Identifying candidate plants for climate-smart management of Silver Maple (*Acer saccharinum*) communities

Abstract

Climate change exposes plant communities to a variety of stressors that may require species to relocate to track suitable conditions. For most plants, this process is unlikely to happen on its own due to the rapid speed of climate change coupled with barriers to dispersal. However, limited information is available on candidate species that could be planted to create climate-resilient communities. This study aims to identify species that can be planted to build 'climate-smart' wetland forest communities in the Northeastern United States. We selected Silver Maple (Acer saccharinum) as a species characterizing these communities for its large latitudinal range and unique ability to tolerate flood conditions in wetland communities, which are especially threatened in the Northeast. We used multivariate analyses using 645 plots from comparable plant surveys from state and Federal agencies to test for significant differences between communities across USDA hardiness zones. Our study found that hardiness zones are a significant predictor of differences between forested wetland plant communities. This suggests that forested wetland communities can be maintained with a variety of native plant species as temperatures warm with climate change. From these results, we generated a list of common species associated with multiple hardiness zones that can be used to support climate-informed management of communities.

Introduction

Climate change poses an unprecedented threat to global species diversity (Bellard et al., 2012). Plants with long generation times and short seed dispersal distances are especially threatened by shifts in temperature and precipitation due to their limited mobility, with the majority of species failing to relocate as quickly as the climate is changing (Corlett and Westcott, 2013; Neilson et al., 2005). However, land managers face challenges identifying which species to relocate, especially in the context of maintaining plant community health.

Climate change can increase the vulnerability of native plant communities by increasing the frequency of extreme events such as flooding and drought (Reyer et al., 2012) and altering the ecology of native insects and pathogens (Weed et al., 2013). For example, climate-associated drought has resulted in outbreaks of native mountain pine beetle (*Dendroctonus ponderosae*) and killed conifer species across 1.2 Mha across the southwestern United States (Weed et al., 2013). Warmer winter temperatures have been associated with reduced winter mortality rates in insects and resulting range expansions (Weed et al., 2013). Ultimately, these stressors are likely to cause native biodiversity to degrade over time even if novel invasive species are not introduced.

Maintaining native biodiversity is critical to ecosystem integrity for several reasons. First, under climate change, it is likely that some species will lose large portions of their ranges or go

extinct, causing the ecosystem to lose valuable services (Harrison et al., 2014). Increased biodiversity ensures that functional redundancy exists within ecosystems, meaning that if one species goes extinct, another will be able to take its place (Reich et al., 2012). On a broader scale, biodiversity is important when considering the benefits of interactions between species. For example, some tree species share carbohydrates through mycorrhizal networks during different times of year depending on the needs of either species, providing mutual benefit to both species (Philip et al., 2010). Relocating entire communities in response to climate change rather than individual species helps to ensure that these mutualisms will continue to take place while providing functional redundancy for uncertainties associated with climate change.

Climate-suitable planting, or assisted migration, has been proposed as a strategy to allow plants to relocate in response to climate change, maintaining ecosystem resistance and resilience and mitigating biodiversity loss (Aitken & Whitlock, 2013; Williams & Dumroese, 2013). Hoegh-Guldberg et al. (2008) provide a multistep process for determining when species should be relocated to maximize species survival while minimizing risk. Primary measures include improving conventional conservation practices such as habitat restoration and improving landscape connectivity to allow species to migrate on their own. If this is not possible, it may be necessary to manually relocate species to prevent extinction. Alternatively, if relocating species would be too large of a disturbance to the novel environment, or if no acceptable sites are available, species can be stored as seed until conditions become more favorable. However, little information is available on which species should be involved in assisted migration, or where species should be planted to accomplish this (Williams & Dumroese, 2013).

Floodplain forest communities are one of the most threatened community types in the eastern United States (Kearsley, 1999). These communities are dominated by Silver Maple (*Acer saccharinum*), which is particularly resilient to flooding events. Silver Maple communities were also chosen as a candidate for assisted migration in the Northeast due to their geographic range, which stretches from Mississippi to southern Quebec (Gabriel, 1990). This places the Northeastern United States well within the northern bounds of the species' climate niche, meaning that this region is likely to remain a favorable habitat for Silver Maple as the climate continues to warm. However, species associated with Silver Maple may have narrower suitable climate niches that will require these species to migrate north over time, making it necessary to determine whether associated species from farther south will be better candidates for northern Silver Maple communities under a warmer climate.

Community-level modeling is important to addressing climate-smart planting of Silver Maple communities because it increases the likelihood of preserving biotic interactions between species that may otherwise be lost on an individual level. Examining whole communities also allows us to determine where species associated with Silver Maple will need to be translocated to in the future.

We use USDA hardiness zone, which is defined by the minimum annual temperature in a given region, as a proxy for climate. We selected hardiness zones as an easily accessible (PRISM Climate Group, 2021) climate proxy because extreme minimum temperatures are shown to have

ecological significance in multiple studies (Parker & Abatzoglou, 2016), and are projected to shift under climate change (Hanberry & Fraser, 2019). Therefore, we use hardiness zones as a proxy for future climate conditions as a space for time substitution. Our research seeks to first answer whether Silver Maple communities are different across hardiness zones, and second to determine whether differences in community composition can be used to identify 'climate-smart' species candidates for restoration.

Methods

To investigate differences in Silver Maple communities along a latitudinal gradient, we analyzed an existing dataset synthesizing plant abundance data from several plot-based surveys. We performed analyses using R version 4.1.2 (R Core Team, 2021) and ArcGIS Pro version 2.9.2. We compiled plot-level plant survey data from the National Park Service (NPS), the Bureau of Land Management (BLM), the Forest Inventory & Analysis (FIA), the multi-state North Carolina Vegetation Survey (NCVS), and the National Ecological Observatory Network (NEON) (Petri et al., n.d.). The values extracted from each dataset were longitude, latitude, exotic status (native or introduced), USDA species code (unique species identifier), percent cover, and dataset name. One of the sets of survey data used (NCVS WV) did not include exotic status for the plants surveyed. For this dataset, we generated exotic status using the match() function in R by combining exotic statuses for all species present in other datasets and matching exotic statuses based on USDA species code. We provided exotic statuses manually for the remaining unmatched species by searching for their species code on the USDA PLANTS Database (USDA, 2022). Once all datasets had been combined, we removed rows with missing values for species or location, along with species only identified to genus level whose invasive status was unclear (n = 94507).

We subset the dataset to only include sampling plots containing Silver Maple (USDA species code ACSA2). We uploaded the latitude/longitude associated with each plot on this list to ArcGIS Pro version 2.5.2 along with a grid of hardiness zones downloaded from PRISM Climate Group and spatially joined to determine which plots were associated with specific hardiness zones (PRISM Climate Group, 2021). We exported the output of this spatial join as a CSV and matched it to the list of species in Silver Maple plots based on the plot's unique ID. Sorting species by zone indicated that only three plots were associated with hardiness zone 8. Due to this low sample size, we excluded all data from zone 8, and focused our study on Silver Maple plots between hardiness zone 3-7.

Ultimately, our goal was to recommend common species for climate-suitable planting because common species are more likely to successfully establish than rare species. We defined common species as those that appear in more than 10% of plots in their respective hardiness zones and have a mean percent cover of 3% or more in plots where they appear based on the rare species threshold used in Laca et al. (2016). This resulted in a final dataset composed of 10052 records of 197 unique species.

We used non-metric multidimensional scaling (NMDS) to visualize the similarity of Silver Maple community composition based on hardiness zone. NMDS ordination is a statistical method used in ecology to visualize how closely communities associate with one another (Addo-Fordjour et al., 2021; Lemieux-Labonte et al., 2016; Crowther et al., 2013) We conducted the ordination based on the Bray-Curtis dissimilarity index using the metaMDS function in the *vegan* software package version 2.5-7 in R (Oksanen et al., 2020). We produced NMDS plots using *ggplot2* version 3.3.5 (Wickham, 2016). In the context of community ecology, NMDS treats the abundance of all species within a set of plots as a unique dimension, and uses these abundance values to calculate the dissimilarity of plots as a matrix. These matrix values are then used to calculate distances between points on a two or three-dimensional plot, transforming data with an extremely large number of dimensions into a few easily visible dimensions with points representing plots or species. Clusters in data can then be isolated to find plots and species that are closely associated with one another, potentially constituting a community (Laca et al., 2016).

We used the ANOSIM function from version 2.5-7 of the *vegan* package to test for significant differences in community composition across the five hardiness zones (Okansen et al., 2020). We conducted pairwise differences through a PERMANOVA test (n = 999) using the pairwise.adonis2 function (Martinez, 2020). Because PERMANOVA can be sensitive to unequal variance between groups, causing the test to misreport within-group variance as among-group variance, we also conducted a PERMDISP test for homogeneity of variance between hardiness zones using the betadisper() function in version 2.5-7 of the *vegan* package. The null hypothesis of this test is that dispersion is the same across all groups. We set the significance level as p < 0.05.

We used the multipatt function from version 1.7.9 of the *indicspecies* package (De Cáceres & Legendre, 2009) to determine which species are significant indicators of each hardiness zone. This analysis computes an indicator value (IndVal) for each species that is based on two metrics: an A-value and B-value. The A-value provides the probability of a species appearing given a particular group. B-value provides the probability that a species belongs to a particular group provided that the species is present. In the context of our study, we defined groups as hardiness zones. Therefore, the A-value would represent the likelihood of a plant being found in a randomly selected plot within a hardiness zone. We selected candidate species for climate-smart planting based on those with the highest A-value in each hardiness zone category.

Results

Overall, our dataset included a total of 645 plots, 197 unique species, and 10,052 data points across six hardiness zones (Table 1) in the northeastern and east central United States (Figure 1). The majority (65%) of plots were located in hardiness zone 6 (Table 1), which ranges from approximately 36 to 41 degrees N in the eastern United states. Multivariate analysis showed a small but significant difference between Silver Maple community plots based on hardiness zones (ANOSIM, R = 0.141, P = 0.001, n = 999, Figure 2). This difference can be seen

in the NMDS plot (Figure 2), where a general linear trend occurs in separation between zones. The highest difference occurs between zones 3 and 7, which have no overlap on the plot. Pairwise ADONIS (PERMANOVA) results indicated that all hardiness zones had significantly different community assemblages from one another (Table 2). Results of multivariate dispersion analyses showed evidence for heterogeneity among hardiness zones (PERMDISP, F = 4.594, p = 0.001) and post-hoc Tukey HSD tests revealed significant differences in dispersion for pairwise comparisons of zones 3 and 4 (Tukey HSD p = 0.003), zones 3 and 5 (Tukey HSD p = 0.020), and zones 3 and 6 (Tukey HSD p = 0.003). Therefore, some of the differences in community composition between these hardiness zone pairs may be attributed to dispersion effects.

The indicator species analysis showed that 77% (152/197) of the common species observed in sampling plots were significantly associated with specific hardiness zones. Of these species, 66% (100/152) were associated with a single hardiness zone, while the remainder were associated with two or more zones (Table 3). The number of species associated with a single hardiness zone varied widely between zones, with 47 species associated with zone 7 and only two species associated with zone 5. The list of species identified as indicators of one or more hardiness zones is available in Appendix 1.

Zone	Plots	Species	Observations
3	12	79	272
4	53	129	720
5	77	139	1135
6	422	165	5742
7	81	143	2183

Table 1. Summary of dataset showing number of plots, species, and plant observations for hardiness zones 3-7.

rowth zone comparison	Df	F	\mathbb{R}^2	Р
Growai zone comparison	(Zone, residuals)			
4 vs 3	1, 63	4.385	0.06507	0.001
4 vs 5	1, 128	2.763	0.02113	0.001
4 vs 6	1, 473	7.664	0.01595	0.001
4 vs 7	1, 132	7.352	0.05276	0.001
3 vs 5	1, 87	5.345	0.05788	0.001
3 vs 6	1, 432	5.815	0.01328	0.001
3 vs 7	1, 91	6.8635	0.07013	0.001
5 vs 6	1, 497	5.8433	0.01162	0.001
5 vs 7	1, 156	6.4093	0.03946	0.001
6 vs 7	1, 501	6.3668	0.01255	0.001

Table 2. Summary of PERMANOVA test showing pairwise differences in plant community composition between hardiness zones in the eastern United States.

Zone	Unique spp.	Shared spp.	Specific to zone
3	40	18	4
4	7	36	1
5	2	30	0
6	4	9	3
7	47	29	6

Table 3. Multipatt output summary categorized by indicator species unique to individual zones, indicator species shared across hardiness zones, and species that

occur in only one zone.



Figure 1. Geographic distribution of study sites (n=645) superimposed on hardiness zones. Study sites are represented by points.



Figure 2. Non-metric Multidimensional Scaling ordination plot comparing native plant community composition from vegetation plots across hardiness zones 3-7 in the eastern United States.

Discussion

Our study indicates a significant correlation between hardiness zones and Silver Maple community composition for Zones 3-7 (Table 2). This suggests that community assemblages are significantly different between hardiness zones. Given that hardiness zones within the United States are expected to shift by an average of one numeric value over the next several decades (Hanberry & Fraser, 2019), the species driving the differences between hardiness zones (Appendix 1) should be monitored as potential candidates for climate-smart migration in Silver Maple-associated communities. This is especially applicable to species that define a single hardiness zone, which may not have stable populations in riparian communities north of their current hardiness zone.

A comparison of differences in species communities between hardiness zones (PERMDISP test) indicated that Zone 3 had significant differences in dispersion compared to zones 4, 5, and 6, which may have caused the significant difference in community composition to be attributed to dispersion effects for these zones. However, the ordination indicates that Zone 3 communities have low overlap with Zones 5 and 6 (Figure 2), meaning that it is still likely that these zones are significantly different beyond dispersion effects.

Shifts in hardiness zone are projected to occur over the course of several decades, with Hanberry and Fraser (2019) anticipating a hardiness zone shift of one numeric value by 2070 to 2099. On a short-term basis, short-lived species should still be planted within their current hardiness zones. Young trees are also especially vulnerable to extreme cold events (Martín-Alcón et al., 2016), meaning that even long-lived species may benefit from waiting before engaging directly in climate-related migration. Therefore, research over the next few years should focus on monitoring how plants are responding to changes in climate within their current ranges, as well as whether species are already moving themselves at the rate needed to stay within their ideal climate envelopes. If species are able to adapt or migrate without human assistance, these species should not be targeted for human-assisted migration. Species that show signs of population decline under climate change should be assessed for feasibility of relocation over the next few decades. Using the framework outlined in Hoegh-Guldberg et al. (2008), species can be evaluated as candidates for assisted migration based on their likelihood of surviving novel environments, potential benefits, and economic feasibility. Species that are not currently feasible for assisted migration can be stored as seeds or propagules until more suitable conditions are available (Hoegh-Guldberg et al., 2008).

We can illustrate the application of study for management by using a smaller area, such as the state of Massachusetts, as a case study. Massachusetts is currently predominantly located in hardiness zone 5, which our study shows has only two unique indicator species . However, 30 additional species define zone 5 as well as other neighboring zones, meaning that a total of 32 species are available to landowners as planting recommendations for the state's current climate. To ensure that plants survive the transition between hardiness zones, it may be best to focus on species that define zone 5 as well as warmer zones, meaning that they will be likely to do well under the current climate as well as future climate conditions. After continued monitoring over the next few decades, landowners can shift focus to planting species that define zone 6.

Selecting species that define the current hardiness zone as well as warmer hardiness zones may be especially useful candidates for climate-smart migration because they can also be used as candidate taxa for assisted migration of plant genomes to move warm-adapted genes of locally present species rather than new species from warmer communities. This can be beneficial to communities because it maintains competitive interactions and strongly limits the risk of novel interactions that can lead to invasion (Wallingford et al., 2020). In a study conducted by Wilczek et al. (2014), field experiments indicated that warm-adapted genotypes of *Arabidopsis thaliana* consistently outperformed native genotypes in four common garden experiments on a north-south gradient throughout Europe. Therefore, there is evidence to suggest that migration of warm-adapted populations of existing plant species could boost population fitness under a warming climate even if the novel genotypes do not carry the same adaptations to other local conditions.

Community structure and diversity are increasingly threatened by changes in the environment such as climate, and changing ecology may cause new detrimental relationships among ecological communities, making it necessary to select for species that are likely to

survive the migration process. A large proportion of assisted migration experiments focused on restoring populations of rare species have failed (Godefroid et al., 2011), meaning that it may be more reasonable for land managers to focus on planting common species that are more likely to survive.

While common species may be more likely to survive, the risks associated with planting common species should still be considered by land managers. Given the unprecedented nature of climate-related assisted migration, it is currently unknown whether species will have detrimental impacts after migration because of the potential for novel interactions between species (Wallingford et al., 2020). This is especially concerning given the differential survival rate of relocated common species in comparison to rare species (Wang et al. 2019; Godefroid et al., 2011; Wilczek et al., 2014). In the past, introductions of other common weedy species near the species' original native range have had negative impacts. For example, Black Locust (Robinia pseudoacacia), which is native to the Appalachian mountains in the eastern United States, has become invasive in the neighboring state of Indiana in disturbed oak savanna communities (Peloquin & Hiebert, 1999). Black Locust invasion is facilitated by its ability to fix nitrogen, which often acts as a limiting nutrient in plant communities, as well as its ability to rapidly multiply through root suckers. When Black Locust is introduced to a community, it can significantly reduce species richness by outcompeting other native species and providing a competitive advantage to nitrogen-responsive species, which can also expand in the presence of Black Locust. This example suggests that while common species may have better survival rates than rare species following assisted migration, adding novel species should be done with caution, and communities should be monitored for novel interactions following species introduction.

Beyond creating the potential for new invasive species, relocating plants increases the risk of transporting foreign pathogens. Crossing genetically distant populations can also result in outbreeding depression, and the introduction of locally maladaptive alleles to the population (Aitken & Whitlock, 2013). Given the potential risks of this approach, land managers need to know which species will support community structure and function under future climate conditions to ensure community survival.

Despite the inherent risks associated with climate-related assisted migration, several criteria can be used to assess the risk of a species dominating a new environment. Species that are generalists, stress-tolerant, and have rapid growth and reproductive rates are considered much more likely to dominate ecosystems than species that lack these traits (Wallingford et al., 2020). However, migrating species differ from invasive species because they may have competitors and predators in their new range that match those found in their original range, providing a mechanism to regulate population growth in weedy range-shifting species (Wallingford et al., 2020). In the event that relocated species do not have competitors and predators with broad enough ranges to provide population control, relocating entire communities provides additional opportunities to retain competitive interactions and keep individual species populations under control.

Further investigation into climate-smart migration is still necessary to ensure that migration efforts are effective. Current literature models range shifts of plant species under climate change in isolation (Iverson et al., 2007; Pedlar et al., 2012; Williams & Dumroese, 2013), but little research has been done to date on climate-related shifts in the context of specific plant communities. For example, Iverson et al. (2007) looks at range shift models in multiple individual plant species, but not the community as a whole. On the opposite end of the spectrum, Alexander et al. (2017) uses models to examine overarching plant community dynamics in response to climate change, but does not focus on specific communities of plants. Therefore, further research is needed to address the knowledge gap of how specific plant communities will need to be managed to respond to climate change. Adopting a community-based focus may also help to develop different monitoring and management recommendations for single-taxa and community-level migration.

Conclusion

Climate change poses a threat to plant communities by altering temperature and precipitation regimes to differ from those plants have evolved to tolerate. While many plants may migrate or adapt in response to these changes, climate change has been shown to outpace the rate of plant migration in forested communities (Knott et al., 2020). Therefore, human intervention will be needed to ensure that plants are able to track their ideal climate envelopes. Our research indicates that Silver Maple-associated communities differ between hardiness zones, and that different species serve as community indicators across the latitudinal range of Silver Maple. We recommend that species defining single zones and species be monitored for population decline over the next few decades to select potential candidates for assisted migration. We also suggest that species that define the current and future hardiness zones of a given area be recommended for planting to ensure that candidate species survive the current climate and tolerate future climates.

Acknowledgements

I would like to thank Dr. Annette Evans, Dr. Bethany Bradley, Audrey Barker Plotkin, Carrie Brown-Lima, Dr. Scott Auerbach, and the UMass Amherst Spatial Ecology Lab for supporting me through the development of this project.

Appendix

Appendix 1

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