



# Experimental plant invasion reduces arthropod abundance and richness across multiple trophic levels

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Plant invasions are known to have negative impacts on native plant communities, yet their influence on higher trophic levels has not been well documented. Past studies investigating the effects of invasive plants on herbivores and carnivores have been largely observational in nature and thus lack the ability to tease apart whether differences are a cause or consequence of the invasion. In addition, understanding how plant traits and plant species compositions change in invaded habitats may increase our ability to predict when and where invasive plants will have effects that cascade to animals. To assess effects on arthropods, we experimentally introduced a non-native plant (*Microstegium vimineum*, Japanese stiltgrass) in a community re-assembly experiment. We also investigated possible mechanisms through which the invader could affect associated arthropods, including changes in native plant species richness, above-ground plant biomass, light availability and vegetation height. In experimentally invaded plots, arthropod abundance was reduced by 39%, and species richness declined by 19%. Carnivores experienced greater reductions in abundance than herbivores (61% vs 31% reduction). Arthropod composition significantly diverged between experimentally invaded and control plots, and particular species belonging to the abundant families Aphididae (aphids), Formicidae (ants) and Phalacridae (shining flower beetles) contributed the most to compositional differences. Among the mechanisms we investigated, only the reduction in native plant species richness caused by invasion was strongly correlated with total arthropod abundance and richness. In sum, our results demonstrate negative impacts of *M. vimineum* invasion on higher trophic levels and suggest that these effects occur, in part, indirectly through invader-mediated reductions in the richness of the native plant community. The particularly strong response of carnivores suggests that plant invasion could reduce top-down control of herbivorous species for native plants.

Non-native, invasive plants can affect the composition, structure, and function of native ecosystems (Simberloff 1996, Ehrenfeld 2003, Mack and D'Antonio 2003), at times suppressing the regeneration of native plant species and reducing plant diversity (Maron and Marler 2008, Adams and Engelhardt 2009). Invasive plants may also have cascading effects that move up through the food web to influence other trophic levels, yet much less is known about these impacts. The effects of plant invasions on arthropods in particular may have strong ecological consequences. Arthropods influence ecosystems not only as important links in the food web, but also as pollinators, decomposers, and predators of pest insects ( Losey and Vaughan 2006).

Reported effects of invasive species on arthropod composition, diversity or abundance appear to be idiosyncratic. Some studies have reported lower arthropod diversity, abundance or richness in invaded areas relative to uninvaded, reference areas (Slobodchikoff and Doyen 1977, Mgobozi et al. 2008, Wu et al. 2009), while others found higher arthropod diversity or

abundance in invaded habitats (Sax 2002, Harris et al. 2004, Pearson 2009). Differences among studies may reflect differences in the particular groups of arthropods or plant invaders under investigation. For example, Lindsay and French (2006) found that the invasive weed *Chrysanthemoides monilifera* reduced the abundance of ants, thrips and spiders, but increased numbers of millipedes, pseudoscorpions and isopods. Idiosyncratic patterns may also result from the lack of experimentation. Thus far, studies have compared arthropod composition among naturally invaded and uninvaded, reference areas (Sax 2002, Harris et al. 2004, Standish 2004, Lindsay and French 2006, Mgobozi et al. 2008, Pearson 2009), but, to our knowledge, have not experimentally manipulated invader presence (but see the restoration treatments of Gratton and Denno (2005)). The observation of lower arthropod abundance in invaded versus reference areas could reflect a cause of the invasion (e.g. spread of invader due to the absence of natural enemies) or a consequence of the invasion (e.g. presence of the invader reduces arthropod abundance), or alternatively may result from underlying environmental differences between areas where the invader is present versus absent (e.g. divergence in resource availability).

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The ability to predict whether arthropod groups will respond positively or negatively to plant invasions could also be improved by a better understanding of the mechanisms through which invasive plants alter arthropod habitats. Invasive plants can affect a variety of community and ecosystem characteristics that may influence associated arthropods. For example, the increase in millipede abundance associated with *Chrysanthemoides* invasion has been suggested to result from the darker, moister microclimate created by the invader (Lindsay and French 2006). Similarly, reductions in tick survival caused by invasion of the exotic grass *Microstegium vimineum* were associated with higher temperature and reduced humidity during the tick questing season (Civitello et al. 2008). To better predict the extent of plant invader effects, more studies are needed to identify the traits of invaders as well as associated changes in the plant community and microenvironment that may underlie responses by arthropods.

We used a community re-assembly experiment to study the impacts on arthropod communities and potential mechanisms underlying invasion by Japanese stiltgrass *Microstegium vimineum*. First documented in the United States in 1919 (Fairbrothers and Gray 1972), *M. vimineum* has now spread to more than 20 eastern states (USDA-NRCS 2005). It is a persistent invader that can grow in diverse light environments (Flory 2010) and is found in riparian zones, flood plains, damp fields, swamps and alongside human-disturbed areas (Fairbrothers and Gray 1972, Cole and Weltzin 2004). Negative impacts of *M. vimineum* invasion on native herbaceous communities have been recently documented in observational and experimental studies (Oswalt et al. 2007, Adams and Engelhardt 2009, Flory and Clay 2009, 2010). Experimental evidence has shown that *M. vimineum* can reduce native herbaceous plant biomass by up to 64% and diversity by up to 38%; invaded areas also exhibited significantly different native species composition than control areas (Flory and Clay 2010). Removing the invader from field sites with a grass specific herbicide allowed for the return of native graminoids and forbs, and up to 123% more native tree regeneration than in areas where invasions were left intact (Flory and Clay 2009).

Although the effects of *M. vimineum* on native plants are well documented, how this invasion affects arthropod abundance or diversity remains unknown. Because herbivorous insect damage levels are typically low in the introduced range of *M. vimineum* (Bradford et al. 2010, pers. obs.), we anticipated negative effects of the invader on arthropods, particularly herbivorous insects. The reduction in herbaceous plant diversity that accompanies *M. vimineum* invasion also led to the expectation that arthropod diversity would decline, given the documented positive relationship between arthropod diversity and plant diversity in some systems (Crisp et al. 1998, Siemann 1998, Siemann et al. 1998, Knops et al. 1999, Haddad et al. 2001, 2009, but see Root 1973, Andow 1991, Hawkins and Porter 2003). Here, we describe an experiment that introduced *M. vimineum* together with native plant species to simulate the scenario where the invader and native species are simultaneously colonizing an area. This pattern of invasion occurs often when *M. vimineum* and native species colonize a newly disturbed site at the same time (e.g. following timber harvest, water scouring, etc.).

Furthermore, differences in plant community composition in our assembly experiment converged on differences observed between naturally invaded and invader-removed habitats (Flory and Clay 2009). We used this experimental addition of the invader to test the following specific questions: 1) does *M. vimineum* invasion reduce arthropod abundance, richness, evenness or diversity? 2) are impacts of *M. vimineum* consistent across trophic groups? And 3) does *M. vimineum* invasion alter arthropod composition (abundances of individual species)? In addition, we quantified changes in total plant productivity, native plant species diversity, light availability, and vegetation height to address, 4) through what mechanisms may *M. vimineum* affect the arthropod community?

## Methods

### Study site

We conducted the study at the Indiana Univ. Research and Teaching Preserve, Bayles Road site (39°13'9"N, 86°32'29"W) near Bloomington, Indiana, USA. The experiment was established in a 60 × 60 m opening in an area that was historically bottomland hardwood forest. We located plots in a space that was mowed regularly for at least the prior 20 years and was previously dominated by the grasses *Poa pratensis* and *Lolium arundinaceum* as well as several old field weeds. This habitat is representative of where *M. vimineum* commonly invades (Cole and Weltzin 2004, Flory 2010), often after natural or anthropogenic disturbances (Oswalt et al. 2007).

### Experimental design

First, we tilled the field every two weeks for six weeks during late summer 2005 to reduce the resident seed bank. Then, in September 2005, we randomly arranged 32 plots (5.25 × 5.25 m) at 2.5 m spacing. Each plot was surrounded by 60 cm tall silt fence buried 10 cm to prevent movement of seeds among plots. In September 2005, we sowed all 32 plots with a mixture of 12 native herbaceous species corresponding to recommended seeding rates (-seeds m<sup>-2</sup>) for natural areas restoration (Heartland Restoration Services, Ft. Wayne, Indiana, USA): *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 were collected by Heartland Restoration Services, Ft. Wayne, Indiana, USA. To impose the invasion treatment, we sowed locally collected *M. vimineum* seeds in half of the plots (n = 16) at a rate of -690 seeds m<sup>-2</sup> corresponding to observed seedling densities at nearby invaded sites (SLF pers. obs.).

In addition to the invader treatment, we also applied a tree planting treatment to inform future restoration strategies. Native trees were added to plots either as seeds or as one-year-old saplings. For the seed treatment, in the fall of 2005 half of the plots with *M. vimineum* (n = 8) and half

of the plots without *M. vimineum* ( $n = 8$ ) were planted with nine species of native trees (seeds  $\text{plot}^{-1}$ ): *Carya laciniosa* (20), *Fraxinus pennsylvanica* (190), *Juglans nigra* (34), *Liquidambar styraciflua* (1470), *Liriodendron tulipifera* (685), *Platanus occidentalis* (1855), *Quercus alba* (22), *Quercus macrocarpa* (40) and *Quercus palustris* (28). We purchased seeds from Vallonia State Tree Nursery, Vallonia, Indiana, USA. Tree seeding rates were adjusted to account for unequal germination rates to achieve similar numbers of each tree species per plot. We planted the five large-seeded species (*Carya laciniosa*, *Juglans nigra*, and *Quercus alba*, *Q. macrocarpa* and *Q. palustris*) on a  $12 \times 12$  grid with 0.4 m between each seed, and we sowed the smaller seeded species haphazardly throughout the plots. For the sapling treatment, in the remaining plots ( $n = 16$ ) we planted four one-year old seedlings of each of the nine tree species ( $6 \times 6$  grid, 0.75m apart) in early spring 2006.

## Data collection

We used sweep net methods to sample arthropods (heavy canvas Bioquip net, 40 cm diameter, 60 cm long handle, with 15 sweeps per plot). We acknowledge that sweep net methods alone may limit our ability to completely characterize the arthropod response. However, the large number of individuals collected was sufficient to assess the invader's effect on aerial, above-ground arthropods, particularly carnivores and herbivores, which were the focus of this study. Samples were collected during the third growing season post-establishment in the early afternoon on 19 June 2008 (sunny, 28°C) and 10 September 2008 (sunny, 22.2°C). These two dates were chosen to capture early and late season arthropod responses in the third year of re-assembly. Our results should therefore not be misinterpreted to represent effects that may be seen in different years or stages of re-assembly. Specimens were stored in Ziploc bags and frozen immediately. In the laboratory, we used three standard testing sieves with mesh sized 4.00 mm, 2.36 mm and 1.00 mm to sort each set of sweeps. Each specimen was classified to order, family and recognizable taxonomic unit (RTU), with the exception of aphids, caterpillars, and small (<5 mm long) flies and wasps. Of the specimens classified to RTU, 25% were also identified to genus and/or species using taxon-specific keys (e.g. we did not key out singletons, see also Rudgers and Clay 2008). Aphids were only identified to family because of the high abundance of specimens and nymphs. Caterpillars were uncommon and difficult to identify after specimens had been frozen. Flies and wasps <5 mm were sorted only to order due to their small size and difficulties in identification. Spiders were classified to species or RTU within each plot to obtain estimates of spider species richness, and counts of the most abundant species were tracked across plots: *Araneus pratensis*, *Argiope trifasciata* (Araneidae), *Oxyopes salticus* (Oxyopidae) and *Xysticus* nymphs (Thomisidae). A representative of each species or RTU was preserved in a reference collection stored at Rice Univ., Houston, Texas, USA. We also classified each specimen by trophic position into the following groups: carnivores (predators and parasitoids), parasitoids only, herbivores or decomposers. No other trophic group (e.g. pollinators, fungivores) was abundant enough to allow for robust statistical analysis.

## Exploring possible mechanisms: plant response variables

We evaluated multiple possible mechanisms through which the invader could affect arthropods. To quantify the diversity and abundance of native plants, we destructively harvested six  $30 \times 30$  cm quadrats from each plot during the first week of September 2007. All vegetation was removed to ground level, sorted to species in the lab, dried to constant weight, and weighed. We completed a second round of destructive harvests the first week of September 2008, using four quadrats per plot, but we only quantified native plant and *M. vimineum* biomass, rather than sorting the samples by species. Quadrat locations for 2007 and 2008 did not overlap. On 19 June and 10 September 2008 we measured the height of the tallest vegetation at four regularly spaced locations within each plot. At those same four locations, we also measured light as photosynthetically active radiation (PAR) under litter/thatch (ground level), at 0.5 m, and above the canopy (full sun).

## Data analysis

### Repeated measures M/ANOVA

To test for an overall arthropod response to the treatments, we conducted factorial MANOVA on total abundance, arthropod richness (number of RTUs), diversity (Shannon index, H) and evenness (Shannon J) averaged across the two dates, with the independent factors of invader treatment (invaded or control), tree planting treatment (tree seeds or saplings) and all interactions. An initial multivariate analysis was preferred for two reasons: differences among treatments may be evidenced by a suite of responses rather than by one single variable, and initial MANOVA helps to protect against type I error (Scheiner 2001). Plot was the unit of replication. Following significant treatment effects in the multivariate model, we then applied repeated measures ANOVA with the repeated factor of date (June or September), and we corrected for inflated type I error associated with the four response variables using Holm's method (Holm 1979). If an effect of treatment on total abundance or richness was significant, we then examined the response of each trophic group separately, including carnivores (which combined predators and parasitoids), parasitoids alone, herbivores, or decomposers. Within each type of response (abundance or richness), we again corrected for multiple response variables (i.e. multiple trophic groups) using Holm's method. Because spiders constituted 40% of the total carnivore population, we also tested the effects of treatments on spider abundance and richness. To further explore responses of carnivores and herbivores, we analyzed the ratio of herbivores to carnivores (square-root transformed). To meet assumptions of normality of residuals and homogeneity of variances, abundances for all trophic groups required log transformation.

To assess possible spatial autocorrelation in arthropod responses, we also included x- and y-coordinates for each plot as covariates in the analyses. While the y-coordinate explained significant variation in some responses, such as arthropod abundance and richness, it did not qualitatively alter the significance of the treatment effects, and in fact slightly reduced p-values, making results stronger. For

simplicity, we present results of analyses without these additional spatial location covariates.

### Rarefaction

Effects of treatments on arthropod richness are not necessarily independent of the treatment effects on abundance because the probability of detecting a new species increases with the number of individuals collected (Gotelli and Colwell 2001). To evaluate whether the response of arthropod richness was driven by differences in abundance between the treatments, we generated sample-based rarefaction curves using each plot as a replicate (Colwell and Coddington 1994) in EstimateS (Colwell 2009) with 500 randomization runs (re-sampled with replacement). We chose Chao1 as the best estimator of richness (Chao 1984).

### Nonmetric multidimensional scaling analysis

To examine treatment effects on arthropod composition, we applied nonmetric multidimensional scaling analysis (NMS) with a Bray–Curtis distance measure, 10 000 iterations and 500 restarts (PRIMER ver. 6, Clarke and Gorley 2007). We only included RTUs that occurred in >5% of the samples following recommendations in McCune and Grace (2002). To test for treatment and date effects, we used analysis of similarities (ANOSIM) (PRIMER, Clarke and Gorley 2007). ANOSIM detects differences in species assemblages between two or more groups (Clarke et al. 2006). Due to the lack of effects of the tree planting treatment (unpubl.), we tested for invasion treatment by date interactions using two-way crossed ANOSIM (10 000 permutations) including the independent factors of treatment (invaded/control) and date (June/September), as well as one-way ANOSIM with four levels (one for each date × treatment combination), which yielded similar results. To identify which arthropod taxa contributed most to the differences among invader treatments, we used SIMPER analysis (Clarke and Gorley 2007). Because dates differed in species composition, SIMPER was applied within each date (Supplementary material Appendix 1).

### Exploring possible mechanisms: indirect effects of the invader

The mechanisms driving arthropod declines could involve both the direct effects of invader presence as well as indirect effects, for example, mediated through changes in plant composition. To explore possible indirect effects, we included the following potential mechanisms as covariates in repeated measures ANCOVA: total plant productivity (above-ground biomass (g)), native plant species richness, the above-ground biomass of native plant species, and percentage reduction in light availability at ground level and at 0.5 m above ground level. To compare the strengths of potential direct versus indirect pathways for arthropods, we contrasted two repeated measures statistical models (SAS 2004 ver. 9.1.3, SAS Inst.). The first model included only the invasion and tree planting treatments (direct + indirect effects model). The second model also included the potential indirect pathway as a covariate, including the covariate × treatment interactions (direct effects model; see also methods in Rudgers and Clay 2008). A significant covariate × treatment interaction would indicate that the relationship between the covariate and the response variable depended on the

presence of the invader, and this was retained in the model if statistically significant. We examined the responses of total arthropod abundance, richness, and evenness with each potential mechanism as a covariate. Low replication of plots precluded the ability to test all mechanisms simultaneously (e.g. with structural equation modeling). In addition, to examine trophic group responses, we used herbivore abundance as a covariate for carnivore abundance. If the arthropod response was highly correlated with the indirect pathway (i.e. the covariate), and the invasion treatment in this covariate model became non-significant relative to the direct + indirect effects model, we interpreted this as evidence of an indirect pathway of the invader effect. It should be noted that these models test for correlation, not causation (e.g. while arthropod abundance may track plant diversity, plant

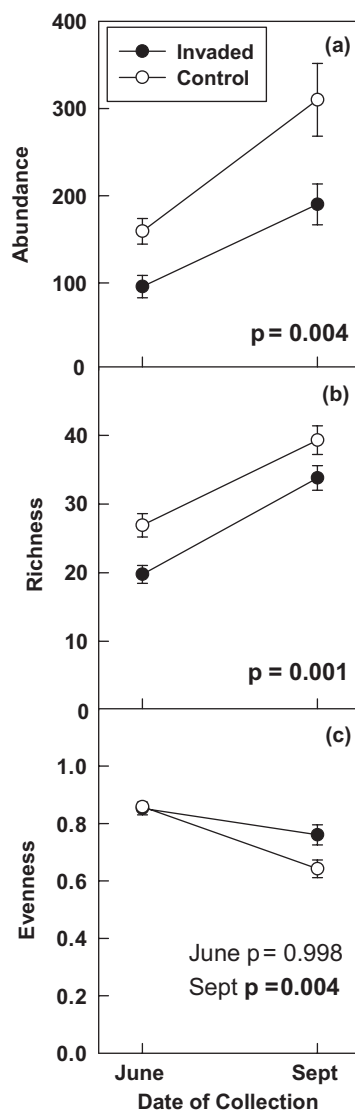


Figure 1. Differences between invaded and control plots in total arthropod abundance (a), richness (b), evenness (c) and diversity (d) for two sampling dates, June and September 2008. Symbols show means per plot ± SE. p-values are shown for the main effect of the invader treatment, and are given separately for each date when the invader × date interaction was significant in repeated measures ANOVA. p-values appear in bold if significant following Holm's correction.

diversity may also reflect past arthropod herbivory). In addition, including a covariate necessarily reduces power, which would increase type II error. However, we used these analyses in an exploratory manner to suggest causal hypotheses that could be tested with future experiments.

## Results

Across the two census dates, we collected 12 899 arthropod individuals. These included 324 RTUs, spanning 80 families and 11 arthropod orders.

### Does *M. vimineum* invasion reduce arthropod abundance, richness, evenness or diversity?

Invasion reduced both arthropod abundance and richness (Fig. 1, Table 1). The MANOVA showed significant effects across all arthropod responses for the invader treatment (Pillai's trace = 0.34,  $F_{4,25} = 3.2$ ,  $p = 0.029$ ), but not for the tree planting treatment (Pillai's trace = 0.09,  $F_{4,25} = 0.7$ ,  $p = 0.630$ ) or the invader  $\times$  tree planting interaction (Pillai's trace = 0.03,  $F_{4,25} = 0.2$ ,  $p = 0.946$ ). Averaged over the two dates, there were 39% fewer arthropod individuals and 19% fewer RTUs in the presence of *M. vimineum* (Fig. 1a–b). Despite the declines in abundance and richness, arthropod evenness was 18% higher in the presence of the invader, but only in September (Fig. 1c), as indicated by a significant interaction between date  $\times$  invader treatment (Table 1). For arthropod diversity, although there was a significant date  $\times$  invader interaction (Table 1), post-hoc comparisons between invaded and control plots on each date were non-significant (Tukey HSD June,  $p = 0.166$ ; September,  $p = 0.098$ ); this lack of response in diversity likely reflects the opposing effects of invasion on arthropod richness (decreased) and evenness (increased). Our different methods for re-establishing native trees (seeding vs sapling) had no significant effect on overall arthropod responses (Table 1).

When samples were rarefied to similar abundances, the effect of the invasion treatment on arthropod richness was no longer significant as indicated by the 95% confidence intervals around Chao1 (Fig. 2). Thus, the difference in arthropod richness between invaded and control plots was largely due to the increased probability of detecting new species when greater numbers of individuals were present. Saturating rarefaction curves for both June and September

data indicated that increased sampling effort would not alter the patterns observed (Fig. 2).

### Are impacts of *M. vimineum* consistent across trophic groups?

The presence of *Microstegium vimineum* significantly reduced arthropod abundance and richness within specific trophic groups. Carnivores (predators and parasitoids) declined in abundance by 61% in invaded plots (Table 2, Fig. 3a). Within the carnivore group, parasitoids (> 5 mm in length) were reduced by 70% (mean abundance per plot  $\pm$  SE: control,  $1.44 \pm 0.26$ ; invaded,  $0.44 \pm 0.47$ ; Table 2), and spiders by 45% (Table 2, Fig. 3d). Despite 31% lower herbivore abundance in invaded plots, effects of the experimental invasion on herbivore abundance only showed a trend towards significance ( $p = 0.057$ , Table 2, Fig. 3b). Thus, the ratio of herbivores to carnivores was significantly higher in invaded plots (control,  $2.92 \pm 0.54$ ; invaded,  $4.97 \pm 0.87$ ;  $F_{1,28} = 5.68$ ,  $p = 0.024$ ). The stronger effect on carnivores was not driven by a higher relative abundance, as herbivores were the more abundant trophic group. Invasion also caused significant reductions in the richness of carnivores (32% lower), and marginally significant reductions (following Holm's correction) in parasitoid richness (57%) and herbivore richness (15%) (Table 2, Fig. 3c). The only trophic group not significantly affected by invasion was the decomposers (Table 2, Fig. 3), which were likely underrepresented by our sweepnet methods. Decomposers represented just 8% of the total individuals per sample. Planting seeds versus saplings to re-establish native trees did not affect arthropod trophic groups or interact with the invasion treatment (Table 2).

### Does *M. vimineum* invasion alter arthropod composition?

Arthropod species composition diverged between the invasion treatments as demonstrated by non-metric multidimensional scaling analysis and ANOSIM (Fig. 4; date  $R = 0.821$ ,  $p = 0.0001$ ; invader  $R = 0.201$ ,  $p = 0.0001$ ). In June, one ant species (*Monomorium* sp., minimum group) and aphids contributed most to the differences in composition between treatments (Supplementary material Appendix 1). The ant was the most abundant taxon and the aphids were the third most abundant taxon that we observed, thus these influences

Table 1. Results from repeated measures ANOVA for total arthropod abundance, richness, evenness and diversity responses to the invader treatment, tree planting treatment, and time. p-values that were significant following Holm's (1979) correction for the four response variables are shown in bold.

|                                     | DF   | Abundance |                  | Richness |                  | Evenness |                  | Diversity |              |
|-------------------------------------|------|-----------|------------------|----------|------------------|----------|------------------|-----------|--------------|
|                                     |      | F         | p                | F        | p                | F        | p                | F         | p            |
| Invader treatment                   | 1,28 | 10.0      | <b>0.004</b>     | 12.7     | <b>0.001</b>     | 3.1      | 0.087            | 0.0       | 0.868        |
| Tree planting treatment             | 1,28 | 0.1       | 0.732            | 0.0      | 0.972            | 0.1      | 0.722            | 0.6       | 0.461        |
| Invader $\times$ Tree               | 1,28 | 0.4       | 0.554            | 0.4      | 0.530            | 0.0      | 0.985            | 0.1       | 0.760        |
| Date                                | 1,28 | 26.5      | <b>&lt;0.001</b> | 56.8     | <b>&lt;0.001</b> | 48.7     | <b>&lt;0.001</b> | 2.6       | 0.122        |
| Date $\times$ Invader               | 1,28 | 1.4       | 0.246            | 0.2      | 0.648            | 7.8      | <b>0.009</b>     | 10.4      | <b>0.003</b> |
| Date $\times$ Tree                  | 1,28 | 0.2       | 0.634            | 3.0      | 0.093            | 0.3      | 0.609            | 0.3       | 0.575        |
| Date $\times$ Invader $\times$ Tree | 1,28 | 0.0       | 0.898            | 0.2      | 0.673            | 0.2      | 0.625            | 0.5       | 0.471        |

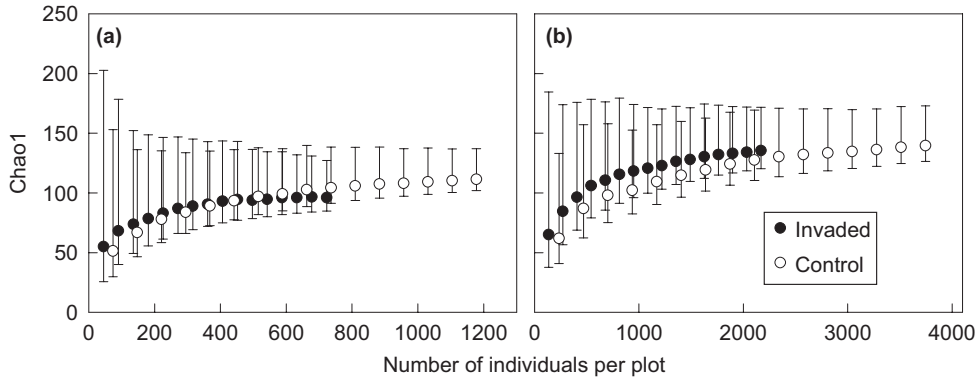


Figure 2. Rarefaction curves plotting Chao1 versus the number of individuals sampled in response to *M. vimineum* invasion treatment for June (a) and September (b) 2008. Bars show 95% CI.

likely reflect the high abundances of these particular clades. In September, invasion reduced the abundance of aphids by 46% and one beetle species by 76% (no. 20, *Olibrus* sp., Phalacridae; note: current *Olibrus* taxonomy precludes identification to species, M. Gimmel pers. comm.), and these two taxa contributed most to compositional dissimilarity (Supplementary material Appendix 1). These two taxa were also the two most abundant in September. All RTUs contributing >3% to the compositional differences were more prevalent in control plots than invaded plots, with only one exception: individuals of one leafhopper species (*Dikraneura abnormis*, Typhlocybininae, Cicadellidae) were 540% more abundant in invaded plots in September (Supplementary material Appendix 1).

### Through what mechanisms may *M. vimineum* affect the arthropod community?

Native plant species richness was the singular indirect mechanism underlying the reduction in arthropod species richness and abundance. Native plant species richness was positively correlated with both arthropod richness and abundance. When statistical models accounted for changes in native plant species richness, this covariate was highly positively correlated with arthropod richness ( $F_{1,27} = 18.53$ ,  $p < 0.001$ ), and the *M. vimineum* treatment no longer significantly reduced arthropod richness (Fig. 5;  $F_{1,27} = 0.03$ ,  $p = 0.861$ ). The same pattern was observed for arthropod abundance, where native plant species richness was positively

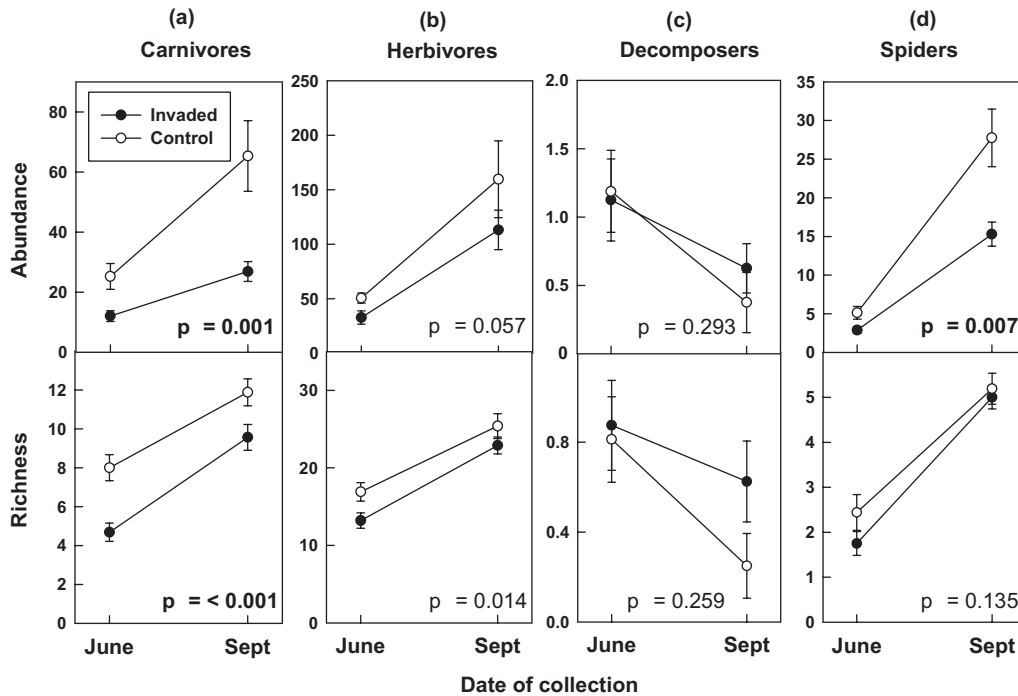


Figure 3. Differences between invaded and control plots in arthropod RTU richness and abundance for carnivores (a), herbivores (b), decomposers (c) and spiders (d) per plot for two sampling dates, June and September 2008. Symbols show means per plot  $\pm$  SE. p-values are shown for the main effect of the invader treatment in repeated measures ANOVA and are bolded if significant following Holm's correction.

Table 2. Results from repeated measures ANOVA for responses in the abundance and richness of four trophic groups (carnivores, herbivores, parasitoids and decomposers) as well as spiders to the invader treatment, tree planting treatment and time. Spiders were included separately because they accounted for 40% of the carnivore group. p-values that were significant following Holm's (1979) correction for the five groups are shown in bold.

|                         | DF   | Abundance  |                |            |                |             |              |             |              |         |                |
|-------------------------|------|------------|----------------|------------|----------------|-------------|--------------|-------------|--------------|---------|----------------|
|                         |      | Carnivores |                | Herbivores |                | Parasitoids |              | Decomposers |              | Spiders |                |
|                         |      | F          | p              | F          | p              | F           | p            | F           | p            | F       | p              |
| Invader treatment       | 1,28 | 13.4       | <b>0.001</b>   | 3.9        | 0.057          | 6.4         | <b>0.017</b> | 1.2         | 0.293        | 8.5     | <b>0.007</b>   |
| Tree planting treatment | 1,28 | 0.1        | 0.760          | 0.0        | 0.840          | 1.8         | 0.197        | 0.1         | 0.732        | 0.0     | 0.927          |
| Invader × Tree          | 1,28 | 0.2        | 0.641          | 0.0        | 0.857          | 0.6         | 0.438        | 0.1         | 0.752        | 0.0     | 0.864          |
| Date                    | 1,28 | 56.2       | < <b>0.001</b> | 56.3       | < <b>0.001</b> | 3.5         | 0.073        | 7.5         | <b>0.011</b> | 182.4   | < <b>0.001</b> |
| Date × Invader          | 1,28 | 0.2        | 0.653          | 1.2        | 0.292          | 0.4         | 0.523        | 1.9         | 0.177        | 3.5     | 0.073          |
| Date × Tree             | 1,28 | 0.5        | 0.474          | 4.9        | 0.036          | 0.1         | 0.728        | 4.9         | 0.035        | 1.2     | 0.279          |
| Date × Invader × Tree   | 1,28 | 0.1        | 0.783          | 0.4        | 0.527          | 11.8        | <b>0.002</b> | 0.1         | 0.819        | 2.6     | 0.121          |

|                         | DF   | Richness   |                |            |                |             |              |             |       |         |                |
|-------------------------|------|------------|----------------|------------|----------------|-------------|--------------|-------------|-------|---------|----------------|
|                         |      | Carnivores |                | Herbivores |                | Parasitoids |              | Decomposers |       | Spiders |                |
|                         |      | F          | p              | F          | p              | F           | p            | F           | p     | F       | p              |
| Invader treatment       | 1,28 | 17.3       | < <b>0.001</b> | 6.9        | 0.014          | 4.2         | 0.049        | 1.3         | 0.259 | 2.4     | 0.135          |
| Tree planting treatment | 1,28 | 0.0        | 0.855          | 0.1        | 0.755          | 0.5         | 0.498        | 0.2         | 0.626 | 3.1     | 0.089          |
| Invader × Tree          | 1,28 | 1.7        | 0.206          | 0.1        | 0.716          | 1.1         | 0.312        | 0.2         | 0.626 | 4.8     | 0.036          |
| Date                    | 1,28 | 61.4       | < <b>0.001</b> | 52.5       | < <b>0.001</b> | 2.2         | 0.151        | 6.1         | 0.020 | 90.0    | < <b>0.001</b> |
| Date × Invader          | 1,28 | 0.8        | 0.378          | 0.2        | 0.659          | 0.1         | 0.715        | 0.9         | 0.352 | 0.6     | 0.436          |
| Date × Tree             | 1,28 | 4.5        | 0.042          | 3.0        | 0.093          | 0.1         | 0.715        | 4.3         | 0.046 | 4.7     | 0.039          |
| Date × Invader × Tree   | 1,28 | 0.3        | 0.580          | 0.4        | 0.556          | 8.7         | <b>0.006</b> | 0.9         | 0.352 | 0.4     | 0.558          |

correlated ( $F_{1,27} = 5.96$ ,  $p = 0.022$ ), and the *M. vimineum* treatment became non-significant ( $F_{1,27} = 0.49$ ,  $p = 0.490$ ). In addition to native plant species richness, both the above-ground biomass of native plant species ( $F_{1,27} = 9.04$ ,  $p = 0.006$ ), and total above-ground biomass ( $F_{1,27} = 4.06$ ,  $p = 0.054$ ) were positively correlated with arthropod richness; however, the *M. vimineum* treatment remained significant (native plant biomass,  $F_{1,27} = 11.35$ ,  $p = 0.002$ ) or nearly so (total plant biomass,  $F_{1,27} = 3.81$ ,  $p = 0.061$ ) in models with either covariate. Neither the above-ground biomass of native plant species ( $F_{1,27} = 0.24$ ,  $p = 0.627$ ) nor total

above-ground biomass ( $F_{1,27} = 1.37$ ,  $p = 0.252$ ) were significant covariates for arthropod abundance. None of the following covariates explained significant variation in arthropod abundance or richness: percentage reduction in light availability at ground level, reduction in light at 0.5 m above ground level, or average vegetation height (all  $p > 0.2$ ). Finally, although herbivore abundance was positively correlated with carnivore abundance ( $F_{1,27} = 4.88$ ,  $p = 0.036$ ), the invader treatment remained significant in this covariate model ( $F_{1,27} = 16.41$ ,  $p < 0.001$ ), suggesting that effects of the invader on carnivores did not occur exclusively through indirect changes in herbivore abundance.

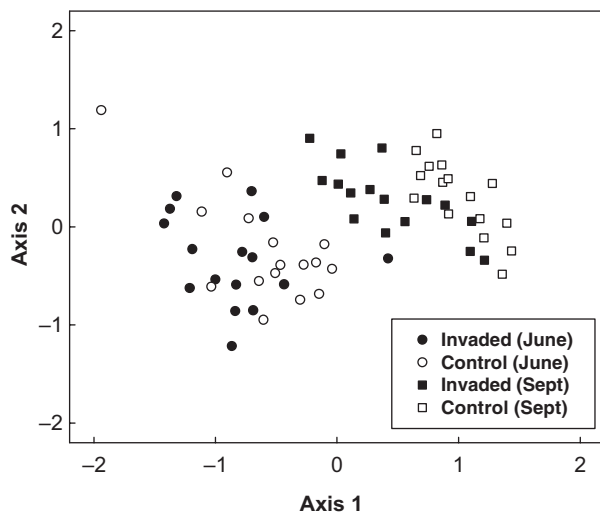


Figure 4. Nonlinear multi-dimensional scaling ordination of the cumulative abundances of each arthropod RTU. Each point represents a plot sampled either in June or September. The distance between points is proportional to the amount of compositional difference.

## Discussion

*Microstegium vimineum* invasion reduced arthropod abundance, decreased species richness and altered community composition. Comparable reductions in abundance, richness or diversity in areas invaded by other non-native plant species have been observed for beetles (Topp et al. 2008), epigeic invertebrates (Standish 2004), salt-marsh arthropods (Wu et al. 2009), sand-burrowing arthropods (Slobodchikoff and Doyen 1977) and spiders (Mgobozi et al. 2008), although none of these studies experimentally manipulated invader presence, preventing the assignment of causality. In contrast, the arthropod responses observed in our study were undoubtedly caused by the presence of the invasive plant because the invader was experimentally introduced. Our study also revealed two new patterns in arthropod response to invasion: plant invasion increased the ratio of herbivores to carnivores in the system, and the invader-mediated reduction in native plant species richness was a primary mechanism through which the invader altered arthropod composition and abundance. We reiterate that the effects of

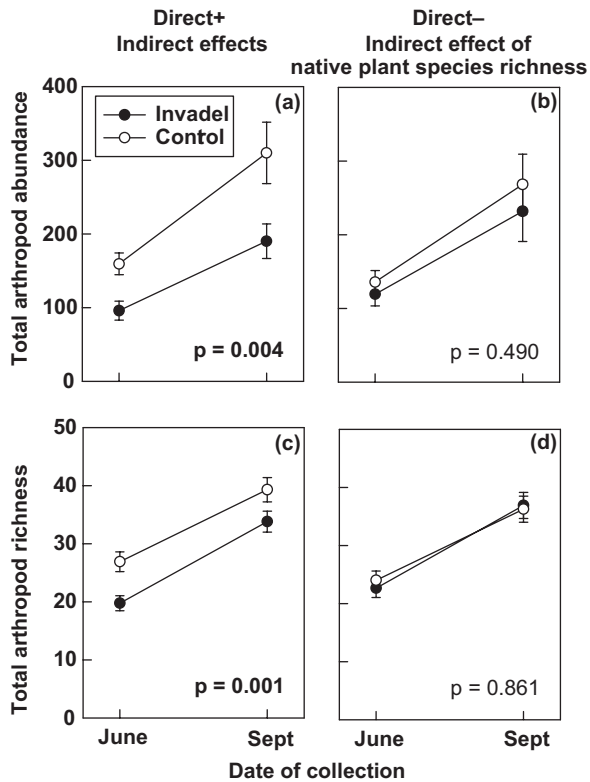


Figure 5. Effects of the *M. vimineum* invader treatment on total arthropod abundance and richness with no consideration of covariates in the direct + indirect effects models (a, c), and with native plant species richness included as a covariate in the direct – indirect effects models (b, d). Symbols show least squares means per plot  $\pm$  SE for two sampling dates, June and September 2008. p-values are given for the main effect of the invader treatment in repeated measures ANOVA, and shown in bold if significant following Holm's correction.

*M. vimineum* were not on established native plant species, but on the process of native community re-assembly. Also, these results represent the effect of the invader *M. vimineum* in the third year of re-assembly and should not be misinterpreted to represent effects over different years or stages of re-assembly. In contrast to the strong effect of invader presence, we found no effect of our tree restoration treatment (seeds vs saplings) on arthropods.

Invasions have been documented to succeed due to their release from natural enemies in the novel habitat (Keane and Crawley 2002, Colautti et al. 2004, Liu and Stiling 2006). This prediction from theory (and evidence from other systems), combined with the observation of low to no herbivory on *M. vimineum* at our sites, suggested that herbivores would be strongly reduced in invaded plots. As expected, herbivore abundances were reduced in *M. vimineum*-invaded plots. Unexpectedly, however, we found the novel result that the negative impact of invasion was greater for carnivores than herbivores. Similarly, in an 11-year study of arthropod responses to plant diversity, Haddad et al. (2009) saw a comparable shift towards an herbivore-dominated trophic structure when plant species richness was reduced. Furthermore, Marshall and Buckley (2009) found significantly more individuals in the herbivorous families Acrididae (grasshoppers)

and Cicadellidae (leaf hoppers) in areas that were naturally invaded by *M. vimineum* relative to reference sites, although this observational study reported no overall difference in arthropod richness or abundance. The higher ratio of herbivores to carnivores in invaded plots could translate into reduced top-down control of herbivorous species (Hairston et al. 1960), ultimately increasing herbivore damage to native plant species (Halaj and Wise 2001). This finding suggests that it would be useful to examine damage levels to native plants in order to explore the possible consequences of this altered herbivore:carnivore ratio.

The mechanisms underlying differential impacts of the invasion on carnivores versus herbivores remain unclear. Comparison of statistical models suggested that the reduction in carnivores due to *M. vimineum* was not exclusively an indirect consequence of the reduction in the abundance of herbivores. It is possible that other characteristics of *M. vimineum* influence carnivores directly. Specifically, in our study, spiders accounted for a large percentage (40%) of the carnivores, suggesting that the negative effect of *M. vimineum* on spiders accounts, in part, for the greater impact on carnivores than herbivores. Spiders rely on habitat structure for web-building (Gunnarsson 1990, Halaj et al. 2000), and a loss of native plant species richness due to invasion could diminish specific types of plant architectural complexity that are important to spiders (Borges and Brown 2001, Topp et al. 2008). For example, Pearson (2009) found direct effects of invasive spotted knapweed (*Centaurea maculosa*) on spiders; the invader provided more favorable structures for *Dicrytina* to build webs than did native plant species. These results were in the opposite direction of the decreases in spiders we observed for *M. vimineum*. Because grasses typically provide low structural complexity, *M. vimineum* may reduce habitat quality or quantity for some carnivores, such as web-building spiders. In support of this hypothesis, similarly negative effects on predators have been found for the grass *Phragmites* in salt marsh invasions (Gratton and Denno 2005). Our analysis did not show spider or carnivore abundances to be correlated with average plant height, yet both responses were positively correlated with native plant species richness (unpubl.). Improved measurements of plant architectural complexity could enhance understanding of the specific mechanisms of effects on carnivores. In addition, a more detailed network approach to arthropod species interactions (Heleno et al. 2009) could further illuminate trophic consequences of the invasion.

Native plant species richness appears to be a key indirect pathway through which *M. vimineum* invasion reduces arthropod abundance and richness. Of the covariates we tested, plant species richness was the only factor that was both highly positively correlated with arthropod responses and eliminated the statistical significance of the invasion treatment effect. This result suggests that plant richness, rather than total resource availability (primary productivity), is a more important driver of arthropod dynamics in this system. However, because covariate models do not imply causality, an alternative hypothesis is that *M. vimineum* alters plant species richness by changing the composition of the arthropod community (e.g. by increasing the herbivore:carnivore ratio and reducing top-down control of herbivores on native plants). Higher plant species richness might signal



the presence of greater varieties of plant structures, food sources for specialist arthropods, and microhabitats, all of which provide opportunities for increasing arthropod species richness. A positive correlation between arthropod richness and plant species richness has also been documented in other systems (Siemann et al. 1998, Haddad et al. 2001, but see Root 1973, Andow 1991, Hawkins and Porter 2003). We suggest that the impact on arthropods may also result from microclimatic changes induced by *M. vimineum* invasion. Although measures of light levels were not correlated with arthropod responses in our study, *M. vimineum* has been documented to increase the temperature and decrease the humidity of invaded plots early in the growing season, likely due to the suppression of native species (Civitello et al. 2008). These changes may reduce habitat suitability for certain arthropod species and would be worth exploring in future studies.

Although our sweepnet methods detected no effect of *M. vimineum* on decomposers, the effect of this invasion on soil arthropod communities may be another area for future investigation. When an invasive plant decreases native plant species abundance and richness, as does *M. vimineum* (Flory and Clay 2009, 2010), the reduction in the native litter and the growing amount of non-native litter may alter the decomposer community, with consequences for the ecosystem (Mayer et al. 2005, Wardle 2006). Furthermore, there is evidence that, compared to the soil below native plant species, the soil beneath *M. vimineum* has a higher pH and a higher nitrification rate, differs in the structure and function of the microbial community, and supports significantly higher earthworm densities (Kourtev et al. 1999, 2002, Ehrenfeld et al. 2001). If *M. vimineum* is the direct cause of these belowground differences, insight into soil arthropod composition could expand understanding of how the invader affects resource cycling and ecosystem functioning (Ehrenfeld et al. 2001).

Arthropods are critical to the functioning of terrestrial ecosystems, making it important to understand how to maintain their diversity and composition (Losey and Vaughn 2006). The experimental nature of our study provided strong evidence that plant invasions have significant impacts on arthropod communities. In sum, our results showed several arthropod trophic groups to be affected by plant invasion, with unexpected and particularly strong effects of invasion on carnivores.

*Acknowledgements* – The authors would like to thank: A. Cady, S. Chamberlain, C. Dietrich, C. Favret, L. Liu, S. Menke and A. Savage, and for their help in processing and/or identifying arthropods, E. Chaneton, N. M. Haddad and A. Moles for constructive comments on the text, the Rice Undergraduate Honors Research in Ecology and Evolutionary Biology class of 2009 for useful discussion, and the USDA Forest Service Hoosier National Forest, The Nature Conservancy, and the Godwin Professorship of Natural Science at Rice Univ. for funding.

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Supplementary material (available online as Appendix O18382 at [www.oikos.ekol.lu.se/appendix](http://www.oikos.ekol.lu.se/appendix)). Appendix 1.