% or more of the silver maple plots (after Alonso et al. 2016). SPCIS plots measure percent cover, so all subsequent analyses were performed on percent cover estimates for "common" species. We define common species as those that are found in 3% or more of the SPCIS plots that also contain silver maple.

We then extracted the relevant environmental variables for each plot. This could be done with any spatial environmental variables; in this case, we focused on temperature gradients using USDA hardiness zones. Hardiness zones, which are based on annual minimum temperature, are commonly used by land managers to generate planting recommendations (e.g. Widrlechner et al. 2012) and can be important for delineating vegetative communities as minimum temperatures often limit plant distributions (Parker & Abatzoglou 2016). Additionally, hardiness zones are projected to shift by at least one zone throughout over 80% of the contiguous U.S. land area by 2070–2099 (Hanberry & Fraser 2019), making them a useful proxy for evaluating potential shifts in communities with climate change. We extracted current (1990–2020) hardiness zones created by the PRISM climate group (PRISM Climate Group 2021) for each silver maple plot.

SPCIS plots are often spatially clustered due to data collection focused within relatively undisturbed parks, forests, and natural areas. To reduce potential spatial autocorrelation, we created a 10 × 10 km grid based on findings from Negret et al. (2020) and randomly sampled one plot from each grid cell. Additionally, SPCIS plots oversample hardiness zones 5–6 due to higher sampling in Illinois and West Virginia. Uneven sampling could mask the effect of temperature on community composition. To account for uneven sampling between zones (Table 1), we limited samples to 36 randomly selected plots from zones 4 to 7 (the maximum available in zone 4 after accounting for spatial autocorrelation). Zones 3 and 8 include far fewer plots—therefore, we include all spatially thinned plots present in these zones ($n = 12$ and 13 plots, respectively), resulting in a total of 169 plots sampled per iteration. Zones 1 and 2 were not included because no records of silver maple were found in these zones from the SPCIS database (Fig. 2).

We randomly sampled plots with replacement for 100 iterations (i.e. all 1,137 plots were available to select from in each iteration) to create a representative sample of each hardiness zone for analysis. We chose this method to incorporate the diversity of plots within each hardiness zone while accounting for variation in community assemblages between plots within a single hardiness zone. From a total of 1,137 plots containing silver maple, 1,052 plots were randomly sampled in at least one iteration of our analysis. For each iteration, we visualized the variation of silver maple community composition across hardiness zones using non-metric multidimensional scaling (NMDS) through the metaMDS function in the *vegan* package (version 2.5.7, Oksanen et al. 2021) in R (R Core Team 2022). NMDS is a statistical method used to visualize how similar ecological communities are to each other (Crowther et al. 2013; Lemieux-Labonté et al. 2016; Addo-Fordjour et al. 2021). The initial input to the function consists of a data frame containing species names, plot IDs, and percent cover for each of the randomly sampled points in the model iteration. From here, the metaMDS function calculates a Bray–Curtis dissimilarity index

Table 1. Summary of dataset showing included and total (in parentheses) number of plots, species, and plant observations for native species in hardiness zones 3–8 (range of silver maple) included across 100 model iterations. Some plots were excluded by random chance due to the 10 km fishnet sampling method used to account for oversampling. Zones 1 and 2 are not included because no plots containing silver maple were found in these zones in our database.

Zone	*Plots*	*Species*	*Observations*
3	20 (20)	51 (51)	167 (167)
4	74 (74)	127 (127)	807 (807)
5	236 (237)	163 (163)	3,468 (3479)
6	477 (559)	186 (186)	7,859 (9312)
7	196 (198)	177 (177)	3,740 (3809)
8	49 (49)	101 (101)	1,031 (1031)

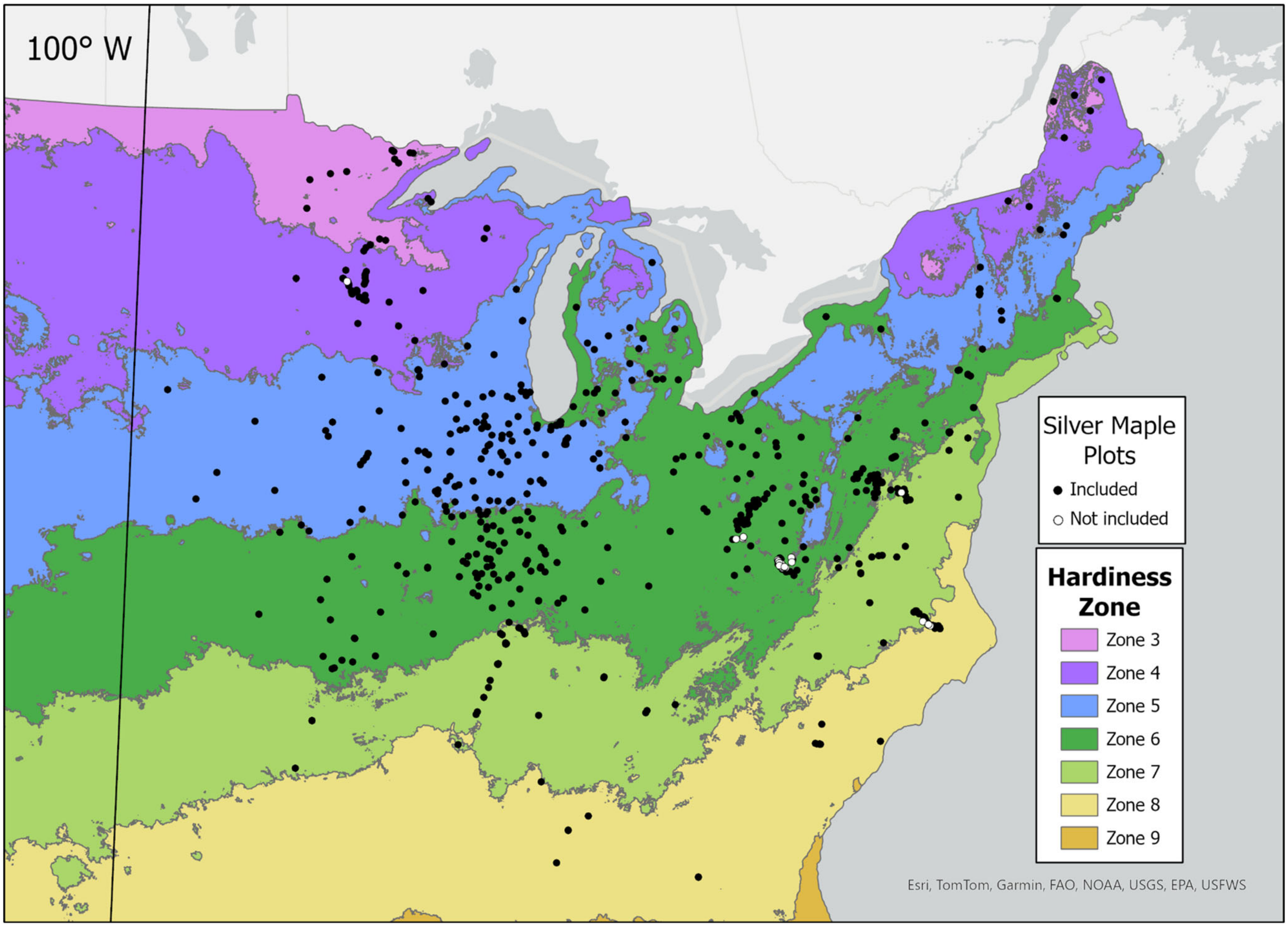

Figure 2. Geographic distribution of study sites ($n = 1{,}137$) superimposed on U.S. Department of Agriculture (USDA) hardiness zones. Study sites are represented by points. Points are color-coded based on whether they are (black) or are not (white) included in the analysis. White plots are not included by chance due to the 10 km fishnet sampling method used to prevent oversampling, meaning that these plots are close to several other silver maple plots included in the study. Zones 1 and 2 are not included because no plots containing silver maple were found in these zones in our database.

for each of the plots and plots them into multidimensional space to show how similar or different the communities are. The Bray–Curtis dissimilarity index compares pairs of plots and ranks them based on their similarity on a scale from 0 to 1, with combinations scoring 0 being identical and combinations scoring 1 being entirely different. Points that are closer together indicate similar communities, while points that are distant are different from each other. We constructed each NMDS plot using the metaMDS function ($k = 3$; trymax = 50; noshare = TRUE; maximum number of iterations = 1e6; convergence criterion = 1e-9 to reduce stress and encourage model convergence). We conducted a PROTEST analysis to test whether the NMDS outputs among iterations were significantly correlated with each other. The null hypothesis of this test is that concurrences between NMDS plots are due to chance, while the alternative hypothesis indicates that NMDS outputs are highly similar between iterations. The R script is appended as Supplement S1.

To test whether the silver maple community composition differed significantly overall across hardiness zones, we used the analysis of similarities (ANOSIM) test using a Bray–Curtis dissimilarity matrix (Oksanen et al. 2021). This is the same dissimilarity matrix used in the NMDS, but it includes hardiness zone values to group outputs. To test for pairwise differences between hardiness zones, we used permutational multivariate analysis of variance (PERMANOVA) tests based on 999 permutations (Martinez 2020). Because PERMANOVA can be sensitive to unequal variance between groups, we also conducted a PERMDISP test for homogeneity of variance between hardiness zones. We aggregated the PERMANOVA and PERMDISP outputs by calculating the averages across model iterations. To determine whether particular zones were contributing to the heterogeneity of variance between hardiness zones, we ran a post hoc Tukey honestly significant difference (HSD) test for every combination of hardiness zones for each model iteration. We averaged the p-values for each hardiness zone combination to identify any zone combinations responsible for the heterogeneity of variance.

To determine which species are associated with each hardiness zone, we conducted an indicator species analysis using the multipatt test in the *indicspecies* package (version 1.7.9, De Cáceres &

Legendre 2009). This tool characterizes the composition of a community in order to inform and prioritize species for conservation monitoring and ecological management (De Cáceres & Legendre 2009; Urban et al. 2012; De Cáceres 2013). Indicator species are highly characteristic of a particular group (in this case, hardiness zone). Indicator species analysis uses indicator values to identify the association strength between a single species and a community assemblage (De Cáceres 2013). Indicator values are calculated based on a species' *fidelity* (probability of finding a species at a site associated with a particular hardiness zone) and *specificity* (probability a site belongs to a particular hardiness zone based on the presence of a species). Therefore, a species may be present but not an indicator species if it does not occur in a high proportion of sites within a group (low fidelity) or if it occurs across many groups (low specificity). We conducted the indicator analysis for each sampling plot iteration ($n = 100$) and corrected for multiple tests using a false discovery rate p-value correction, which can maintain statistical power over large numbers of trials (Salas-López et al. 2022). Species were identified as indicators of a hardiness zone when the multipatt indicator value met the significance threshold ($p < 0.05$) in at least one iteration. The proportion of iterations in which a species was significantly associated with the hardiness zone can be found in Table S1.

Results

The SPCIS database had 1,137 silver maple plots east of 100°W longitude that contained a total of 27,939 records of 1,659 native species (Table 1). After plots were randomly subsampled to account for oversampling and spatial autocorrelation and only species present in 3% or more plots were retained, our final dataset included 1,052 plots containing 17,072 records of 189 species (11% of total native species) ranging from hardiness zones 3–8 (Table S1; Fig. 2). While our sampling method reduced the number of plots included in densely sampled areas, none of the 189 common species were lost.

Our analyses showed marginally significant differences between silver maple communities across hardiness zones (ANOSIM, $R = 0.047$, $p = 0.080$). Pairwise ADONIS (PERMANOVA) results indicated that most hardiness zones had significantly different community assemblages from one another (Table S2), but the overall effect sizes were small, with the greatest difference occurring between the coolest and warmest zones 3 and 8 ($R^2 = 0.144$, Table S2). These patterns are reflected in the overlap of zones in our NMDS output (Fig. 3). We observed overall consistency in NMDS outputs among the 100 iterations (PROTEST analysis; $p = 0.090$). We found evidence for heterogeneity of dispersion among hardiness zones, indicating higher variability in community composition within some hardiness zones (PERMDISP, $F = 6.414 \pm 1.205$ [95% CI], $p = 0.001$). Post hoc Tukey HSD tests revealed that this could be attributed to significant differences in dispersion between zone 3 and all other zones, and between zones 5 and 8, but no significant differences between any other zone combinations were found (Table S3). This parallels the NMDS output, which shows smaller polygons (reduced community variance) for zones 3 and 8 (Fig. 3).

The strong overlap in the ordination results was reflected in the broad climate tolerance of many of the species. The majority of common species ($n = 145/189$) were found in at least four different hardiness zones (Table S1; Fig. 4A). However, the breadth of species distribution does not necessarily reflect the status of species as indicators of their community. Across the 189 common species included in our analyses, 87 were identified as indicator species. Of these, most were associated with one hardiness zone (36 species) or 2 adjacent hardiness zones (29 species) (Table S1; Fig. 4B & 4C). Most of these species with narrow hardiness zone associations were associated with the warmer hardiness zones (Table S1). Across growth forms, herbaceous indicator species (forbs) were most likely to be associated with a single hardiness zone, whereas indicator species from other growth forms tended to be associated with two or more hardiness zones (Fig. 4D).

Discussion

Climatic conditions exert a strong influence over the geographic distribution of plant communities (Whittaker 1970), and climate change is projected to drive shifts in plant communities, particularly toward higher latitudes or altitudes (IPCC 2023). Unfortunately, few native plant species are likely to keep up with the rapid pace of climate change due to their slow dispersal rates (Bradley et al. 2024). As a result, climate-informed conservation of plant communities will likely need to leverage management strategies such as assisted gene-flow (Aitken & Whitlock 2013) or assisted migration (Hof et al. 2017) to enhance species or community resilience (e.g. Millar et al. 2007). For silver maple communities, our results suggest there are only minor differences in community composition across hardiness zones, indicating that these community assemblages share many of the same common plant species across a broad latitudinal gradient. Given the broad climatic distribution of these species, large-scale assisted migration of taxa across hardiness zones may be unnecessary to maintain the biodiversity of silver maple communities as temperatures rise. Instead, focusing on conservation strategies that preserve or enhance the adaptive potential of currently established populations, such as reducing stressors on existing populations or via assisted gene flow, may be sufficient for promoting climate resilience in silver maple communities across the eastern United States.

Conservation and restoration practices often focus on common species within a community because they play a key role in maintaining ecosystem function under stress (Smith & Knapp 2003) and are able to establish across a wide range of habitats (Mazaris et al. 2008), potentially improving overall establishment success. While the distributions of species based on occurrences are useful initial measures of climatic tolerance, an indicator species assessment identifies species that are particularly abundant and associated with hardiness zones and might be a better metric of climatic tolerance of a population. Out of our 87 indicator species, we identified 51 that are indicators in silver maple communities across more than one hardiness zone.

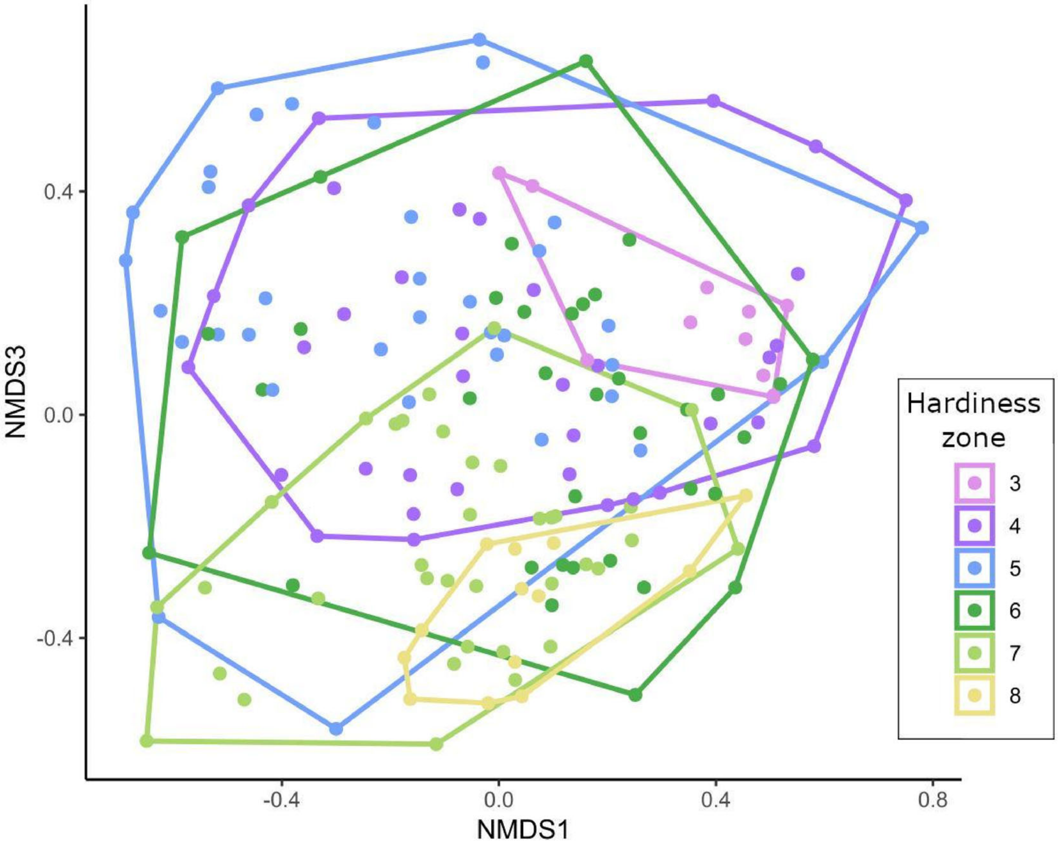

Figure 3. Non-metric multidimensional scaling ordination plot comparing native plant community composition from vegetation plots across U.S. Department of Agriculture (USDA) hardiness zones 3–8 from silver maple communities in the eastern United States (Stress value = 0.231). Plots are generated using species names, plot IDs, and percent cover data. Plots are grouped by hardiness zone. Larger polygons indicate greater variability in community composition for a particular hardiness zone. Greater overlap in polygons represents increased similarity in community composition between hardiness zones.

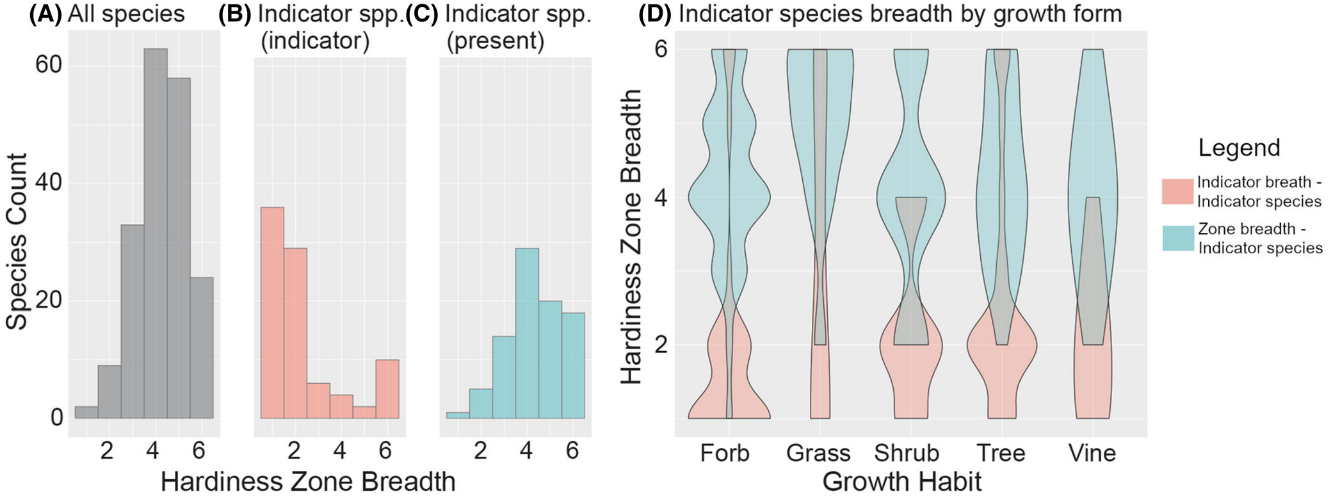

Figure 4. Histograms of hardiness zone breadth for common and indicator species. (A) Distribution of hardiness zone breadth for all 189 common species. (B) Hardiness zone breadth over which the 87 indicator species were counted as indicators. (C) Hardiness zone breadth over which the 87 indicator species were present. (D) Hardiness zone breadth of indicator species presence (blue) versus indicator status (pink) grouped by growth habit. A wider column indicates a greater number of species.

These broadly distributed taxa, such as the forb false nettle (*Boehmeria cylindrica*) or the grass Virginia wildrye (*Elymus virginicus*), could be ideal candidates to explore the benefits of assisted gene flow. Likewise, assisted gene flow may also be a beneficial management strategy for long-lived species, such as red maple (*Acer rubrum*), where long generation times make it more challenging for populations to adapt to rapidly changing environmental conditions (Neilson et al. 2005). Assisted gene flow may help increase the genetic diversity of these focal taxa, particularly given that the trailing edges of populations are thought to have the highest genetic diversity (Hampe & Petit 2005), which in turn may confer adaptive resilience to current and future climate change (Aitken & Whitlock 2013). While our analytical approach illustrates one way to identify potential assemblages of species that could be candidates for assisted gene flow, the potential benefits must be balanced against potential risks for small or isolated populations. These include the risk of introducing novel deleterious alleles to populations adapted to current climatic conditions, which may disrupt existing community and population dynamics (Bucharova et al. 2017; Grummer et al. 2022). Moreover, potential fitness benefits associated with assisted gene flow may not be realized quickly enough to help with rapid climate change, particularly in long-lived species such as trees (Grummer et al. 2022).

Although some indicator species were associated with multiple hardiness zones, the majority (65) were associated with one or two zones, suggesting these taxa will likely need to shift their distributions to track suitable climatic conditions in the future. Many of these indicator species are associated with warmer hardiness zones, making them good candidates for assisted migration into cooler silver maple communities across the east coast. For example, the tree bald cypress (*Taxodium distichum*), the vine supplejack (*Berchemia scandens*), and shrub meadow holly (*Ilex decidua*) are indicator species in hardiness zones 7–8 and are rarely present outside of these warmer climates. The narrow indicator species association suggests that these populations are important components of silver maple communities in warmer climates. For species like these with narrow climate tolerances, assisted migration may be an effective approach for building climate resilience, especially given that rates of native plant range expansion are already lagging far behind estimated rates required to track suitable climatic conditions (Bradley et al. 2024). While human-mediated interventions such as assisted migration can help species keep pace with rapid climate change, managers should weigh the potential benefits of introducing species against potential negative interactions that might harm a recipient community. For example, Wallingford et al. (2020) suggest avoiding species that are fast-growing and aggressive in their native range or reported as invasive outside of their native range. Similarly, genetic consequences, such as outbreeding depression or disruption of nonclimatic adaptive gene complexes, should also be considered when proposing assisted migration as a community restoration strategy (Hoffmann et al. 2021).

Lastly, our analyses identified some taxa, such as the forb Canada mayflower (*Maianthemum canadense*) and the tree Bur oak (*Quercus macrocarpa*), that are indicators of silver maple communities only at their coldest range margin (hardiness zone 3) in the eastern United States. Given the lack of existing silver maple plots in colder zones, these species do not have any clear-cut communities into which they could move. Instead, practitioners could target these species by managing cooler microsites that act as climate refugia, for example, in areas with sufficient canopy cover and soil moisture (Ashcroft & Gollan 2013).

Selecting species assemblages based solely on associations with temperature should be weighed against climate-driven shifts in other environmental variables, such as precipitation, which can also influence the composition, dynamics, and selection regimes of plant communities (USGCRP et al. 2017). For example, climate change is projected to influence abiotic conditions such as the frequency and magnitude of flood events (Demaria et al. 2016), which are known to influence community assemblages of floodplain forests (Havrdová et al. 2023). Thus, while our results are useful for identifying candidate suites of species to consider for regional restoration, practitioners should also consider local site characteristics when determining which species assemblages to target for climate-informed management.

Climate-informed conservation requires developing management strategies that consider and allow for future environmental changes (Millar et al. 2007; Stein et al. 2014; Gann et al. 2019). Yet, identifying candidate species for climate-informed management of a given plant community remains a challenge given the scarcity of tools to identify potential climate impacts on plant populations within a community context. New datasets such as SPCIS in the United States (Petri et al. 2023) enable scientists and practitioners to consider full plant communities and provide an important advance for assessing community associations. While spatially extensive, this dataset still suffers from spatial biases due to variation in sampling effort and may undersample some important restoration target species and communities. Our analysis of silver maple communities illustrates an important first step toward identifying appropriate assemblages of candidate species for climate-informed conservation and restoration. A similar approach could be applied to other species representative of different plant communities to identify candidate species lists for climate-informed restoration. Candidate species lists can inform the testing of the appropriateness of using seeds from local versus warm-adapted provenances (e.g. Bucharova et al. 2017) in silver maple communities, and a similar approach can be applied in other threatened ecosystems. Leveraging macroscale plant community datasets allows us to generate regionally applicable recommendations for climate-informed planting by identifying plants that are likely more (or less) resilient to future climatic changes at restoration sites.

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Literature Cited

Addo-Fordjour P, Boakye EK, Rahmad ZB (2021) Logging and topographic effects on tree community structure and habitat associations in a tropical upland evergreen forest, Ghana. Journal of Forestry Research 32:1361–1372. https://doi.org/10.1007/s11676-020-01203-w

Aitken SN, Whitlock MC (2013) Assisted gene flow to facilitate local adaptation to climate change. Annual Review of Ecology, Evolution, and Systematics 44:367–388. https://doi.org/10.1146/annurev-ecolsys-110512-135747

Alonso M, George M, Laca E (2016) Plant community patterns in California oak woodlands. Agro Sur 44:25–34. https://doi.org/10.4206/agrosur.2016.v44n2-04

Ashcroft MB, Gollan JR (2013) Moisture, thermal inertia, and the spatial distributions of near-surface soil and air temperatures: understanding factors that promote microrefugia. Agricultural and Forest Meteorology 176:77–89. https://doi.org/10.1016/j.agrformet.2013.03.008

Bradley BA, Beaury EM, Gallardo B, Ibáñez I, Jarnevich C, Morelli TL, Sofaer HR, Sorte CJB, Vilà M (2024) Observed and potential range shifts of native and nonnative species with climate change. Annual Reviews in Ecology, Evolution, and Systematics 55:23–40. https://doi.org/10.1146/annurev-ecolsys-102722-013135

Brown DG, Johnson KM, Loveland TR, Theobald DM (2005) Rural land-use trends in the conterminous United States, 1950–2000. Ecological Applications 15:1851–1863. https://doi.org/10.1890/03-5220

Bucharova A, Durka W, Hölzel N, Kollmann J, Michalski S, Bossdorf O (2017) Are local plants the best for ecosystem restoration? It depends on how you analyze the data. Ecology and Evolution 7:10683–10689. https://doi.org/10.1002/ece3.3585

Burghardt KT, Tallamy DW, Philips C, Shropshire KJ (2010) Non-native plants reduce abundance, richness, and host specialization in lepidopteran communities. Ecosphere 1:art11. https://doi.org/10.1890/ES10-00032.1

Butterfield BJ, Copeland SM, Munson SM, Roybal CM, Wood TE (2017) Prestoration: using species in restoration that will persist now and into the future. Restoration Ecology 25:S155–S163. https://doi.org/10.1111/rec.12381

Corlett RT, Westcott DA (2013) Will plant movements keep up with climate change? Trends in Ecology & Evolution 28:482–488. https://doi.org/10.1016/j.tree.2013.04.003

Crowther TW, Stanton DWG, Thomas SM, A'Bear AD, Hiscox J, Jones TH, Voříšková J, Baldrian P, Boddy L (2013) Top-down control of soil fungal community composition by a globally distributed keystone consumer. Ecology 94:2518–2528. https://doi.org/10.1890/13-0197.1

De Cáceres M (2013) How to use the indicspecies package (ver. 1.7. 1) R Project, 29

De Cáceres M, Legendre P (2009) Associations between species and groups of sites: indices and statistical inference. Ecology 90:3566–3574. https://doi.org/10.1890/08-1823.1

Demaria EMC, Palmer RN, Roundy JK (2016) Regional climate change projections of streamflow characteristics in the Northeast and Midwest U.S. Journal of Hydrology: Regional Studies 5:309–323. https://doi.org/10.1016/j.ejrh.2015.11.007

Etterson JR, Cornett MW, White MA, Kavajecz LC (2020) Assisted migration across fixed seed zones detects adaptation lags in two major North American tree species. Ecological Applications 30:e02092. https://doi.org/10.1002/eap.2092

Forester BR, DeChaine EG, Bunn AG (2013) Integrating ensemble species distribution modelling and statistical phylogeography to inform projections of climate change impacts on species distributions. Diversity and Distributions 19:1480–1495. https://doi.org/10.1111/ddi.12098

Gabriel WJ (1990) *Acer saccharinum* L. USFS Southern Research Station, Washington, D.C.

Gann GD, McDonald T, Walder B, Aronson J, Nelson CR, Jonson J, et al. (2019) International principles and standards for the practice of ecological restoration. Restoration Ecology 27:S1–S46. https://doi.org/10.1111/rec.13035

Gray LK, Gylander T, Mbogga MS, Chen P, Hamann A (2011) Assisted migration to address climate change: recommendations for aspen reforestation in western Canada. Ecological Applications 21:1591–1603. https://doi.org/10.1890/10-1054.1

Grummer JA, Booker TR, Matthey-Doret R, Nietlisbach P, Thomaz AT, Whitlock MC (2022) The immediate costs and long-term benefits of assisted gene flow in large populations. Conservation Biology 36:e13911. https://doi.org/10.1111/cobi.13911

Hampe A, Petit RJ (2005) Conserving biodiversity under climate change: the rear edge matters. Ecology Letters 8:461–467. https://doi.org/10.1111/j.1461-0248.2005.00739.x

Hanberry BB, Fraser JS (2019) Visualizing current and future climate boundaries of the conterminous United States: implications for forests. Forests 10:280. https://doi.org/10.3390/f10030280

Harrison PA, Berry PM, Simpson G, Haslett JR, Blicharska M, Bucur M, et al. (2014) Linkages between biodiversity attributes and ecosystem services: a systematic review. Ecosystem Services 9:191–203. https://doi.org/10.1016/j.ecoser.2014.05.006

Havrdová A, Douda J, Doudová J (2023) Threats, biodiversity drivers and restoration in temperate floodplain forests related to spatial scales. Science of the Total Environment 854:158743. https://doi.org/10.1016/j.scitotenv.2022.158743

Hoegh-Guldberg O, Hughes L, McIntyre S, Lindenmayer DB, Parmesan C, Possingham HP, Thomas CD (2008) Assisted colonization and rapid climate change. Science 321:345–346. https://doi.org/10.1126/science.1157897

Hof AR, Dymond CC, Mladenoff DJ (2017) Climate change mitigation through adaptation: the effectiveness of forest diversification by novel tree planting regimes. Ecosphere 8:e01981. https://doi.org/10.1002/ecs2.1981

Hoffmann AA, Miller AD, Weeks AR (2021) Genetic mixing for population management: from genetic rescue to provenancing. Evolutionary Applications 14:634–652. https://doi.org/10.1111/eva.13154

IPCC (2023) Climate change (2023) synthesis report. Pages 184. In: Core Writing Team, Lee H, Romero J (eds) Contribution of working groups I, II and III to the sixth assessment report of the Intergovernmental Panel on Climate Change. IPCC, Geneva, Switzerland. https://doi.org/10.59327/IPCC/AR6-9789291691647

Iverson L, Prasad A, Matthews S (2008) Modeling potential climate change impacts on the trees of the northeastern United States. Mitigation and Adaptation Strategies for Global Change 13:487–516. https://doi.org/10.1007/s11027-007-9129-y

Karmalkar AV, Thibeault JM, Bryan AM, Seth A (2019) Identifying credible and diverse GCMs for regional climate change studies—case study: northeastern United States. Climatic Change 154:367–386. https://doi.org/10.1007/s10584-019-02411-y

Lemieux-Labonté V, Tromas N, Shapiro BJ, Lapointe F-J (2016) Environment and host species shape the skin microbiome of captive neotropical bats. PeerJ 4:e2430. https://doi.org/10.7717/peerj.2430

Marks CO, Atia H (2020) Seedling submergence tolerances accurately predict riparian tree species distributions: insights to help design environmental flows. Wetlands 40:1923–1934. https://doi.org/10.1007/s13157-020-01375-5

Marks CO, Yellen BC, Nislow KH (2021) Species distributions on successional and flooding gradients in Connecticut River floodplain forests. Northeastern Naturalist 28:577–602. https://doi.org/10.1656/045.028.0415

Martinez AP 2020 pairwiseAdonis: pairwise multilevel comparison using adonis. R package version 0.3.

Mazaris AD, Tzanopoulos J, Kallimanis AS, Matsinos YG, Sgardelis SP, Pantis JD (2008) The contribution of common and rare species to plant species richness patterns: the effect of habitat type and size of sampling unit. Biodiversity and Conservation 17:3567–3577. https://doi.org/10.1007/s10531-008-9480-7

Millar CI, Stephenson NL, Stephens SL (2007) Climate change and forests of the future: managing in the face of uncertainty. Ecological Applications 17: 2145–2151. https://doi.org/10.1890/06-1715.1

Narango DL, Tallamy DW, Marra PP (2018) Nonnative plants reduce population growth of an insectivorous bird. Proceedings of the National Academy of Sciences of the United States of America 115:11549–11554. https://doi.org/10.1073/pnas.1809259115

Negret PJ, Marco MD, Sonter LJ, Rhodes J, Possingham HP, Maron M (2020) Effects of spatial autocorrelation and sampling design on estimates of protected area effectiveness. Conservation Biology 34:1452–1462. https://doi.org/10.1111/cobi.13522

Neilson RP, Pitelka LF, Solomon AM, Nathan R, Midgley GF, Fragoso JMV, Lischke H, Thompson K (2005) Forecasting regional to global plant migration in response to climate change. Bioscience 55:749–759. https://doi.org/10.1641/0006-3568(2005)055[0749:FRTGPM]2.0.CO;2

Oksanen J, Blanchet FG, Friendly M, Kindt R, Legendre P, McGlinn D, Minchin PR, O'Hara RB, Simpson GL, Solymos P (2021) vegan: Community Ecology Package R package version 2.5–7. 2020

Parker LE, Abatzoglou JT (2016) Projected changes in cold hardiness zones and suitable overwinter ranges of perennial crops over the United States. Environmental Research Letters 11:034001. https://doi.org/10.1088/1748-9326/11/3/034001

Parmesan C, Morecroft MD, Trisurat Y, Adrian R, Anshari GZ, Arneth A, et al. (2022) Terrestrial and freshwater ecosystems and their services. Pages 197–377. In: Pörtner H-O, Roberts DC, Tignor M, Poloczanska ES, Mintenbeck K, Alegría A, Craig M, Langsdorf S, Löschke S, Möller V, Okem A, Rama B (eds) Climate change 2022: impacts, adaptation and vulnerability. Contribution of working group II to the sixth assessment report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, UK and New York, NY, USA

Pearson RG, Dawson TP (2003) Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? Global Ecology and Biogeography 12:361–371. https://doi.org/10.1046/j.1466-822X.2003.00042.x

Petri L, Beaury EM, Corbin J, Peach K, Sofaer H, Pearse IS, et al. (2023) SPCIS: standardized plant community with introduced status database. Ecology 104:e3947. https://doi.org/10.1002/ecy.3947

PRISM Climate Group (2021) Oregon State University https://prism.oregonstate.edu (accessed Oct 2021)

Prober SM, Byrne M, McLean EH, Steane DA, Potts BM, Vaillancourt RE, Stock WD (2015) Climate-adjusted provenancing: a strategy for climate-resilient ecological restoration. Frontiers in Ecology and Evolution 3:65. https://doi.org/10.3389/fevo.2015.00065

R Core Team (2022) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/

Reich PB, Tilman D, Isbell F, Mueller K, Hobbie SE, Flynn DFB, Eisenhauer N (2012) Impacts of biodiversity loss escalate through time as redundancy fades. Science 336:589–592. https://doi.org/10.1126/science.1217909

Richardson DM, Hellmann JJ, McLachlan JS, Sax DF, Schwartz MW, Gonzalez P, et al. (2009) Multidimensional evaluation of managed relocation. Proceedings of the National Academy of Sciences 106:9721–9724. https://doi.org/10.1073/pnas.0902327106

Salas-López A, Violle C, Munoz F, Menzel F, Orivel J (2022) Effects of habitat and competition on niche partitioning and community structure in neotropical ants. Frontiers in Ecology and Evolution 10. https://doi.org/10.3389/fevo.2022.863080

Smith MD, Knapp AK (2003) Dominant species maintain ecosystem function with non-random species loss. Ecology Letters 6:509–517. https://doi.org/10.1046/j.1461-0248.2003.00454.x

Stein BA, Glick P, Edelson N, Staudt A (2014) Climate-smart conservation: putting adaption principles into practice. National Wildlife Federation, Washington D.C.

Twardek WM, Taylor JJ, Rytwinski T, Aitken SN, MacDonald AL, Van Bogaert R, Cooke SJ (2023) The application of assisted migration as a climate change adaptation tactic: an evidence map and synthesis. Biological Conservation 280:109932. https://doi.org/10.1016/j.biocon.2023.109932

Urban NA, Swihart RK, Malloy MC, Dunning JB (2012) Improving selection of indicator species when detection is imperfect. Ecological Indicators 15: 188–197. https://doi.org/10.1016/j.ecolind.2011.09.031

USGCRP Wuebbles DJ Fahey DW Hibbard KA 2017 Climate Science Special Report U.S. Global Change Research ProgramWashington, D.C.

Vogler JB, Vukomanovic J (2021) Trends in United States human footprint revealed by new spatial metrics of urbanization and per capita land change. Sustainability 13:12852. https://doi.org/10.3390/su132212852

Wallingford PD, Morelli TL, Allen JM, Beaury EM, Blumenthal DM, Bradley BA, et al. (2020) Adjusting the lens of invasion biology to focus on the impacts of climate-driven range shifts. Nature Climate Change 10: 398–405. https://doi.org/10.1038/s41558-020-0768-2

Whittaker RH (1970) Communities and ecosystems. Macmillan, London

Widrlechner MP, Daly C, Keller M, Kaplan K (2012) Horticultural applications of a newly revised USDA Plant hardiness zone map. HortTechnology 22: 6–19. https://doi.org/10.21273/HORTTECH.22.1.6

Willis SG, Foden W, Baker DJ, Belle E, Burgess ND, Carr JA, et al. (2015) Integrating climate change vulnerability assessments from species distribution models and trait-based approaches. Biological Conservation 190:167–178. https://doi.org/10.1016/j.biocon.2015.05.001

Supporting Information

The following information may be found in the online version of this article:

Supplement S1. R script used to conduct silver maple community analysis.

Table S1. Spreadsheet of common species associated with silver maple plots.

Table S2. Pairwise ADONIS (PERMANOVA) outputs grouped by USDA hardiness zone.

Table S3. Summary of *p*-values for Tukey HSD pairwise comparisons of dispersion between USDA hardiness zones to test for heterogeneity of variance.

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