Diversity declines in *Microstegium vimineum* (Japanese stiltgrass) patches

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Abstract

The spread of invasive plant species and their impacts on plant communities have received international attention as global trade and global environmental change enhance the colonization and establishment of introduced species and threaten the integrity of native ecosystems. Because introduced species vary in their impact, studying the relationship between invasion and native communities is necessary to guide allocation of finite management resources. By studying adjacent pairs of invaded and uninvaded plots across an eastern United States forested landscape, we demonstrate *Microstegium vimineum* was associated with local declines in species richness and cover of native species. Negative impacts of M. vimineum on species richness did not emerge until August when M. vimineum cover and height were greatest, highlighting the value of following study subjects through the growing season. In contrast, native species cover was already lower in invaded plots early in the growing season. *M. vimineum* invasion was not the only important driver of species richness and community composition within the study region; abiotic environmental gradients, such as soil nitrate concentration and pH, across the six study sites were also important in affecting species richness and cover, but lessened in explanatory power through the growing season. We conclude that *M. vimineum* has effects on community structure that may have long-term consequences for biodiversity. Studies which track sites through time and consider multiple scales are required as invaders impact multiple biotic and abiotic factors operating at different spatial and temporal scales.

Key words: invasion, Maryland, native plants, richness, spatial scale
1. Introduction

Invasive plants are considered a global threat to ecosystems. They have been charged with homogenizing regional biotas (McKinney, 2004) and causing local declines of native species (Lodge et al., 2000; Mack et al., 2000). However, studies that seek to assess the impact of invasive plants on native ecosystems are usually conducted at fine spatial scales and not designed to separate the local effects of an invasive species from the effects of regional variation in environmental factors on plant communities (e.g., Dickens et al., 2005; Yurkonis et al., 2005; Gerber et al., 2008). This is despite evidence that plant biodiversity patterns reflect abiotic gradients, such as nutrient availability, even in highly invaded systems (Corney et al., 2004; Erskine Ogden and Rejmanek, 2005).

Making management decisions regarding invasive species involves predicting the outcome of taking no action, and weighing that against various control options. As such, research that elucidates the impacts of taking no action is crucial. One way to gauge the impact of an invasive species is to test if it is impacting the biodiversity of recipient plant communities, as is generally assumed but not necessarily always the case. For example, if an invading species uses resources in different ways than resident species, then the invading species may have little impact on the native vegetation (Levine and D’Antonio, 1999). In contrast, if an invader changes the disturbance regime or resource supply rates, large and sometimes cascading impacts may be expected (D’Antonio and Vitousek, 1992; Jager et al., 2007).
Despite growing concern about the impact of invasive species, biogeography and environmental heterogeneity can swamp the effects of local interspecific interactions between an invading species and the resident community (Huston, 1999). Thus, multiple spatial scales need to be studied to reliably discern the relative importance of invasion on diversity (Pauchard and Shea, 2006). Likewise, the factors that make a community susceptible to invasion, and the factors that make a species invasive can both vary over time (Davis et al., 2000). Accordingly, it is possible that the impact of invasion varies not just spatially, but also temporally (Clarke et al., 2005; Bjerknes et al., 2007). Thus, the impact of an invading species needs to be studied across sites and through time, otherwise it is possible to miss the patterns entirely.

Just as methodology must reflect the fact that many herbaceous species have a brief window of maximum production, it must also take into account the constraints inherent in studying invasive species. While experimental methods are necessary to definitively determine patterns and mechanisms, an experimental approach using invasive species has limitations. Greenhouse studies are often criticized for being too artificial, however adding an invasive species to an uninvaded area raises ethical issues. Removal studies rely on an untested assumption that removing a plant will delete its impact, but we know that many invaders have legacies such as altered soil nutrient cycling (Valtonen et al., 2006). Oldfield studies that monitor vegetation over many decades spanning the invasion of multiple species have been used to shed light on the impact of invasion (e.g., Meiners et al., 2001, 2004). However, long-term studies are uncommon (Puth and Post, 2005), and the
immediacy of invasion sometimes necessitates shorter-term studies to provide guidelines to management.

Carefully designed observational studies can make an important contribution to our understanding of the impact of invasion and the mechanisms underlying successful invasions. Here we describe a study of invaded sites across a fragmented forested landscape, with paired invaded and uninvaded plots immediately adjacent to one another at each study site. Uninvaded areas are frequently used as control plots (Kotanen, 1997; Alvarez and Cushman, 2002; Ortega and Pearson, 2005); however, paired plots that are immediately adjacent to each other located at multiple sites separated by several kilometers is an uncommon but advantageous design (Chabrerie et al., 2008). With such a design both local and regional scales can be observed. An invasive species with a patchy distribution is ideal as it allows for observation of uninvaded plots located very close to invaded plots, minimizing covarying environmental variables that could confound the study.

We studied the impact of *Microstegium vimineum* (Japanese stiltgrass) on native vegetation in the Chesapeake and Ohio Canal National Historical Park, located adjacent to the Potomac River in Maryland, USA. *M. vimineum* is a grass native to Asia that was introduced into Tennessee by 1919 (Fairbrothers and Gray, 1972). Since that time it has spread through the eastern United States. It is a shade tolerant forest herb that thrives in disturbed locations (Winter et al., 1982; Barden, 1987; Horton and Neufeld, 1998). *M. vimineum* appears to elevate soil nitrification rates and pH levels and is associated with
different soil microbiota than adjacent natives (Ehrenfeld et al., 2001; Kourtev et al., 2002). Overland flow, deer, and humans spread the species easily, though it apparently is unpalatable to deer (Barden, 1987; Mehrhoff, 2000). It exhibits phenotypic plasticity (Claridge and Franklin, 2003; Cole and Weltzin, 2004), apparently able to compensate for suboptimal levels of one resource when there was a sufficient supply of some other resource. *M. vimineum* does not appear to exhibit allelopathy (Barden, 1987; Cole and Weltzin, 2005). It uses the C4 photosynthetic pathway, and though it germinates in April, it reaches peak productivity in August and does not set seed until September (Barden, 1987). Despite high levels of management concern over *M. vimineum*, the extent to which it is associated with declines in native species is unknown.

We predicted that invaded plots would support a different plant community than uninvaded plots at a local scale and that species richness would be lower in invaded plots. We further predicted a positive correlation between native and exotic species richness at a landscape scale in keeping with existing research (e.g., Stohlgren et al., 2003). *M. vimineum* grows most rapidly in July and August, and is still small in June. We therefore predicted that a negative association between *M. vimineum* and other species at local scales would be greater in August than in June. We predicted that soil nutrients and light levels would be lower in invaded plots than uninvaded plots, reflecting the species’ abilities to alter resource levels. We hypothesized that direct interactions, such as facilitation and competition, as opposed to indirect interactions such as those impacting dispersal, would
explain the impact of *M. vimineum* on other species, and as such predicted that the seed bank in invaded and uninvaded plots would not differ.

2. Methods

To test our predictions, we conducted a botanical survey along the Chesapeake and Ohio Canal National Historical Park (C&O), USA, in 2005. This survey allowed selection of six sites in May 2006 that supported *M. vimineum*. At each site we delineated two adjacent plots, one invaded with *M. vimineum* and one uninvaded, that appeared to be similar in environmental conditions. Aboveground vegetation was surveyed three times during the growing season. Samples from the soil seedbank were germinated in the greenhouse, and abiotic environmental variables were measured in the field in the summer of 2006.

2.1 Study sites

The six study sites are situated in C&O where it transects the Ridge and Valley physiographic province, spanning the area between Hagerstown and Cumberland in Allegany and Washington counties of Maryland, USA. The park was once a location of high levels of disturbance with the construction and operation of the canal in the 1800s. The canal ceased operations in 1924, and has been owned by the National Park Service since 1938. Most of the park is forested and recent human disturbance to the study sites is minimal. White-tailed deer were frequently noted at study sites. The climate is temperate and mesic deciduous forest is the dominant cover type. Sites are named for the nearest C&O milemarker (110, 128, 156, 162, 166, 170). C&O is a linear park, which
approximately follows the north bank of the Potomac River for 297 km. Hence, as the milemarker names would indicate, sites were at least 6.4 km (4 miles) apart, and the whole study area encompassed an approximately linear stretch of 96.5 km (60 miles).

2.2 Site selection

Potential sites were identified using information from a botanical survey conducted in the summer of 2005. When potential locations were revisited in May 2006, the first site encountered that met a list of a priori criteria was selected to minimize bias in site selection. Site selection continued until six sites were identified. More than six sites would not have been logistically feasible to sample. The criteria used for selecting study sites included identifying a 6m x 4m plot with at least 50% cover of *M. vimineum* (“invaded” treatment) immediately adjacent to a plot of the same size with less than 15% cover of *M. vimineum* (“uninvaded” treatment), as determined by visual estimation. Sites had to be free of any obvious environmental gradients that would mask or confound the relationship between *M. vimineum* and other species, such as fence lines or abrupt changes in forest cover. Sites had to be out of view of any trail or road, though owing to the linear nature of C&O, all sites were within 500 m of a trail. All sites were located in deciduous forest, none were placed immediately adjacent to the canal, river or other water, and all plots were on flat ground and located on substrate of alluvial origin (Southworth et al., 2001). At four sites the overstory was dominated by *Acer negundo*, one site was dominated by *Liriodendron tulipifera* (site 128), and one by *Platanus occidentalis* (site 162).
2.3 Field methods

At each of the six study sites, a 2 m buffer strip separated the 4 x 6 m invaded and uninvaded plots. Each plot was divided into a grid of 24-1 m² subplots. Two subplots within the plot were excluded from vegetation sampling to allow a place to stand for accessing all surveyed subplots without trampling vegetation. Vegetation was sampled in mid-June, mid-August, and mid-September 2006 to test for seasonal effects of *M. vimineum* on extant communities. Percent cover of each species and of bare ground was estimated to the nearest cover class in each subplot using a modified Braun-Blanquet scheme (cover classes: <1%, 1-4%, 5-9%, 10-25%, 26-50%, 51-75%, 76-91%, 92-96%, 97-99%, >99%; Mueller-Dombois and Ellenberg, 1974). Percent cover was noted in two vertical strata (<1 m and between 1 and 2 m), allowing for a theoretical maximum of 200% cover. The Integrated Taxonomic Information System (available at www.itis.gov) was used to determine species origin and Gleason and Cronquist (1991) was used as a taxonomic reference. Height of *M. vimineum* was also recorded in June, August and September, and was determined by measuring to the nearest centimeter a randomly selected plant in each subplot in which it was found and averaging for each site.

Environmental conditions were measured in invaded and uninvaded plots to test for regional environmental gradients that may not have been evident during site selection and to discern associations between *M. vimineum* and abiotic factors. Soil moisture, depth of leaf litter, and soil compaction were measured in six subplots per plot; each plot was divided into units of four subplots, and within each of these units the measurement location
was placed randomly. Soil moisture was determined in the field using a Hydrosense moisture probe (Campbell Scientific, Logan, UT) in June and September of 2006. To limit damage to the soil moisture probe, only two soil moisture measurements were taken per invaded and uninvaded plot at site 156, which consisted of very rocky substrate. Depth of leaf litter was measured with a ruler, distinguishing between litter from *M. vimineum* and all other litter. Material was designated as litter if it was possible to distinguish its origin, and otherwise considered duff and not measured. Soil compaction was measured in June using a spring operated pocket penetrometer (Forestry Suppliers, Inc., model 77114). In late summer (July-August), light levels were recorded in the four corners of each plot during cloudless times of day at two heights, ground level and 1.2 m above soil surface, using a recently calibrated LI-191 Line Quantum Sensor attached to a LAI-2070 Control Unit (Li-Cor, Lincoln, NE). We measured ambient light levels immediately before and after plot measurements in the nearest canopy opening and used simple regression to determine the ambient light levels for the times of plot light measurement. Light levels under the canopy are reported as a percentage of these calculated ambient light levels.

Soil samples were collected in late June 2006 from four randomly selected subplots per plot for soil chemistry analysis. We tested levels of nitrate and ammonium on KCl extractions of the soil samples using a flow injection analyzer (Lachat instruments, Loveland, CO). pH was measured using an electronic pH probe (Thermo Electron corporation, Beverly, MA) on water slurries. For pH analysis, two soil samples were
combined to provide two measurements per plot, with the exception of site 156, for which there was only enough soil for one measurement per plot with all soil samples combined.

2.4 Greenhouse methods

Soil cores for a seedbank germination trial were taken from the six study sites at the time of site selection in late May 2006 and placed in the greenhouse at the University of Maryland Center for Environmental Science’s Appalachian Laboratory in Frostburg, MD. Seedbank soil cores were taken using a stratified random design. In each plot, three randomly located 2 cm diameter soil cores were removed from each of the 24 1 m² subplots to a depth of 10 cm. To make the germination trial more manageable, we combined the soil cores from pairs of neighboring subplots into a single 34 cm x 25 cm plastic tray and placed the combined and mixed soil on sterilized sand. The resulting 144 trays were watered daily with dechlorinated tap water through August. In September, lower temperatures kept trays moist and watering was reduced to once every other day. Placement of the trays in the greenhouse was re-randomized every two weeks to minimize potentially confounding microclimatic effects. As plants germinated, they were transferred out of the germination trays so they could be grown out until identifiable without competing with remaining seeds. The germination trial was completed in October 2006.

2.5 Statistical analysis

Intermediate values for vegetation cover were used for analysis (e.g., where 10-25% cover was noted in the field, 17.5% was used for analysis). We calculated total, exotic, and native
species richness; and percent cover of native species and *M. vimineum* for each plot and survey month. Cumulative species richness was also calculated for the entire study period. Seedbank richness was determined using the accumulated number of species per plot from the germination trial.

The study was a randomized complete block design where site was the block and nested invaded/uninvaded treatments at each site were fixed effects. Species were either accumulated across subplots, in the case of species richness estimates, or averaged across subplots, in the case of plant cover and abiotic variables.

We tested whether site and plot (invaded or uninvaded) are associated with differences in species richness, and percent native or exotic cover using a repeated measures ANOVA with plot and site as between subject effects and time as the within subject effect. When model results were significant, we conducted additional two-way ANOVAs for each time period to allow for specific comparisons among means. Results were Bonferroni adjusted in those cases where multiple means were compared (see Figure 1). As abiotic variables were not repeatedly measured through time with the exception of soil moisture, we used a two-way ANOVA to test for differences in pH, soil nitrate, soil ammonium, soil moisture in June and September, light at ground, light at 1.2 m, and soil compaction among plots and sites. In addition to using species richness and cover as summary variables of community structure, we used a multivariate approach to preserve species level data and learn more about site and plot differences in community structure. Non-metric
Multidimensional Scaling (NMS) of community structure (standing vegetation and seed bank) determined how similar community structure in the invaded and uninvaded plots were across sites and time (standing vegetation only as soil samples for germination trials were collected only once) using the Bray-Curtis distance measure. To evaluate whether invaded/uninvaded plots and sites were different in ordination space, we conducted a MANOVA on the NMS axis scores. The dimensionality of the final NMS results, and hence the number of NMS axes used in the MANOVA, optimized stress of the ordination and final instability.

We conducted Pearson correlations between hypothesized causative variables (percent cover *M. vimineum*, environmental variables) and community descriptors (percent cover native species, species richness) for the June, August, and September sampling dates. An analysis of covariance (ANCOVA) was conducted to test the relative importance of discrete (invaded/uninvaded) and continuous (soil nutrients, light availability, soil moisture, soil pH, soil compaction, litter depth) variables in affecting species richness. ANCOVAs were run separately for the three sampling dates.

All statistical analyses were performed using SAS (v8.2, SAS Institute, Inc., Cary, NC) or PC-ORD 4 (MjM software, Glenden Beach, OR). An α level of 0.05 was used throughout all analyses to determine significance. All variables were tested for normality and none required transformation. One site (128) was removed from the NMS analysis because the
uninvaded plot was mostly bare ground. However, all plots and sites were used in all other statistical analyses, as the exclusion of site 128 did not influence the results.

3. Results

3.1 Species richness and native species cover

Species richness in aboveground herbaceous vegetation was highest in June and decreased through time (Table 1, Figure 1a). Both plot and site were equally important in driving patterns of species richness (Table 1) but the relative importance of each factor changed through time. Species richness did not differ between invaded and uninvaded plots in June (ANOVA; \( F_{6,5} = 5.31, P_{\text{model}} = 0.04, P_{\text{plot}} = 0.39 \)) but differed among sites \( (P_{\text{site}} = 0.03) \). In contrast, invaded and uninvaded plots diverged in species richness in August (ANOVA; \( F_{6,5} = 12.28, P_{\text{model}} = 0.007 \)) and September (ANOVA; \( F_{6,5} = 11.82, P_{\text{model}} = 0.008 \)) when plot effects \( (P_{\text{plot}} = 0.004 \text{ and } 0.006 \text{ in August and September, respectively}) \), were more explanatory than site effects \( (P_{\text{site}} = 0.01 \text{ and } 0.01 \text{ in August and September}) \). These patterns in species richness reflect changes in native species richness among plots through time, as exotic species richness was relatively low (five species per plot), did not differ between invaded and uninvaded plots, and only changed little through time (Table 1). Cumulative native and exotic species richness were positively correlated in uninvaded plots but not in invaded plots \( (\text{Pearson correlation}; \text{uninvaded plots: } P=0.014, \ r=0.90, n=6; \text{invaded plots: } P=0.206, \ r=0.60, n=6; \text{Figure 2}) \).
In both invaded and uninvaded plots, native species cover remained the same across the three sampling times (Table 1, Figure 1b) but was lower in invaded plots than uninvaded plots (Table 1) in June (ANOVA; $F_{6,5}=10.78$, $P_{\text{model}}=0.01$, $P_{\text{plot}}=0.02$) and August (ANOVA; $F_{6,5}=4.98$, $P_{\text{model}}=0.05$, $P_{\text{plot}}=0.01$) but not in September (ANOVA; $F_{6,5}=2.16$, $P_{\text{model}}=0.21$, $P_{\text{plot}}=0.13$). In contrast, sites did not differ in native species cover (Table 1). Average percent cover of $M. \text{ vimineum}$ in invaded plots increased through time but remained low and did not change throughout the season in uninvaded plots (Figure 1). Differences between invaded and uninvaded plots remained high throughout the growing season (Table 1), whereas sites did not differ in $M. \text{ vimineum}$ cover. Average height of $M. \text{ vimineum}$ increased from 23.5 cm ($\pm 2.7$ SE) in June to 37.2 cm ($\pm 2.8$ SE) in August, to 41.7 cm ($\pm 2.8$ SE) in September (ANOVA; $F_{2,15}=5.56$ $P=0.05$). Four of the six uninvaded plots supported >50% cover of native species with $\text{Verbesina alternifolia}$, $\text{Agrostis perrenans}$, $\text{Pilea pumila}$ being the most abundant species. One uninvaded plot (site 166) supported 35% cover of native species and significant amounts of exotic species (13% cover $\text{Alliaria petiolata}$). The sixth uninvaded plot (site 128) was mostly bare ground.

### 3.2 Comparison of community composition between invaded and uninvaded plots

To complement the repeated measures ANOVAs, we conducted a NMS on the plot data and ran a MANOVA on the 3 NMS axes to test for differences among plots and sites through time. With $M. \text{ vimineum}$ removed from the dataset, invaded and uninvaded plots separate as distinct communities in ordination space (Figure 3; Wilks’ Lamda$_{\text{plot}}$, $F_{3,20}=3.9$, $P=0.02$). However, differences between sites were greater than differences between
invaded and uninvaded plots (Wilks’ Lambda_{site}, F_{12,53}=62.8, P<0.001). Community composition did not differ between June, August and September after accounting for site and plot differences (Wilks’ Lambda_{time}, F_{6,40}=0.71, P=0.64).

Seedbank richness ranged from 5 to 18 species in invaded plots and from 6 to 21 species in uninvaded plots. Seedbank richness did not differ between invaded and uninvaded plots or between sites (ANOVA; F_{6,4}=1.40, P=0.39). Similarly, seedbank species composition did not differ between invaded and uninvaded plots in ordination space (MANOVA on 2 NMS axes, Wilks’ Lambda_{plot}, F_{2,4}=2.24, P=0.22), but differed among sites (Wilks’ Lambda_{site}, F_{10,8}=6.09, P=0.009). Aboveground richness and seedbank richness were not correlated (Pearson correlation; P=0.086, r=0.516, n=12).

### 3.3 Environmental variables

Soil nitrate concentration, June soil moisture, and soil pH differed among study sites (Table 2). Only M. vimineum litter depth differed between invaded and uninvaded plots (Table 2). Soil nitrate and species richness in plots were positively correlated (total richness P=0.004, r=0.76; exotic richness P=0.004, r=0.76; native richness P=0.017, r=0.67; n=12). Percent cover of native species was correlated with different factors in June than in August. In June, cover of native species varied with soil pH and soil ammonium, but not with percent cover of M. vimineum (Table 3). In August this pattern reversed, with no relationship apparent between native species cover and soil pH and ammonium (Table
3). *Microstegium vimineum* cover in both June and August was negatively correlated with native species cover in August (Table 3).

### 3.4 Explanatory models

Total species richness within plots was best explained by a model (ANCOVA; $F_{2,9}=9.75$, $P=0.006$ in June, $F_{2,9}=21.17$, $P<0.001$ in August, $F_{2,9}=15.97$, $P=0.001$ in September) which included if the plot was invaded ($P=0.090$, $P<0.001$, and $P=0.002$ in June, August and September, respectively), and the soil nitrate level of the plot ($P=0.002$, $P<0.001$ and $P<0.001$ in June, August and September, respectively). Native cover through time was best explained by a model (ANCOVA; $F_{2,9}=8.34$, $P=0.009$ in June, $F_{2,9}=9.60$, $P=0.006$ in August, $F_{2,9}=5.00$, $P=0.035$ in September) which included if the plot was invaded ($P=0.059$, $P=0.006$ and $P=0.098$ in June, August and September, respectively) and soil pH ($P=0.007$, $P=0.030$ and $P=0.030$ in June, August and September, respectively).

### 4. Discussion

#### 4.1 Vegetation patterns in space and time

*M. vimineum* was associated with reductions in native species richness and percent cover (Figure 1a,b, Table 1), especially in August when *M. vimineum* covered more horizontal (Figure 1c) and vertical space than in June. This negative association of an invasive species with existing native communities across a range of sites is consistent with other documented patterns of invasive species impacts (e.g., Richardson et al., 1989; Alvarez and Cushman, 2002; Jackson, 2005; Reinhart et al., 2005). However, differences in the six
sampled sites were clearly also responsible for some of the observed variation in species richness (Table 1, Figure 3), suggesting that biogeographic variation in species composition can be as important as local effects of invasion in determining species richness. In contrast, sites did not differ in native plant cover (Table 1), which suggests that differences in species richness among sites were not simply an artifact of sample size (Colwell and Hurtt, 1994), assuming that plant cover correlates with abundance.

Differences in environmental conditions across sites contributed to observed differences in community structure (Table 2). In particular, soil nitrate was an important covariate that explained species richness across plots and sites, and pH was an important covariate in explaining native species cover across plots and sites. pH was also an important variable related to differences in community structure in the NMS ordination (Figure 3). In June, cover of native species was correlated with soil chemistry, and not correlated with *M. vimineum* cover. But in August, the pattern reversed (Table 3). This suggests that while abiotic factors may explain cover of native species during parts of the growing season when *M. vimineum* occupies a smaller part of the community, by August, when *M. vimineum* is at or close to peak cover and biomass, the importance of abiotic factors on native species cover may be overshadowed by the impact of *M. vimineum*. Species composition was markedly different among sites (Figure 3) such that differences in species identity among sites could have played an important role in the response to *M. vimineum* and the interaction with the abiotic factors measured. However, the results of the NMS analysis show that community composition changed little through time and, hence, species
richness is unlikely a reflection of seasonal species turnover. We therefore conclude that species richness and cover are both the result of interspecific interactions with *M. vimineum* at local scales and environmental variation at landscape scales. Which process dominates depends on the breadth of the environmental gradient that was sampled, the strength of interspecific interactions between the invader and the established community, and the time of year.

4.2. Local and regional processes

We observed a positive relationship between soil nitrate and species richness at the landscape scale suggesting that more species, native and exotic, can be packed into the environment where more resources are available (Goldberg and Miller, 1990). Indeed, exotic richness and native richness were positively correlated in uninvaded plots (Figure 2), a relationship found repeatedly in the literature at various spatial scales (e.g., Smith and Knapp, 1999; Stohlgren et al., 1999; Sax, 2002; McKinney, 2004; Tabacchi and Planty-Tabacchi, 2005). This suggests exotic and native species are responding to the same environmental drivers, such as soil nitrate, in the landscape (Stohlgren et al., 2003; Davies et al., 2005). Conversely, native and exotic species richness were not correlated in invaded plots (Figure 2), suggesting that the interaction with *M. vimineum* overshadows the direct response of native and exotic species to the abiotic environment, corroborating our finding that *M. vimineum* is an important driver of community structure in our study system.
Invaded and uninvaded areas within the same site started with the same potential for species richness, as witnessed by similar seedbanks in invaded and uninvaded plots but this potential was clearly not reached in invaded plots. Unlike other researchers (Ehrenfeld et al., 2001; Belote and Weltzin, 2006), we found that soil resources and light supply did not differ between invaded and uninvaded plots (Table 1). Regardless, given its generally known supplementing effects on nitrogen and depleting effects on light, *M. vimineum* may have the capacity to facilitate the growth of or to compete with native species.

The expected outcome of these concurrent local and regional patterns is an increase in species richness where species are released from competition for soil nitrogen, such as in low productivity environments, and a decrease in native species richness in places that are highly productive and limited by light availability. Most *M. vimineum* invasions are likely to occur in high productivity environments where disturbances provide a pulse of resources and light is the limiting resource. Thus, we predict that the latter possibility will be most commonly observed especially when highly productive plant communities decrease ground level light availability to the light compensation point of many deciduous forest herbs (0.5-2% of full sunlight; Hicks and Chabot, 1985). In our study system, this level was almost reached in invaded areas (Table 2).

An alternative explanation for the local differences observed among invaded and uninvaded plots is that the invaded plots may have experienced a local disturbance that resulted in a greater susceptibility of plots to *M. vimineum* invasion (Davis et al., 2000).
Such impacts would be expected to be mediated through differences in the forest canopy or through differences in soil conditions. In either case, both *M. vimineum* and native species would be directly affected by this difference in available resources. However, light above the herbaceous level and total leaf litter did not differ between invaded and uninvaded plots. Soil conditions were also generally comparable between invaded and uninvaded sites, suggesting that differences among invaded and uninvaded plots were probably not associated with small-scale disturbances.

4.3. Conclusions and management recommendations

*M. vimineum* is an invasive species that can establish dominance in the understory of deciduous forests in the eastern United States, and management actions may be required to curb the success of the species. While our study suggests that *M. vimineum* has a negative impact on species richness, it only does so later in the growing season when *M. vimineum* has matured, suggesting that late season native species are the most vulnerable to this late season invader. While local extinction events may currently be offset by immigration from the region and by a persistent seed bank, the long-term negative consequences of continued *M. vimineum* invasion on biodiversity loss may be far greater. First, *M. vimineum* dominated areas may serve as sink habitats (Pulliam, 1988) for native species that allow seeds of native species to immigrate and germinate but do not allow plants to mature and reproduce (Mason et al., 2007). Second, while richness did not differ among invaded and uninvaded plots in June, the observed difference in native species cover in June (Figure 1b)
suggests that population sizes of some species may have been reduced. This may create genetic bottlenecks and the local extinction of small populations, eventually affecting the richness and composition of invaded areas. Only long-term monitoring of invaded areas, and genetic analysis of populations growing within and outside *M. vimineum* patches, may shed light on these latent effects of invasion (Sax and Gaines, 2008). Interpretation of monitoring results, however, will require site-specific information about reference conditions, as abiotic conditions may be as important as invasive species in affecting biodiversity patterns.

Ultimately, human management may be easier than resource management. Thus, a program of vigorous outreach and education to all who visit natural areas about the spread of invasive species, such as *M. vimineum*, is called for. Simple strategies such as brushing off bootlaces with a wire brush, avoiding patches of invasive plants when in seed, and wearing footwear which minimizes seeds carried away from the site, have the potential to impact the rate of spread of this species.

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Ecography 28(5), 573-582.


### Tables and Figures

#### Table 1. Plant community

<table>
<thead>
<tr>
<th></th>
<th>Within subject effects</th>
<th>Between subject effects</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Time</td>
<td>Plot</td>
</tr>
<tr>
<td>df</td>
<td>F</td>
<td>P</td>
</tr>
<tr>
<td>----------------------</td>
<td>------------------------</td>
<td>-------------------------</td>
</tr>
<tr>
<td>Total sp. richness</td>
<td>2,10 17.65 &lt;0.001 1.5</td>
<td>12.46 0.02 1.10 11.22 0.01</td>
</tr>
<tr>
<td>Native sp. richness</td>
<td>2,10 18.76 &lt;0.001 1.5</td>
<td>18.24 0.008 1.10 13.54 0.006</td>
</tr>
<tr>
<td>Exotic sp. richness</td>
<td>2,10 4.29 0.05 1.5</td>
<td>2.11 0.21 1.10 10.23 0.01</td>
</tr>
<tr>
<td>Native sp. cover</td>
<td>2,10 0.02 0.98 1.5</td>
<td>10.54 0.02 1.10 3.92 0.08</td>
</tr>
<tr>
<td><em>M. vimineum</em> cover</td>
<td>2,10 37.48 &lt;0.001 1.5</td>
<td>63.91 &lt;0.001 1.10 0.67 0.66</td>
</tr>
</tbody>
</table>

Repeated measures two-way analysis of variance results for plant community variables collected in June, August, and September 2006 in invaded and uninvaded plots at six study sites. P-values ≤ 0.05 are bolded.
Table 2. Abiotic variables

<table>
<thead>
<tr>
<th>Model</th>
<th>Plot</th>
<th>Site</th>
<th>Mean ± ste</th>
<th>invaded</th>
<th>uninvaded</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>df</td>
<td>F</td>
<td>P</td>
<td>F</td>
<td>P</td>
</tr>
<tr>
<td>Ammonium</td>
<td>6,5</td>
<td>3.41</td>
<td>0.10</td>
<td>0.93</td>
<td>4.09</td>
</tr>
<tr>
<td>Nitrate</td>
<td>6,5</td>
<td>13.97</td>
<td>0.006</td>
<td>5.46</td>
<td>0.07</td>
</tr>
<tr>
<td>Light ground</td>
<td>6,5</td>
<td>1.80</td>
<td>0.27</td>
<td>2.17</td>
<td>0.20</td>
</tr>
<tr>
<td>Light 1.2m</td>
<td>6,5</td>
<td>1.70</td>
<td>0.29</td>
<td>1.10</td>
<td>0.34</td>
</tr>
<tr>
<td>Soil moisture</td>
<td>6,5</td>
<td>27.36</td>
<td>0.001</td>
<td>0.00</td>
<td>1.0</td>
</tr>
<tr>
<td>June</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Soil moisture</td>
<td>6,5</td>
<td>0.39</td>
<td>0.86</td>
<td>0.32</td>
<td>0.60</td>
</tr>
<tr>
<td>September</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>pH</td>
<td>6,5</td>
<td>26.88</td>
<td>0.001</td>
<td>0.00</td>
<td>0.99</td>
</tr>
<tr>
<td>Soil compaction</td>
<td>6,5</td>
<td>3.21</td>
<td>0.11</td>
<td>5.01</td>
<td>0.08</td>
</tr>
<tr>
<td>Total litter</td>
<td>6,5</td>
<td>1.77</td>
<td>0.27</td>
<td>0.17</td>
<td>0.70</td>
</tr>
<tr>
<td>Microstegium</td>
<td>6,5</td>
<td>2.33</td>
<td>0.19</td>
<td>9.00</td>
<td>0.03</td>
</tr>
</tbody>
</table>

Two-way analysis of variance results for abiotic variables collected in invaded and uninvaded plots at the six study sites. All sampling was done in June 2006 except where indicated. P-values ≤ 0.05 are bolded.
Table 3. Change over time

<table>
<thead>
<tr>
<th></th>
<th>Percent cover native species in June</th>
<th>Percent cover native species in August</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>P</td>
<td>r</td>
</tr>
<tr>
<td>Soil pH</td>
<td>0.014</td>
<td>-0.683</td>
</tr>
<tr>
<td>Soil ammonium</td>
<td>0.022</td>
<td>0.652</td>
</tr>
<tr>
<td>Percent cover <em>M. vimineum</em> in June</td>
<td>0.161</td>
<td>-0.432</td>
</tr>
<tr>
<td>Percent cover <em>M. vimineum</em> in August</td>
<td>0.343</td>
<td>-0.300</td>
</tr>
</tbody>
</table>

Correlations (Pearson product-moment) of biotic variables (*M. vimineum* cover in June and August) and resource variables (soil pH, soil ammonium) with native cover in June and August. P-values ≤ 0.05 are bolded. N=12.
Figure 1. Plant community

(a) Species richness

- "a" invaded
- "a" uninvaded

(b) Native cover (%)

- "a" invaded
- "a" uninvaded

(c) Microstegium virens cover (%)

- "a" invaded
- "b" uninvaded

Legend:
- "a" invaded
- "b" uninvaded
Difference in species richness (a), native species abundance (b), and *M. vimineum* abundance (c) among invaded and uninverted plots for the June, August and September sampling dates. Native and exotic species are not represented separately in (a) as exotic species richness was low (5 species), did not differ among plots and changed little through time. To emphasize differences between invaded and uninhibited plots, pairwise comparisons were made only within each month and P-values Bonferroni corrected to account for multiple comparisons among plot means.
Cumulative native species richness and exotic species richness were positively correlated in uninvaded plots (black circles) but not in invaded plots (grey squares).

Pearson correlation; uninvaded plots: \( P=0.014, r=0.90, n=6 \); invaded plots: \( P=0.206, r=0.60, n=6 \).
Figure 3. Similarity of plant communities

Similarity of standing vegetation community composition between invaded and uninvaded plots and sample months (standing vegetation only). Hollow triangles represent invaded plots and solid triangles represent uninvaded plots. Numbers indicate site (110, 128, 156, 162, 166, 170) and capital letters represent sample months (J=June, A=August, S=September). Microstegium vimineum data were removed from the dataset for this analysis so that the rest of the community could be compared. The uninvaded plot at site 128 was primarily bare ground. With site 128 removed, native cover, soil compaction, soil pH explain the variation seen among plots. With site 128 included, soil moisture explains most of the variation.