

Non-native grass invasion alters native plant composition in experimental communities

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Abstract Invasions of non-native species are considered to have significant impacts on native species, but few studies have quantified the direct effects of invasions on native community structure and composition. Many studies on the effects of invasions fail to distinguish between (1) differential responses of native and non-native species to environmental conditions, and (2) direct impacts of invasions on native communities. In particular, invasions may alter community assembly following disturbance and prevent recolonization of native species. To determine if invasions directly impact native communities, we established 32 experimental plots (27.5 m²) and seeded them with 12 native species. Then, we added seed of a non-native invasive grass (*Microstegium vimineum*) to half of the plots and compared native plant community responses between control and invaded plots. Invasion reduced native biomass by 46, 64, and 58%, respectively, over three growing seasons. After the second year of the experiment, invaded plots had 43% lower species richness and 38% lower diversity as calculated from the Shannon index. Nonmetric multidimensional scaling ordination showed a significant divergence in composition between invaded and control plots. Further, there was a strong negative relationship between invader and

native plant biomass, signifying that native plants are more strongly suppressed in densely invaded areas. Our results show that a non-native invasive plant inhibits native species establishment and growth following disturbance and that native species do not gain competitive dominance after multiple growing seasons. Thus, plant invaders can alter the structure of native plant communities and reduce the success of restoration efforts.

Keywords Biomass · Diversity · *Microstegium vimineum* · Japanese stiltgrass · Species richness · Species evenness · Species-accumulation curve · Ordination

Introduction

Biological invasions are commonly considered to have strong ecological and economic impacts (e.g. Mack et al. 2000; Pimentel et al. 2000; Byers et al. 2002), but few studies have directly quantified the influence of invasions on native community composition (Parker et al. 1999; Maron and Marler 2008). In addition, it is often unclear if (1) invasions are driving observed differences in native communities, or if (2) invaders and natives are responding differently to changes in the environment (MacDougall and Turkington 2005). Under the first model, community composition is determined by direct competition for

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resources between species in the community, both native and invasive. For example, Maron and Marler (2008) showed that three non-native grassland invaders in the western US directly suppressed established native species through competitive dominance. The second model proposes that the composition of communities is determined not by competitive interactions, but because dispersal limitation or natural or anthropogenic disturbance favors non-native over native species. Supporting this model, Seabloom et al. (2003) found that invasive annual grasses dominate in California grasslands because of disturbance and inadequate dispersal of native perennial species, not because they are competitively superior. The ongoing introduction of non-native species necessitates more rigorous evaluations of the impacts of invasions on the structure and composition of native communities, and the underlying mechanisms facilitating invasions (Parker et al. 1999; Levine et al. 2003). Distinguishing between invasive species as drivers of change in communities versus differential responses of invasive and native species to environmental perturbations will help shape management solutions and more clearly define the effects of invasions on native systems (Byers et al. 2002; Corbin and D'Antonio 2004; MacDougall and Turkington 2005).

Disturbances are known to play a key role in promoting plant invasions (Hobbs and Huenneke 1992; Lonsdale 1999; Mack et al. 2000), but less is known about how invasions alter the assembly of native communities following disturbances. It is not clear if reductions in native species following disturbance are due to the failure of native species to colonize and survive under disturbed conditions or if invasive plants are directly responsible for reducing native plant success (Seabloom et al. 2003; Corbin and D'Antonio 2004; MacDougall and Turkington 2005). Distinguishing between these two possibilities has important implications for the conservation and restoration of native communities, especially in areas prone to natural or anthropogenic disturbance. For example, if native species are competitively dominant but limited by dispersal, then actively restoring natural areas after disturbances by adding seed would allow native species to dominate over non-native invaders. Alternatively, if invaders are responsible for changes in native community assemblages following disturbance, then introductions of native species

would have to coincide with invasive species removal.

To quantify the impacts of invasions in structuring native communities, studies are required that experimentally manipulate the presence of the invasive species (Parker et al. 1999; Byers et al. 2002). Most previous studies to evaluate the effects of invasions have used container experiments (e.g. Dukes 2001; Leicht et al. 2005), observational, non-experimental studies (e.g. Holmes and Cowling 1997; Oswalt et al. 2007), or removal experiments (Gorchov and Trisel 2003; Biggerstaff and Beck 2007; Flory and Clay 2009). Such methods have limited ability to directly and realistically quantify the effects of invaders on native communities (Aarssen and Epp 1990; McLellan et al. 1995; Parker and Reichard 1998). The optimum method for isolating the effects of invasive species on resident communities is through experimental introductions (Parker et al. 1999; Byers et al. 2002). Experimentally adding non-native species to native communities using a randomized approach controls for differences in environmental conditions and initial plant community composition. In addition, experimental field studies provide more realistic biotic interactions (e.g. herbivores, pathogens, mutualists), soil conditions, spatial scale, and climatic variation than container studies with uniform environments. Although experimental introductions can provide better measures of the effects of invasions than other methods, care must be taken to prevent accidental introductions into natural areas and to ensure no invaders remain at the conclusion of the experiment. Despite the advantages of experimental introductions, they have only rarely been used to quantify the impacts of plant invasions on whole plant communities (e.g. Callaway et al. 1999; Corbin and D'Antonio 2004; Davis et al. 2005; Maron and Marler 2008).

Here we evaluate the impact of an invasive annual grass (*Microstegium vimineum* Trin. A. Camus, Japanese stiltgrass) on the biomass, diversity, and composition of native plant communities. *Microstegium* was introduced to North America in the early 20th century (Fairbrothers and Gray 1972) but has only recently been recognized as a widespread invader in eastern deciduous forests. It has been found in forest openings and bottomland areas and along roads, streams, and trails (Barden 1987; Cole and Weltzin 2004) in more than 20 states (USDA and

NRCS 2005). In this study we compare control field plots to experimentally invaded plots following an artificial disturbance to quantify the effects of *Microstegium* on native plant community assembly. Because *Microstegium* grows at high densities and produces abundant biomass (Flory 2009), particularly after natural or anthropogenic disturbances (Glasgow and Matlack 2007; Oswalt and Oswalt 2007; Marshall and Buckley 2008), we hypothesized that invaded plots would have reduced native species biomass and diversity, and altered community composition compared to control plots. The results of this experimental study provide a direct measure of the impact of a plant invasion on native communities and contribute to the development of restoration strategies.

Methods

Experimental design

We conducted this study at the Indiana University Research and Teaching Preserve's Bayles Road site (39°13'9"N, 86°32'29"W) near Bloomington, Indiana. The area was historically covered by bottomland hardwood forest but openings have been maintained for agriculture and biological research on the site for more than 60 years. We established our experiment in a 60 m × 60 m opening surrounded by mature tree species typical of bottomland areas in the lower Midwest including box elder (*Acer negundo*), tulip poplar (*Liriodendron tulipifera*), and sycamore (*Platanus occidentalis*). Prior to our study, the area was dominated by old field species and mowed to prevent tree encroachment.

To establish the experiment, we first tilled the area every 2 weeks for 6 weeks during late summer 2005 to reduce the resident species seed bank and provide homogenous experimental conditions. In September 2005, we randomly arranged 32 plots (5.25 m × 5.25 m) at 2.5 m spacing. Each plot was surrounded by 60 cm tall silt fence buried 10 cm deep to prevent movement of seeds among plots. All plots were sown with 12 native herbaceous species corresponding to recommended seeding rates (~seeds/m²) for natural areas restoration: *Andropogon gerardii* (60), *Asclepias incarnata* (15), *Aster novae-angliae* (35), *Calamagrostis canadensis* (56), *Carex vulpinoidea* (42), *Elymus virginicus* (71), *Helenium autumnale* (33),

Panicum virgatum (41), *Senna hebecarpa* (7), *Scirpus atrovirens* (49), *Scirpus cyperinus* (109), and *Verbena hastata* (33; seeds collected in Indiana by Heartland Restoration Services, Ft. Wayne, IN). These species were chosen because they commonly occur in wet meadows and open woodlands in the Midwest, habitats where *Microstegium* often invades (Redman 1995; Cole and Weltzin 2004; Flory 2009). After the native species were planted in all plots, half of the otherwise identical plots ($n = 16$) were sown with locally collected *Microstegium* seed at a rate of ~690 seeds/m², corresponding to observed seedling densities in locally invaded sites (S. L. Flory, unpublished data). No other treatments were applied. Plots were subjected to ambient abiotic (e.g. light, precipitation, temperature) and biotic (e.g. herbivores, pathogens) conditions. A number of species not planted into the experiment colonized from the surrounding area.

This experimental design allowed us to isolate the effects of *Microstegium* on resident and planted species under controlled conditions. The bottomland semi-shaded field site we chose is typical of habitats where *Microstegium* commonly invades, but invasions also occur at sites with much different environmental characteristics, from deeply shaded forest interiors to full sun wildlife openings (Cole and Weltzin 2004; Flory 2009). The results presented here provide an important measure of the impacts of *Microstegium* on native community biomass, diversity, and community composition, but interactions between this invader and native species may vary across broad scale environmental conditions.

Data collection

To quantify the effects of *Microstegium* on native plant communities, we conducted destructive harvests in early September 2006, 2007, and 2008. Eight 30 cm × 30 cm quadrats were harvested from each plot in 2006, six in 2007, and four in 2008. Quadrat locations for each year did not overlap. All herbaceous vegetation in each quadrat was clipped at ground level, sorted in the lab, dried at 60°C to constant mass, and weighed (±0.01 g). Samples for 2006 and 2007 were sorted to species. The 2008 harvest was only sorted to separate *Microstegium* and all other species. Data was collected as biomass per area, and not number of stems or individuals. It was not possible to distinguish *Microstegium* individuals

in the field because of high density, extensive tillering, and rooting at the nodes. Data for resident species was collected in the same manner for consistency.

Data analysis

To determine if there were differences in *Microstegium* biomass, native biomass, and total community biomass between control and invaded plots and among the 3 years of the study, we averaged biomass values across quadrats within plots and analyzed plot averages with repeated measures ANOVA (Proc TTEST; SAS Institute Inc 2002). The same analysis was used to evaluate differences in native species richness, evenness, and diversity between control and invaded plots for 2006 and 2007. The *Microstegium* addition treatment was a fixed factor and year the repeated factor (Proc GLM, SAS Institute Inc 2002). Plot was the level of replication. We used post-hoc Tukey HSD tests to evaluate differences between treatments within years.

The Shannon diversity index of each quadrat was calculated based on the proportional biomass of each species (Magurran 1988): $H' = -\sum[(p_i)(\ln p_i)]$, where p_i is the proportion of the total quadrat biomass belonging to the i th species (Krebs 1989). Because comparing Shannon values across treatments can provide inaccurate estimates of the magnitude of differences among treatments (Hill 1973; Jost 2006), Shannon values were converted to the effective number of species ($e^{H'}$), the number of species present if all were equally common (MacArthur 1965; Jost 2006). Evenness was calculated as $J' = H'/(\ln S)$, where S = species richness (Pielou 1975).

Estimates of species richness will increase towards an asymptote as sampling intensity increases (Bunge and Fitzpatrick 1993). Therefore, small sample sizes may not accurately estimate species diversity differences between treatments (Gotelli and Colwell 2001). To better analyze differences in species richness between the control and invaded plots for 2006 and 2007, we computed species accumulation curves (i.e. sample-based rarefaction; Gotelli and Colwell 2001) based on the number of plots sampled using EstimateS software (Colwell et al. 2004; Colwell 2005).

Microstegium biomass varied among the experimentally invaded plots so the effect of the invasion

on native species may have depended on *Microstegium* abundance. We used linear regression (Proc REG, SAS Institute Inc 2002) to evaluate the effect of *Microstegium* biomass on native species biomass and diversity.

To determine if the composition of native species was affected by the invasion treatment, we used nonmetric multidimensional scaling analysis (NMS) with a Bray-Curtis distance measure (PC-ORD, McCune and Mefford 1999). We only included species that occurred in at least 5% of the plots (McCune and Grace 2002). Monte Carlo tests were used to test if the NMS ordination was significantly different from random data. We tested for differences between the control and invaded plots using the multi-response permutation procedure (MRPP) in PC-ORD, a non-parametric method for testing multivariate differences between groups (Zimmerman et al. 1985).

Results

No *Microstegium* was found in control plots in 2006 or 2007 but a small amount of *Microstegium* was found in two control plots in 2008 (Fig. 1a). There was significantly more *Microstegium* in invaded than control plots (treatment: $F_{1,30} = 155.87$, $P < 0.0001$) and invader biomass varied across the 3 years (year: $F_{2,60} = 5.18$, $P = 0.0084$). There was also a year \times treatment interaction for invader biomass ($F_{2,60} = 5.12$, $P = 0.0088$). *Microstegium* biomass declined by an average of 27% between 2006 (32.5 g/quadrat) and 2007 (23.9 g/quadrat) but increased by an average of 59% between 2007 and 2008 (37.9 g/quadrat; Fig. 1a).

The *Microstegium* invasion treatment significantly reduced native community biomass (treatment: $F_{1,30} = 49.49$, $P < 0.0001$) and there was a marginal statistical interaction between year and treatment ($F_{2,60} = 3.08$, $P = 0.0532$; Fig. 1b). In 2006, average native biomass was reduced by 46% in invaded plots compared to control plots (28.8 vs. 15.6 g/quadrat). The effect of invasion was even stronger in 2007 where invaded plots (12.4 g/quadrat) contained 64% less native plant biomass than control plots (34.2 g/quadrat; Fig. 1b). In 2008, there was 58% less native biomass in invaded plots compared to control plots (14.4 vs. 34.1 g/quadrat). There was no overall effect

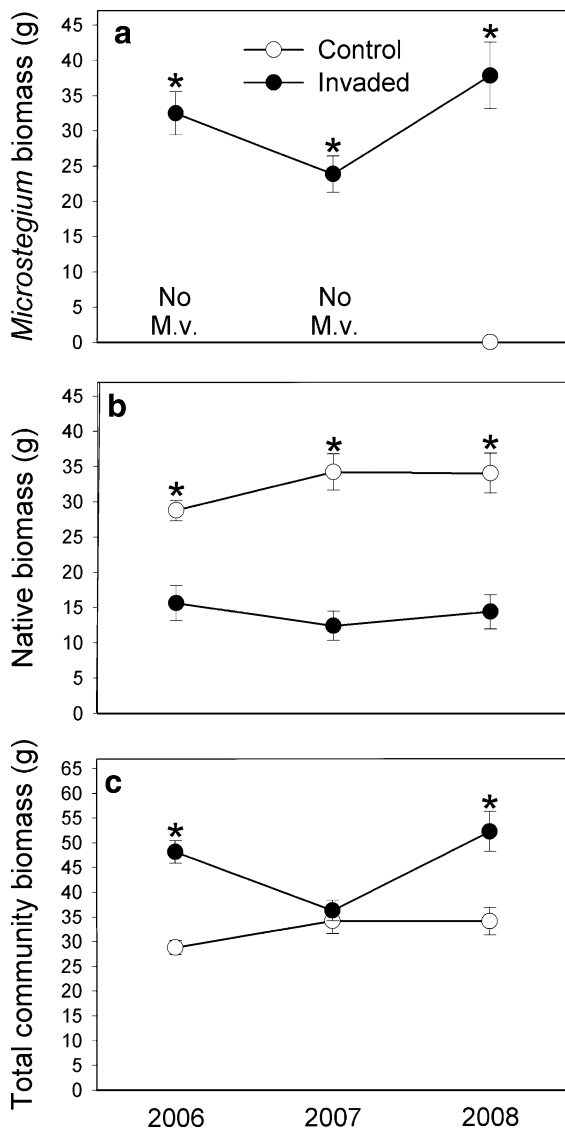


Fig. 1 Average (\pm SE) *Microstegium* (a) native community (b) and total community (c) biomass (g/quadrat) in control and invaded plots in 2006, 2007, and 2008. No *Microstegium* was found in control plots in 2006 or 2007 but two control plots contained small amounts of *Microstegium* in 2008. Asterisks indicate significant differences ($P < 0.001$) between treatments within years

of year on native plant biomass ($F_{2,60} = 0.64, P = 0.5324$). Across the 3 years, total plant community biomass (including *Microstegium*) was greater in invaded than control plots ($F_{1,30} = 28.19, P < 0.0001$) and there was a year \times treatment interaction ($F_{2,60} = 7.66, P = 0.0015$; Fig. 1c). This interaction corresponded to significantly greater total community biomass in

invaded than control plots in 2006 and 2008 but not 2007 (Fig. 1c).

We planted 12 native species in all plots, but identified up to 17 species per plot, indicating that species also germinated from the seed bank or naturally recruited into the plots. In *Microstegium* invaded plots, there was on average 19% lower native species richness in 2006 and 43% lower species richness in 2007 (treatment: $F_{1,30} = 19.48, P = 0.0001$; Fig. 2a). There was significantly lower overall richness across treatments in 2007 than 2006 (year: $F_{1,30} = 92.81, P < 0.0001$) and a stronger effect of the invasion treatment (year \times treatment: $F_{1,30} = 19.96, P = 0.0001$). There was no overall effect of the invasion on species evenness (treatment: $F_{1,30} = 2.65, P = 0.1138$; Fig. 2b) but there was an effect of year ($F_{1,30} = 12.64, P = 0.0013$) and a marginal year \times treatment interaction ($F_{1,30} = 2.99, P = 0.0939$) because of lower species evenness in invaded plots in 2007. Average native species diversity (as calculated from Shannon index) was significantly lower in invaded compared to control plots (treatment: $F_{1,30} = 10.16, P = 0.0033$). There was lower overall diversity across the treatments in 2007 than 2006 (year: $F_{1,30} = 35.70, P < 0.0001$) and 38% lower diversity in invaded than control plots (year \times treatment: $F_{1,30} = 5.78, P = 0.0226$; Fig. 2c). In 2007 13 species occurred in the control plots that were not found in the invaded plots. In contrast, only five species occurred in the invaded plots that were not found in the control plots.

Species accumulation curves for the control and invaded treatments in both years nearly reached an asymptote (Fig. 3), indicating that our sampling procedure captured most of the species richness within the study area. Differences in expected native species richness calculated by rarefaction were consistent with the results from the destructive harvest with fewer native species in invaded plots for 2006. In 2007, there were even greater differences between treatments with *Microstegium* invasion reducing expected species richness by 18% (78 vs. 64 species) when all 16 pooled samples were evaluated (Fig. 3).

There was a strong negative relationship between average *Microstegium* biomass per plot and native species biomass for both 2006 (slope = $-0.55, r^2 = 0.46, F_{1,14} = 11.91, P = 0.004$) and 2007 (slope = $-0.48, r^2 = 0.37, F_{1,14} = 8.34, P = 0.01$; Fig. 4a). There was no statistical relationship between *Microstegium* biomass and native species

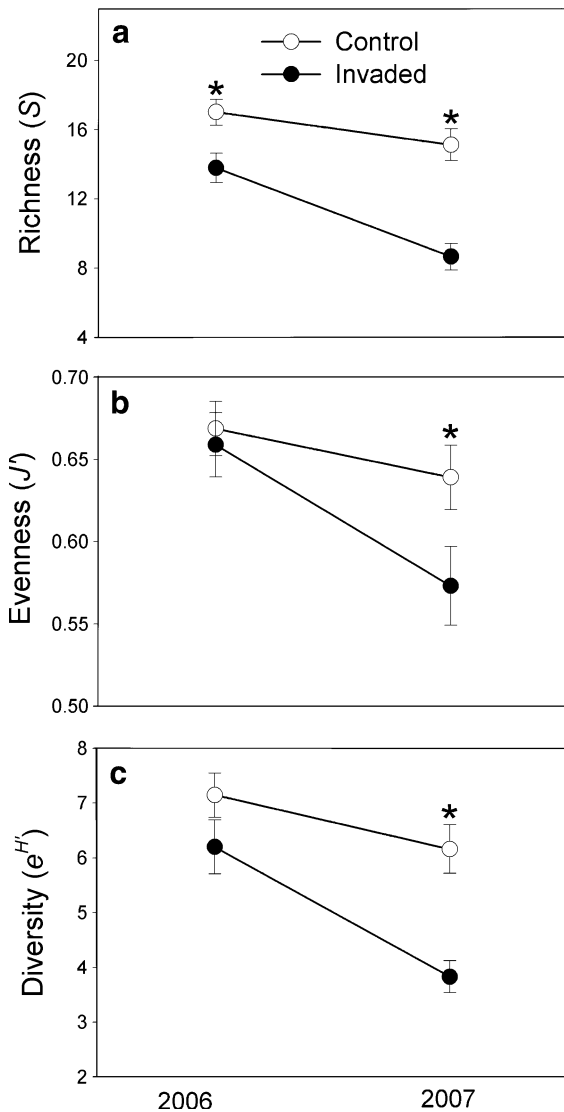


Fig. 2 Average (\pm SE) native species richness (a), evenness (b), and diversity (c) per quadrat in control and invaded plots in 2006 and 2007. Asterisks indicate significant differences ($P < 0.05$) between treatments within years

diversity in 2006 (slope = -0.05 , $r^2 = 0.17$, $F_{1,14} = 1.84$, $P = 0.17$) or 2007 (slope = -0.04 , $r^2 = 0.13$, $F_{1,14} = 2.24$, $P = 0.13$; Fig. 4b). The resident community was not identified by species in 2008. *Microstegium* biomass had a stronger negative effect on native community biomass than on native species diversity.

Nonmetric multidimensional scaling ordination and multi-response permutation procedure revealed that the *Microstegium* invasion treatment caused a significant divergence in native species composition between treatment groups ($P < 0.0001$; Fig. 5). The

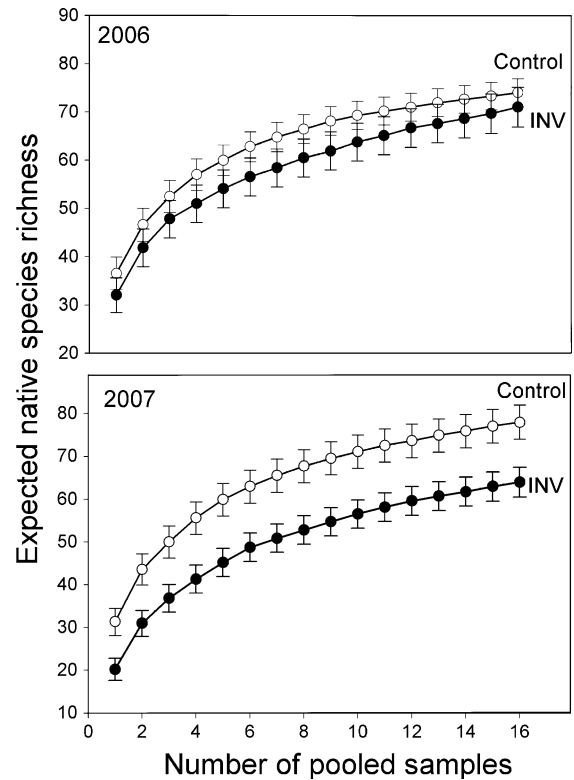


Fig. 3 Species accumulation curves estimated by sample-based rarefaction for the invaded (INV) and control plots in 2006 and 2007. The expected numbers of native species are given for 0–16 pooled samples

optimum ordination included three axes, which explained 35.1, 29.4, and 16.6% of the variation, respectively. Monte Carlo tests showed that the NMS ordination differed from random data ($P = 0.0323$). The biomass of *Microstegium* in the plots explained 72.7% of the variation in axis 1 and percent gravimetric soil moisture (data not shown) explained 52.7% of the variation in axis 2 (Fig. 5).

Discussion

Our results show that an invasive plant can exert significant negative effects on native plant communities over three growing seasons. Native plant biomass was reduced and native species composition shifted due to the invasion (Fig. 6). Reductions in native biomass and richness were evident after one growing season but changes in native species diversity calculated from Shannon index did not occur

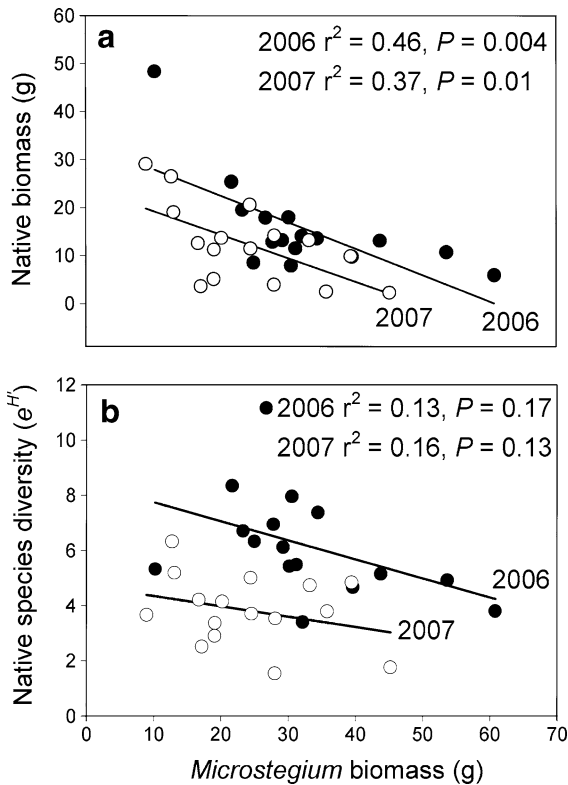


Fig. 4 Relationships between native community and *Microstegium* biomass (g/quadrat; **a**) and between native species diversity ($e^{H'}$) and *Microstegium* biomass (**b**) for 2006 and 2007

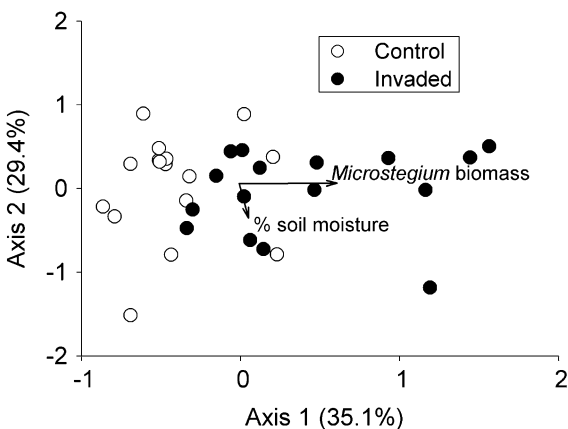


Fig. 5 Nonmetric multidimensional scaling ordination of the average biomass of native species in control plots and plots invaded by *Microstegium*. Each point represents a plot and the distance between points is directly proportional to the difference in composition among the plots. The length of the vectors is proportional to the amount of variation explained by *Microstegium* biomass (72.7%) for axis 1 and percent soil moisture (52.7%) for axis 2



Fig. 6 Example of a control plot (**a**) and a plot invaded by *Microstegium vimineum* (**b**). Note the difference in native plant abundance and diversity

until after the second season. Furthermore, after the second year of invasion, the biomass of the invader was strongly related to reductions in native plant biomass. Importantly, by experimentally introducing the invader, we are assured that differences in the native community are due to the direct effect of the invasion and not the result of differences in environmental conditions or an artifact of the study design. More generally, invasion altered native community assembly following disturbance, suggesting that restoration practices must consider both the establishment of desirable native species and invasions of non-native species.

Recent studies have suggested that invasive plants may be ‘passengers’ in communities that are structured by environmental change or dispersal limitation (Seabloom et al. 2003; Corbin and D’Antonio 2004; MacDougall and Turkington 2005). Native species may then become increasingly dominant over time

following disturbance. Our results show that *Microstegium* suppressed native plant biomass immediately after the experiment was established, and remained dominant over subsequent years. Thus, *Microstegium* appears to be 'driving' the differences in native community structure. Invaded communities also exhibited reduced diversity and altered composition after the second year of the study, and the difference in native plant biomass between control and invaded plots was significantly different following the third growing season. *Microstegium* was also more abundant in the third year of the study than in previous years, suggesting that the invader was maintaining dominance. Further study is needed to determine if invader dominance and native suppression would be sustained over many growing seasons, but we have no evidence to suggest that native species can gain dominance in this system once disturbances cease. *Microstegium* has been invasive for less than 10 years in the lower Midwest so its long term interaction with native communities is unknown.

Our results are consistent with previous studies on the effects of *Microstegium* on native species. Leicht et al. (2005) conducted competition experiments with *Microstegium* and two native grass species in a greenhouse and found that the effect of *Microstegium* on native species was as much as 27 times greater than intraspecific competition. In our previous work, we used a mesocosm experiment in the field to show that *Microstegium* reduced the growth of native graminoids, but only under part shade conditions (Flory et al. 2007). In an observational study, Oswalt et al. (2007) found negative correlations between *Microstegium* cover and woody seedling density and diversity in areas recently harvested for timber. Given these previous results and the experimental data provided here, it is clear that *Microstegium* invasions can have significant negative consequences for native plant communities.

In our study, *Microstegium* was less abundant in 2007 than in 2006 or 2008, possibly due to drought conditions (NOAA and NCDC 2008). Despite this pattern, invader impacts on native species diversity were more pronounced in 2007 than in 2006. Drought can result in increased competition between invaders and natives for limited resources (Hamilton et al. 1999). However, other mechanisms besides direct interspecific competition may also contribute to reduced native biomass. *Microstegium* forms a dense

litter layer that is slow to decompose (Ehrenfeld et al. 2001), which could inhibit native seedling emergence and survival. The stronger effects of invasion on diversity and biomass in 2007 may have resulted from the dense litter layer formed by the senescence of plants from previous years. Although no experimental data on the effects of *Microstegium* litter are available, Lenz et al. (2003) found that the litter of other invasive annual grasses in Australia decreased native species richness and facilitated the growth of the invasive grasses. In addition to the physical effects of litter on native plant species, *Microstegium* can alter soil microbial conditions and nutrient cycling processes (Ehrenfeld et al. 2001). *Microstegium* immobilizes soil nitrogen by uptaking high levels of nitrogen and decomposing slowly, leaving fewer nutrients available for native species (Ehrenfeld et al. 2001). Thus, changes in soil microbial function and nutrient availability may have also contributed to the decline of native species. *Microstegium* may also affect native species through other mechanisms, such as changing soil moisture, light availability, or herbivore pressure. Additional studies are needed to identify and evaluate the strength of specific mechanisms by which *Microstegium* invasions reduce native plant community biomass and diversity.

The availability of resources such as light and water and the degree of litter disturbance may alter the rate of *Microstegium* spread and its effects on native communities (Oswalt and Oswalt 2007; Marshall and Buckley 2008). We conducted our experiment in a forest opening and tilled the soil to provide homogenous experimental conditions. Under natural field conditions, invaded sites likely vary in resource availability and the degree of anthropogenic or natural disturbances, which might alter the effects of invasion on native communities. Further evaluating the effects of *Microstegium* across natural areas with a range of environmental conditions and disturbance regimes would be challenging, but would provide a more complete assessment of the impacts of invasion on native systems.

The overall effect of a plant invasion can be quantified by multiplying total area invaded, abundance, and some measure of impact per unit (Parker et al. 1999). *Microstegium* has invaded more than 20 US states (USDA and NRCS 2005) and observational reports indicate that it is rapidly spreading throughout the eastern US and expanding its range north- and

westward (Redman 1995; Overlease and Overlease 2007). Given the strong per-biomass effects of *Microstegium* on native species documented here, the extent of its range, and high abundance at some field sites (Oswalt et al. 2007; Flory 2009), the cumulative effect of *Microstegium* on native plant communities is clearly very large.

In sum, after one growing season *Microstegium* invaded plots had reduced native biomass. After two seasons, invasion reduced native plant biomass and diversity, and significantly altered native community composition. Three growing seasons after the initial disturbance, native species biomass had still not recovered relative to control plots. Our results have implications for restoration efforts because the success of desirable species is often impacted by invasions of non-native plants. Despite adding a diverse assemblage of native species and recruitment of many additional species from the seed bank and surrounding area, native species were inhibited by the invasion. Future research priorities should be to determine the mechanisms by which *Microstegium* and other invaders suppress native species, and to identify conditions that encourage native species in invaded areas.

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