

Plant Species Composition and Interactions within Communities Invaded by *Persicaria perfoliata* (Polygonaceae)

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Abstract - *Persicaria perfoliata* (Mile-a-Minute Weed), an invasive vine, forms monocultural patches of various sizes within infested landscapes among patches also containing other plants. We compared the species composition of *P. perfoliata*-dominated patches and adjacent nondominated patches in 2 topographically homogeneous sites using 20 paired plots, nonmetric multidimensional scaling, multi-response permutation procedure, and indicator species analyses. Richness and diversity were lower in the *P. perfoliata*-dominated patches but both patch types had uncommon native plants present. The patch types differed significantly in composition, and the nondominated patches were dominated by another nonnative invader, *Microstegium vimineum* (Japanese Stiltgrass), or a native weed, *Ambrosia artemisiifolia* (Common Ragweed). Documenting potentially interacting native and exotic species within an invaded landscape will help predict likely restoration success in response to targeted nonnative-invasive plant removal.

Introduction

Biological invasions of nonnative plants negatively affect the diversity and abundance of native plants (Flory and Clay 2010a, Hejda et al. 2009, Tilman 1999), vertebrates (Horncastle et al. 2005, Nelson et al. 2017), invertebrates (Graves and Shapiro 2003, Morón et al. 2009), ecological communities (Kohli et al. 2004, Richardson et al. 1989), and ecosystem processes (Gordon 1998, Richardson et al. 2007, Standish et al. 2004). Consequently, such impacts may result in excessive management costs (Mason and French 2007). Wilcove et al. (1998) estimated that 57% of the threatened or endangered plants in the US are imperiled by alien plants, and Pimentel et al. (2001) estimated that the US spends approximately \$34 billion per year to control weeds of croplands and pastures and another \$145 million per year to control nonnative invasive plants in natural areas. While a rich literature base exists on certain individual invasive exotic plant species, the scientific community is far from understanding their role within a community or ecosystem context (Kuebbing et al. 2013).

Understanding how native plants, specifically aggressive early successional species, and other nonnative plants interact with associated invasive plants may help us predict the recovery trajectory after the removal of targeted invasive plants. Invasive nonnative plants may be more competitive than native

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species (Maron and Marler 2008), but there is evidence that some invasive plants may be opportunists but not superior competitors (Vilá and Weiner 2004). It is important to differentiate between direct species competition and early opportunistic colonization that takes place immediately after a disturbance. Vilá and Weiner (2004) conducted a meta-analysis on the available literature on competition and found that there was a 47% reduction in biomass of native species caused by direct competition from nonnative species and an 18% reduction in biomass of nonnative species caused by direct competition from a native species. They note, however, that the studies may be biased towards positive outcomes and unusually weak native competitors. In addition, the patches with one or more dominant invasive species in severely invaded areas may be impacted by how multiple invasive species interact with each other in addition to how they interact with any remaining native species over time (Kuebbing et al. 2013). For example, the native *Robinia pseudoacacia* L. (Black Locust) seedlings facilitate the growth of *Ailanthus altissima* (Mill.) Swingle (Tree of Heaven) seedlings likely via nitrogen fixation, but at later stages of growth, interspecific competition results in Tree of Heaven being the stronger competitor. (Nilsen et al. 2018). Pairing aggressive native species that share similar life-history traits with invasive plants has successfully shown some suppression of the nonnative invasive. Examples include the native *Elymus elymoides* Raf. (Squirreltail) and nonnative *Bromus tectorum* L. (Cheat Grass) (Booth et al. 2003) and the native *Gaillardia pulchella* Foug. (Indian Blanket) and the nonnative *Rapistrum rugosum* (L.) All. (Turnipweed) (Simmons 2005). Many invaded sites also suffer from perpetual disturbances, such as deer herbivory or nonnative earthworms, that may enable invasion opportunities or allow them to persist. Any native species present are also responding to these same disturbances (Knight et al. 2009, Whitfeld et al. 2014).

Highly invaded sites that have been infested by a dominant nonnative plant for several years often are characterized by a mosaic of patches of various sizes and abundances of that dominant invasive plant (Kartzinel et al. 2015, Petrovskaya et al. 2017). If this patchy mosaic occurs in a physiographically homogeneous environment, one may hypothesize that patches lacking in the dominant invader include plant species that make local spread by the invader more difficult; these species could include native species, exotic species, or other exotic invaders. More importantly, these patches may serve as a refuge for less-abundant native species and ensure their recovery after removal of the dominant invasive plant. Determining the species composition of patches with a low abundance of a dominant invader adjacent to patches with a high abundance of the dominant invader may provide information about competitive species that could exclude the invader or coexist with the invader especially in response to the invaders' managed reduced dominance.

This study focuses on the invasive *Persicaria perfoliata* (L.) H. Gross (Mile-a-Minute Weed, hereafter abbreviated as MAM; Polygonaceae). MAM is an annual vine with characteristic triangular leaves, ocrea surrounding the stems, and small recurved prickles. This weed can grow up to 6 m in 1 growing season (Okay 1997) and forms various patch sizes and shapes. This plant has invaded at least 15 states of the northeastern and mid-Atlantic US (EDDMaps 2020; Hough-Goldstein et al.

2012, 2015; Kumar and DiTommaso 2005). Although MAM is typically found in low abundance along disturbed riparian areas in Asia (Hough-Goldstein et al. 2015, Hyatt and Akari 2006), it also invades disturbed areas (i.e., construction site, roadsides, and utility rights-of-ways) and recently harvested forests in the US (Cusick and Ortt 1987; Hough-Goldstein et al. 2008, 2015). In its invaded region, it suppresses native flora, decreases plant diversity across landscapes, and is a nuisance to humans due to its sharp recurved prickles and the formation of impenetrable areas made up of multiple large and small patches (Hough-Goldstein et al. 2015, Oliver 1997). Its tendency to overtop other plants and produce masses of intertwining foliage makes these areas appear as monocultures, though a closer look reveals the presence of other species. These infestations also leave a notable thatch of dead plant material each year that slowly decomposes but, if edges are mapped each year, can be used to delineate the existence of previous year's patch locations as well as potentially estimate spread rates as patches possibly increase in size. MAM is a prolific producer of seeds, which are dispersed by gravity, water, birds, and deer in late summer and early fall, can be viable for at least 6 years in seed banks, and may germinate under the previous year's plants, with an average density within MAM patches of 400–1000 seeds per m² and most seed germinating within the first 2 years (Hough-Goldstein et al. 2008, 2015; Okay 1997), ensuring a self-perpetuating population. Thus, any control measures of MAM will likely require multiple years of removal or possible use of pre-emergent herbicides and long-term monitoring.

The objective of this study was to compare the species composition of MAM-dominated (henceforth “dominated”) patches to adjacent patches where MAM was not dominant (henceforth “nondominated”) within an environmentally homogeneous site that has been infested with MAM for at least 5 years. We hypothesized that dominated patches would have fewer native species and be less diverse than the nondominated patches and that the nondominated patches would be dominated instead by 1 or more native species or another invasive plant. Information about these native and other nonnative species may inform management decisions about future removal of MAM, including biocontrol efforts. This information will enable land managers to assess the need for active restoration including planting native species and predict the spread of other nonnative species in response to removing MAM.

Methods

Site description

Our study took place at 2 open, previously forested (harvested at least 60 years ago) sites in southwestern Pennsylvania with infestations of MAM. These privately owned sites were located near Jefferson (39°55'10.14"N, 80°2'15.01"W) and Rogersville (39°53'23.55"N, 80°16'55.61"W) and were 848 m² and 315 m² in size, respectively. Both sites had adjacent forest patches dominated by *Quercus rubra* L. (Northern Red Oak), *Carya* spp. (hickory), and *Acer saccharum* Marshall (Sugar Maple) with some *Acer negundo* L. (Boxelder) and *Ulmus rubra* Muhl. (Red Elm). In the Jefferson site, chemical control with a broad-spectrum herbicide

(Roundup®; Bayer, Leverkusen, Germany) was applied on the MAM only once in 2010 and did not control MAM (hence, its continued dominance). Both infested sites have also had an uncertain number (between 500 and 3000) of *Rhinoncomimus latipes* Korotyaev (Mile-a-minute Weevil, Coleoptera: Curculionidae) released as a biocontrol in 2015 and 2017 in early summer in the Rogersville site, and in 2018 in the Jefferson site, but also with limited impact thus far. Though none were seen during sampling, it is possible that some weevils were still present. At the time of this study, the open, relatively flat, once-forested areas of both sites were infested with MAM. Our study focused only on the open, invaded areas that shared the same topography (flat, e.g., <10% slope and an elevation of about 380 m), similar soils (Guernsey-Dormont-Culleoka Association, which has moderately well-drained, deep soils formed from weathered limestone, sandstone and shale; considered one of the better soils for farming; USDA, NRCS 2020b; Seibert et al. 1983), and similar disturbance histories (aside from the herbicide application at the Jefferson site).

Vegetation sampling

We defined a MAM patch as any area with $\geq 75\%$ cover of MAM thatch from previous years. We selected patches from 3 patch sizes ($>1\text{ m}^2$ and $<10\text{ m}^2$, $\geq 10\text{ m}^2$ and $<30\text{ m}^2$, and $\geq 30\text{ m}^2$) using the remaining MAM thatch from previous years determined from aerial photography taken with an unmanned aerial vehicle (DJI Phantom 3 Advanced; SZ DJI Technology Co., Ltd., Shenzhen, China) and ground-truthed. We fit one 1-m^2 circular plot for potential vegetation sampling within patches that were $<10\text{ m}^2$, two 1-m^2 plots in patches $\geq 10\text{ m}^2$ and $<30\text{ m}^2$, and three 1-m^2 plots in patches $\geq 30\text{ m}^2$ (Fig. 1). We randomly selected a total of 10 plots from the 26 delineated infested patches in the Jefferson site and the 28 delineated infested patches in the Rogersville site. We paired an additional 10 plots not

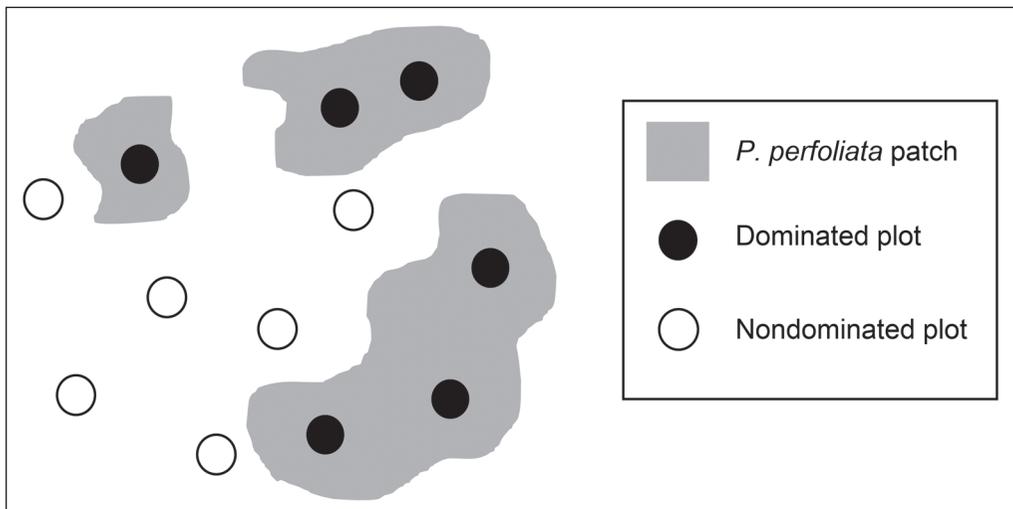


Figure 1. A schematic diagram of dominated patches of *Persicaria perfoliata* (Mile-a-Minute Weed), of various sizes for selecting plots for vegetation sampling. We randomly selected one 1-m^2 circular plot within a patch of $<10\text{ m}^2$, two 1-m^2 plots within patches $\geq 10\text{ m}^2$ and $<30\text{ m}^2$, and three 1-m^2 plots for $\geq 30\text{ m}^2$.

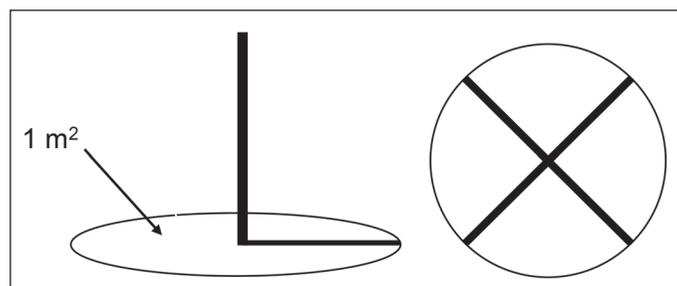
dominated by MAM (e.g., adjacent—within 5 m—but outside of the dominated patch) with these selected plots. The nondominated patches were located in the background matrix and, because the paired sampled plots were at the same frequency and adjacent to the infested plots, they were no more likely to experience edge effects (Fig. 1). We sampled the 20 plots at each of the 2 sites in late June and revisited them in early August in 2019 for some species confirmations. Within each 1-m² plot, we created 4 quadrants (Fig. 2). Within each quadrant, we visually estimated percent cover of each woody tree seedling (less than 1 m in height) rooted in the plot and every shrub, herbaceous, and vine species rooted or with vegetation hanging within the plot boundary (Huebner 2007). These open areas had few if any saplings or trees. We averaged the percent cover of the 4 quadrants and determined frequency (i.e., the number of quadrants containing each species) for each species for each plot. We then averaged the percent cover and frequency values to calculate an importance value (IV) for each species and relativized the IVs by dividing each species IV by the sum of all species IVs. Each plant in the plots was vouchered and identified to species when possible, otherwise to genus. Species nomenclature followed Gleason and Cronquist (1993) and Rhoads and Block (2000), with final accepted names defined by the Integrated Taxonomic Information System (ITIS 2020). We defined species nativity/origin using the USDA PLANTS database (USDA, NRCS 2020a).

Data analyses

In order to evaluate potential site effects, we determined differences between dominated and nondominated plots by analyzing each site separately as well as in combination. In addition, we organized data sets such that MAM percent cover was included or excluded from the analyses, but only the latter is presented herein. Because we already knew the selected dominated plots would show the highest MAM percent cover, the relative abundances of other species present were more evident by removing MAM. Nonetheless, when MAM was included, the other species showed the same rankings in abundance. Because we also did not want to misleadingly increase richness/diversity of the dominated plots with MAM inclusion, we presented only the analysis excluding MAM. We calculated plant species richness, diversity (Shannon–Weiner), and evenness using PC-ORD 7 (McCune and Mefford 2016).

We used nonmetric multidimensional scaling (NMS) and indicator species analysis (ISA) (PC-ORD 7; Kruskal 1964, McCune and Grace 2002) to evaluate

Figure 2. A schematic diagram of a 1-m² plot. We established 4 quadrants within each 1-m² plot and estimated plant cover visually.



plant composition between the dominated and nondominated plots both within site and with sites combined. NMS is a multivariate ordination method best suited for data that may be nonnormal. Plant responses to environment are often non-linear, making NMS an ordination method of choice for many plant ecologists. ISA uses the proportional abundance and frequency of a particular species within 1 group compared to its abundance and frequency in all groups being compared. A perfect indicator (highest ranking) would always be present in a group and not found in any other group (Dufrêne and Legendre 1997). The NMS analyses consisted of 500 real runs, 500 iterations, with a random starting configuration, using a Sorénson (Bray–Curtis) distance measure (PC-ORD 7; McCune and Mefford 2016). To minimize the noise in our dataset with many zeros, we conducted Beals smoothing (Beals 1984) before the analyses. We evaluated data with and without the Beals smoothing, recognizing weaknesses associated with Beals smoothing in that it may produce reliable trends even from a series of random numbers (De Cáceres and Legendre 2008, McCune and Grace 2002).

We used a multi-response permutation procedure (MRPP) also with a Sorénson distance measure to compare the dominated and nondominated plots. These MRPP comparisons were conducted both within each site and with sites combined as well as with inclusion and exclusion of MAM cover (though we present only the exclusion data) (PC-ORD 7; McCune and Mefford 2016). MRPP is a method providing a nonparametric multivariate test of differences between 2 or more groups, which makes no distributional assumptions (e.g., normality and homogeneity; McCune and Grace 2002).

We used analysis of variance (two-way ANOVA; Proc GLM, SAS 9.4; SAS Institute, Inc. 2013) to test for differences in species richness, diversity, and evenness between the dominated plots and nondominated plots. Data met normality and homogeneity assumptions. We made multiple comparisons, including site interactions, with least-squares means and a Tukey adjustment with $\alpha = 0.05$ (SAS 9.4; SAS Institute, Inc. 2013). Tests for significant interactions between site and plot type were included because we wanted to confirm one site was not more likely to be invaded by MAM than the other site, which then could affect the relationship between plot type and the dependent variables.

Results

Species composition

There were 36 and 26 species at the Jefferson and Rogersville sites, respectively, and 54 different species for the combined dataset, with only 8 species common between the sites (for a list of all plant species present at the 2 sites, see supplemental Table S1, available online at <https://www.eaglehill.us/NENAonline/suppl-files/n28-3-N1883-Huebner-s1>, and, for BioOne subscribers, at <https://dx.doi.org/10.1656/N1883.s1>). At the Jefferson site, *Microstegium vimineum* (Trin.) A. Camus (Japanese Stiltgrass), *Persicaria longiseta* (Bruijn) Kitag. (Oriental Lady's Thumb), *Impatiens capensis* Meerb. (Orange Jewelweed), and *Pilea pumila* (L.) A. Gray (Clearweed) were the species with the highest IV for both the

dominated and nondominated plots (Table 1). In the Rogersville site, *Celastrus orbiculatus* Thunb. (Oriental Bittersweet), *Ambrosia artemisiifolia* L. (Common Ragweed), *Oxalis stricta* L. (Common Woodsorrel), and *Acalypha rhomboidea* Raf. (Three-seeded Mercury) were the species with highest IV in the dominated plots, while Common Ragweed, Oriental Bittersweet, Common Woodsorrel, and *Trillium pretense* L. (Red Clover) were the species with the highest IV in the nondominated plots (Table 1). Of all 54 species, including MAM, at both sites, 45 species (83%) were native to the region and 9 species (17%) were non-native.

The most stable NMS ordination for the Beals-smoothed combined data was a two-dimensional solution that had a final stress value of 5.9 (5–10 represents a good ordination with no real risk of false inferences; Clarke 1993) and a final instability value of 0.0 (stable) after 500 iterations (Fig. 3). Although the original combined dataset without Beals smoothing had a final stress value of 4.7 with identical options, only a single-dimensional solution was possible. The two-dimensional ordination was dominated by plots from the Jefferson site on the right, and plots from the Rogersville site on the left showing less dissimilarity between dominated and nondominated plots (Fig. 3). The individual-site species compositions were evaluated separately with Beals smoothing, because the NMS ordination of the original non-smoothed data from each site was too unstable (final stress > 40) with a one-dimensional solution. The most stable NMS ordination for the Jefferson and Rogersville sites with the Beals-smoothed dataset was

Table 1. Rank of relative importance values (IV) of all other species in plots dominated by *Persicaria perfoliata* (Mile-a-Minute Weed) and in nondominated plots.

	Rank	Dominated plots	IV	Nondominated plots	IV
Jefferson	1	<i>Microstegium vimineum</i>	3.568	<i>Microstegium vimineum</i>	3.741
	2	<i>Persicaria longiseta</i>	0.651	<i>Persicaria longiseta</i>	0.510
	3	<i>Impatiens capensis</i>	0.535	<i>Impatiens capensis</i>	0.462
	4	<i>Pilea pumila</i>	0.341	<i>Pilea pumila</i>	0.435
	5	<i>Asclepias syriaca</i>	0.183	<i>Rumex obtusifolius</i>	0.380
	6	<i>Poa saltuensis</i>	0.165	<i>Muhlenbergia schreberi</i>	0.258
	7	<i>Fallopia scandens</i>	0.142	<i>Rosa multiflora</i>	0.243
	8	<i>Ageratina altissima</i>	0.129	<i>Vitis vulpina</i>	0.238
	9	<i>Rosa multiflora</i>	0.111	<i>Viola sororia</i>	0.229
	10	<i>Vitis sp.</i>	0.073	<i>Ageratina altissima</i>	0.228
Rogersville	1	<i>Celastrus orbiculatus</i>	2.556	<i>Ambrosia artemisiifolia</i>	2.116
	2	<i>Ambrosia artemisiifolia</i>	0.910	<i>Celastrus orbiculatus</i>	1.681
	3	<i>Oxalis stricta</i>	0.903	<i>Oxalis stricta</i>	1.172
	4	<i>Acalypha rhomboidea</i>	0.684	<i>Trifolium pretense</i>	0.655
	5	<i>Erechtites hieraciiifolius</i>	0.542	<i>Erechtites hieraciiifolius</i>	0.640
	6	<i>Trifolium pratense</i>	0.315	<i>Acalypha rhomboidea</i>	0.518
	7	<i>Clematis virginiana</i>	0.177	<i>Viola sororia</i>	0.386
	8	<i>Viola sororia</i>	0.162	<i>Clinopodium vulgare</i>	0.180
	9	<i>Lactuca canadensis</i>	0.152	<i>Conyza canadensis</i>	0.154
	10	<i>Bidens frondosa</i>	0.083	<i>Rubus pensilvanicus</i>	0.150

a two-dimensional solution for each site (Jefferson site: final stress = 8.1, final instability < 0.000001 [stable]; Rogersville site: final stress = 7.2, final instability < 0.000001 [stable]; Fig. 4), showing a separation between the dominated and nondominated plots within each site.

MRPP analysis indicated that plant species compositions of the dominated and nondominated plots were statistically different, but with stronger differences

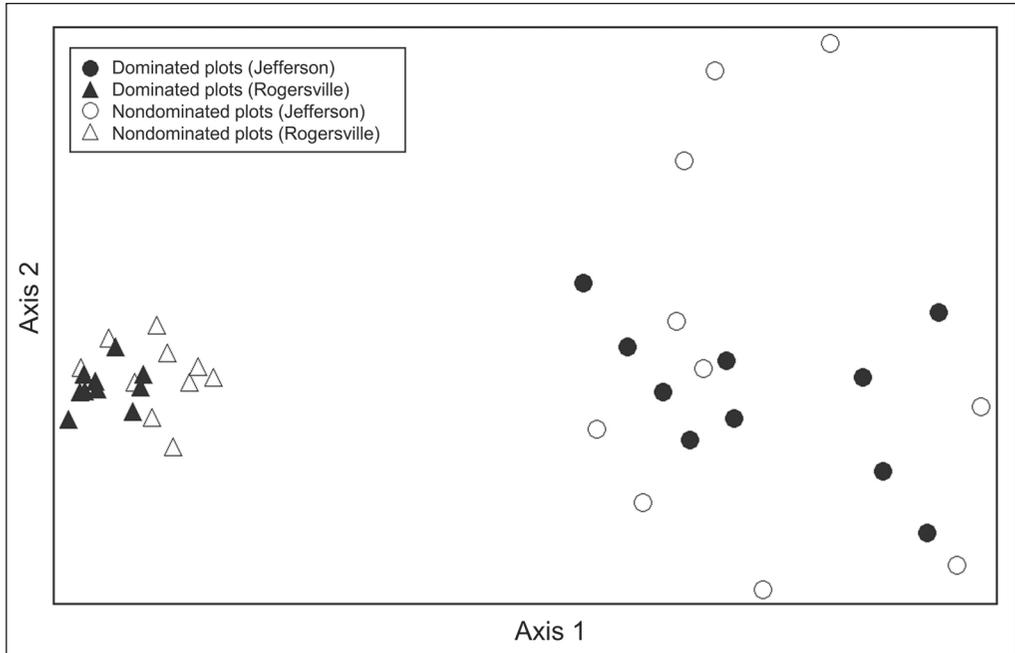


Figure 3. A stable two-dimensional nonmetric multidimensional scaling ordination of the combined sites using Beals-smoothed data grouped by sites ($P = 0.004$, 250 real and 250 randomized run, Sorénsen distance measure).

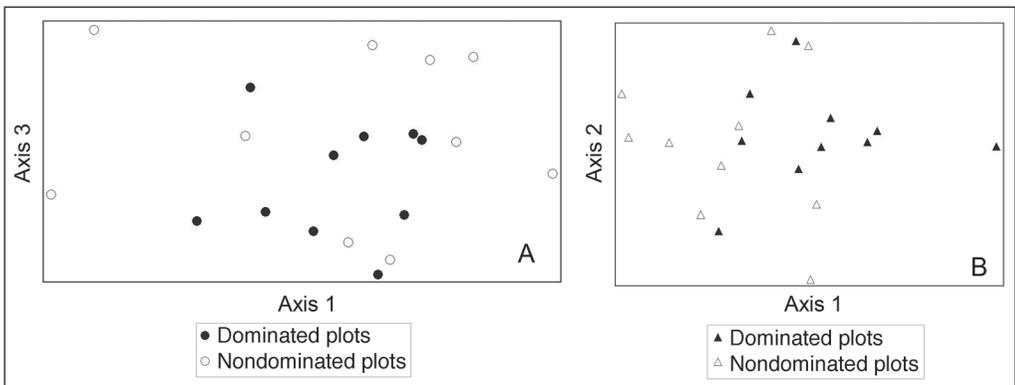


Figure 4. A stable two-dimensional nonmetric multidimensional scaling ordination for each of the 2 sites (A: Jefferson, B: Rogersville) using Beals-smoothed data grouped by plot type ($P = 0.004$, 250 real and 250 randomized run, Sorénsen distance measure; Rogersville: $P = 0.004$, 250 real and 250 randomized run, Sorénsen distance measure).

between the sites than between the plot types (Table 2). The indicator-species analysis showed that a single species, Japanese Stiltgrass, was an indicator species of the Jefferson site and 7 species were indicator species for the Rogersville site, with Oriental Bittersweet being the most important. The plot types within the Jefferson site did not have indicator species because they shared the same dominant species with similar abundances. Within the Rogersville site, the nondominated plots had a native indicator species, Common Ragweed, whereas the dominated plots had the nonnative invasive Oriental Bittersweet as the indicator species (Table 3).

Species richness, diversity, and evenness

The average species richness and diversity differed significantly between sites ($F = 13.88$, $P = 0.0007$ and $F = 15.29$, $P = 0.0004$, respectively) and among plot types ($F = 11.87$, $P = 0.0015$ and $F = 12.48$, $P = 0.0012$, respectively) with no significant interaction between site and plot type. A comparison of the combined plot types among sites with a Tukey adjustment for multiple comparisons showed that richness of dominated plots at the Jefferson site, where Japanese Stiltgrass was abundant, was significantly lower than that of the nondominated plots at the Rogersville site (Fig. 5). Diversity of the dominated plots at the Jefferson site was significantly lower than that of the nondominated plots in both the Jefferson and Rogersville sites as well as the dominated plots of the Rogersville site. Evenness did not differ between dominated and nondominated plots at either site (Fig. 5), indicating the nondominated plots also had a dominant species, a nonnative species

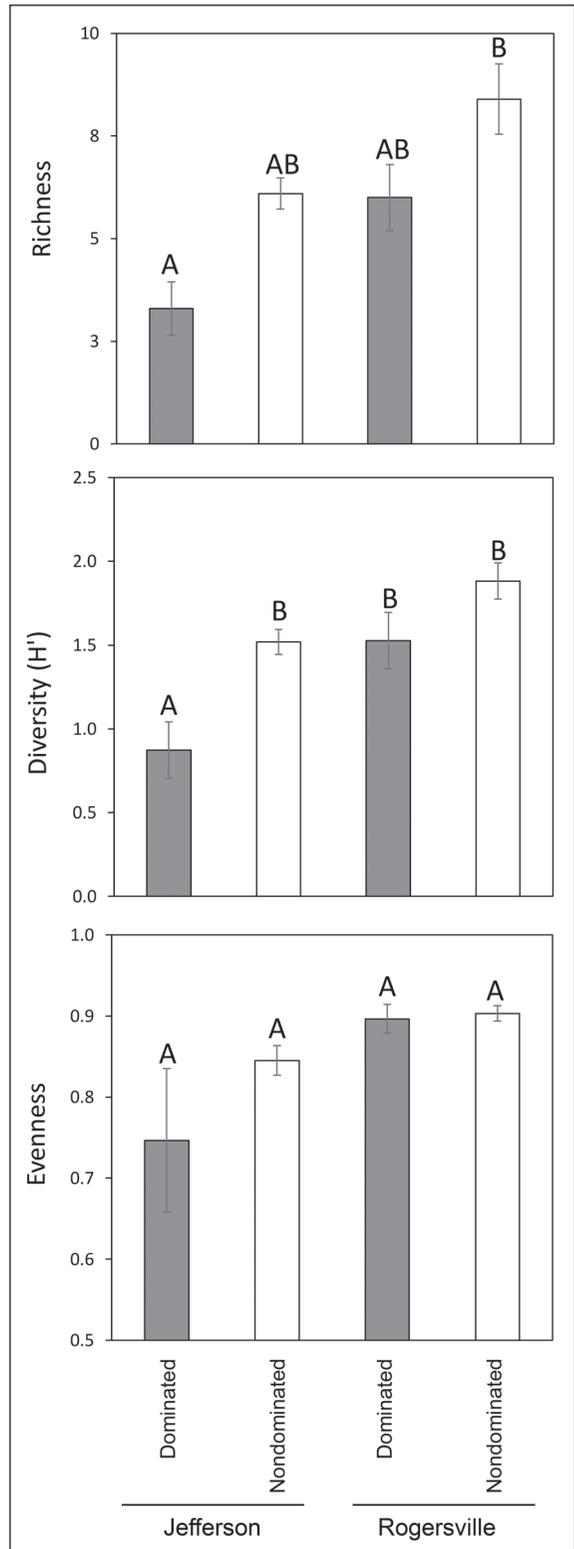
Table 2. MRPP results for differences between sites and between plot types in each site. A is the chance-correct within-group agreement; A = 1 if all items are identical within groups and A = 0 if heterogeneity within groups equals expectation by chance.

Individual factors	A	P
Between sites	0.458	<0.0001
Jefferson (dominated vs nondominated)	0.030	0.029
Rogersville (dominated vs nondominated)	0.040	0.020

Table 3. Indicator species and indicator values in parentheses for species with P-value below 0.05 in each group. No indicator species was detected in the Jefferson plot types.

Groups	Indicator species (indicator value)	P
Jefferson	<i>Microstegium vimineum</i> (1.000)	0.0001
Rogersville	<i>Acalypha rhomboidea</i> (0.734)	0.0002
	<i>Ambrosia artemisiifolia</i> (0.905)	0.0001
	<i>Celastrus orbiculatus</i> (1.000)	0.0001
	<i>Erechtites hieraciifolius</i> (0.734)	0.0001
	<i>Oxalis stricta</i> (0.860)	0.0001
	<i>Rubus pensilvanicus</i> (0.378)	0.0447
	<i>Trifolium pretense</i> (0.694)	0.0001
Plot types - Rogersville		
Nondominated	<i>Ambrosia artemisiifolia</i> (69.9)	0.0006
Dominated	<i>Celastrus orbiculatus</i> (60.3)	0.0300

Figure 5. Mean \pm SE of species richness, diversity, and evenness within and among sites and plot types. Results are based on an ANOVA. Multiple comparisons, including site interactions (no interactions were significant), were made with least-squares means and a Tukey adjustment with $\alpha = 0.05$ (SAS 9.4 software: SAS 2013). Different letters indicate statistically significant differences.



(Japanese Stiltgrass) at the Jefferson site and a native species (Common Ragweed) at the Rogersville site (Table 1).

Discussion

There have been many studies addressing how invasive plants directly or indirectly reduce the diversity and abundance of native plant species (Hejda et al 2009, Molinari and D'Antonio 2014). Our study supports a decrease in species richness and diversity in MAM-dominated patches compared to nondominated patches in highly invaded sites that are physiographically homogeneous. Nonetheless, there may be unmeasured differences in soil or microhabitats that could help explain the differences in species composition and patchiness. Unfortunately, such post-invasion differences likely reflect both pre-invasion and post-invasion soil conditions, making it impossible to separate out conditions caused by the invasion from preferred conditions enabling establishment of the invader. In this study, we defined plant species composition in areas infested by MAM, manifesting that native and nonnative plants may be coexisting in patches. We hope to further explain these patchy species distributions of apparently coexisting native and nonnative species in future research.

The fact that MAM usually forms dense, monocultural patches indicates that its dominance over available resources may prevent germination, survival, and growth of existing native species and of other nonnative species. However, we found several coexisting native and exotic species in our study. Based on the rank of relative IV and ISA indicator values, Japanese Stiltgrass was a dominant species in both dominated and nondominated plots in the Jefferson site, whereas the native Common Ragweed was a dominant species in the nondominated plots, even surpassing another invader (Oriental Bittersweet) in relative cover at the Rogersville site. Japanese Stiltgrass and Oriental Bittersweet are common invasive species in the northeastern US that may further impact ecosystem properties by changing soil fertility such as increasing pH, nitrification, and litter-decomposition rates (Ehrenfeld 2003, Ehrenfeld and Scott 2001, Leicht-Young et al. 2009). Common Ragweed and Common Woodsorrel are native species to the region but are regarded as common weeds in multiple early successional habitats that decrease in abundance as succession proceeds (Bassett and Crompton 1975, Marble et al. 2013). The Rogersville site could conceivably recover to a native-dominated site after removal of MAM without a need to plant additional native species or to remove other exotics, though it would be prudent to remove Oriental Bittersweet as well. In contrast, the Jefferson site will clearly be dominated by Japanese Stiltgrass and Oriental Lady's Thumb, another invasive exotic, after removal of MAM, unless management also includes removal of these species. However, at both the Rogersville and Jefferson sites, there are several native species present that are poised to increase in abundance. This study highlights how seemingly similar invaded sites can differ significantly in plant species compositions. Being aware of the abundances of other species present during any targeted treatments of a single species will improve site

management by providing likely scenarios of new species abundances once the target species is removed or reduced.

Currently, management of MAM mainly relies on pre- and post-emergent herbicides and biological control (Gover et al. 2008, Hough-Goldstein et al. 2015, Mountain 1989). Physical and mechanical removal may be effective for small populations, though there is still a chance viable seeds in the seedbank will germinate later, requiring repeated removal events. It is well documented that removal or suppression of a dominant invasive weed can cause invasion of different invasive plants or dominance by coexisting exotic plants (Erskine Ogden and Rejmánek 2005, Westman 1990). However, the use of the biological control agent MAM Weevil may enable a longer recovery period with relatively slow suppression of MAM, allowing existing or planted native plant species more time to recover or grow (Hough-Goldstein et al. 2009, Hudson et al. 2017). The stem-boring larvae and the adult of this host-specific biocontrol agent cause, respectively, reductions in fitness (growth and reproduction) of and significant feeding damage to MAM. Neither, however, kill the plants immediately (Colpetzer et al. 2004, Smith and Hough-Goldstein 2014). Because other dominant exotic and native species coexist in the invaded sites, a subsequent release of MAM Weevil should be considered in the context of integrating weed management with possible herbicide application for other invasive plants present, giving the native species a possible advantage.

Restoration of invaded natural ecosystems must take all species present at the site into account and not just any initial focal species being removed (Flory and Clay 2010b, Lake et al. 2014). Westman (1990) suggested that the removal of invasive plants without a restoration plan of the native community can result in severe abiotic alteration causing further modifications of the site. The target invasive plant of our study, MAM, is commonly found with the invasive grass Japanese Stiltgrass (Lake et al. 2011), and our data support this at 1 site. Cutting and Hough-Goldstein (2013) and Lake et al. (2014) found that suppression of MAM without also removing Japanese Stiltgrass can result in subsequent domination by Japanese Stiltgrass, as might likely happen should MAM be eradicated at the Jefferson site. In contrast, removal of MAM at the Rogersville site could potentially result in the native Common Ragweed dominating, but with Oriental Bittersweet coexisting in the species mix. In both cases, the greater species richness of the nondominated plots is due to more native species being present, but with each in very low abundance. Increases in these native species are not likely to occur at the Jefferson site without the joint removal of Japanese Stiltgrass, whereas the Rogersville site may see an increase in the less common native species after removing MAM as succession progresses. Succession dominated by native species may progress faster at the Rogersville site if Oriental Bittersweet is also removed.

Though competition is often assumed to be the dominant interaction between native and nonnative plants, with invasive plants being the better competitor, some native species are better competitors, some native species may facilitate invasive plants or vice versa, and some species coexist by occupying different niches (Goody 2019, Nilsen et al. 2018, Stout and Tiedeken 2017). Such interactions may then

result in novel communities or invasional meltdowns (Hobbs et al. 2009, Simberloff 2006, Simberloff and Von Holle 1999). Our study defines the composition of potentially novel plant communities, with 1 site (Jefferson) perhaps on the verge of or in the middle of an invasional meltdown.

The results of our study suggest that MAM affects native plant communities negatively and that restoration after any MAM control efforts should take into account the presence of other dominant exotic and native species. Japanese Stiltgrass and Common Ragweed at the Jefferson and Rogersville sites, respectively, have a high potential for becoming a subsequent dominant species after successful weed management of MAM. These results suggest that knowledge of the plant community that coexists with a dominant invasive plant targeted for removal will help increase the likelihood of restoration success for 2 reasons. First, presence of other dominant exotic species should highlight the need for management of these species as well. Secondly, presence of dominant native plant species, especially with less common native species also present, may indicate greater system resilience to the new disturbance caused by the target species' removal.

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