

Plant invasion impacts on arthropod abundance, diversity and feeding consistent across environmental and geographic gradients

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Abstract Exotic plant invasion not only changes native plant communities, it also alters associated arthropod community diversity and structure. These impacts often are contradictory and context-specific by study location. *M. vimineum* is an Asian grass currently invading the eastern United States that generally escapes herbivory. The invasion impacts on arthropod communities are mixed, and the effects on arthropod food webs are largely unknown. Because *M. vimineum* has a unique $\delta^{13}\text{C}$ value, its carbon flow can be resolved from native plants in recipient food webs. We investigate arthropod communities at *M. vimineum*-invaded sites along a 100-km geographic and environmental gradient in the southeastern U.S. We investigate *M. vimineum* impacts on arthropod abundance and diversity, how *M. vimineum*-derived carbon contributes to arthropod biomass and how environmental variation modifies invasion effects on arthropod communities. We find that *M. vimineum* invasion corresponds with increased arthropod diversity and abundance, but reduced evenness. Herbivore damage to leaves is equivalent between native species and *M. vimineum*, but the type of herbivore damage is not the same between the native and invader plants. We also find that herbivores derive 37 % of their

biomass-carbon from the exotic plant but predators almost none (4 %). Detritivores derive exotic carbon (9 %) proportional to *M. vimineum* in the litter layer. Whereas exotic plant impacts on arthropod communities often seem idiosyncratic by site, we find no context-dependent invasion effects of *M. vimineum* by study location. The consistency suggests that the impacts may be broadly generalizable, at least within well-established parts of the invasion range.

Keywords Enemy release · Invertebrate · Japanese stiltgrass · *Microstegium vimineum* · Nepalese browntop · Food webs · Arthropods · Diversity

Introduction

Plant abundance and type influence arthropod community composition (Kremen et al. 1993; Price and Hunter 2005). Given that exotic plant invasions can dramatically shift vegetation structure by displacing native herbs and tree seedlings (e.g., Callaway and Walker 1997; Flory and Clay 2009), it is then not surprising that these invasions also can change arthropod communities, such as through declines in diversity and abundance (e.g., Wu et al. 2009; Litt and Steidl 2010; Simao et al. 2010; Yoshioka et al. 2010). However, arthropod diversity and abundance also can remain the same or even increase following exotic plant invasion (e.g., Sax 2002; Derraik et al. 2005;

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Bartomeus and Santamaria 2008). These varied responses highlight the need for investigations across a broad range of environmental conditions to determine generalizable invasive species impacts. If such investigations are conducted across regional gradients, with multiple local sites, then broad- and fine-scale environmental heterogeneity arising from variation in topography, climate and land-use can indicate how this heterogeneity might modify invasion impacts (e.g., Warren et al. 2011a). Given that arthropods play a central role in nutrient cycling, community interactions and food webs (Wilson 1987; Losey and Vaughan 2006), knowledge of generalizable invasion effects on arthropod communities helps determine whether plant invaders alter the structure and function of recipient ecosystems in predictable ways.

Whereas the impacts of plant invasion on arthropod community abundance and diversity are well studied (e.g., Schmitz et al. 2004; Bartomeus and Santamaria 2008; Wu et al. 2009; Litt and Steidl 2010; Simao et al. 2010; Yoshioka et al. 2010), much less is known about the extent to which exotic plant biomass is incorporated into recipient food webs. Invasion theory suggests that exotic plants escape herbivory, but empirical evidence is equivocal as to whether they become carbon sources or sinks in invaded communities (Blossey and Notzold 1995; Keane and Crawley 2002; Bossdorf et al. 2005). Herbivores can derive a substantial fraction of their body-carbon from invasive plants (e.g., Bradford et al. 2010). However, the potential lag-time between exotic invasion and the buildup of natural enemies challenges whether results from isolated case-studies can be extrapolated to broad-scale, general patterns (Diez et al. 2010). Even in long-established invasions, the extent that herbivores incorporate exotic plants into the ‘green food web’ (i.e. food webs based on aboveground, live plants) likely depends on the environmental context (e.g., a food shortage prompts a shift to the novel resource). In contrast to green food webs, time since initial invasion should have little influence on ‘brown food webs’ (i.e. those based on plant-detrital inputs to soils) because soil animals are considered to exhibit marked functional redundancy in feeding (Andren et al. 1999). This means that they feed on resources in proportion to resource availability rather than resource type, although they sometimes do select a specific plant (e.g., Smith and Bradford 2003). As such, invasive plant carbon may be incorporated into

detrital-based food webs in relation to its proportion of available plant-detrital biomass.

Microstegium vimineum (Trin.) Camus is an Asian grass that has invaded the eastern United States (see Warren et al. 2011b and references therein). Its geographic range and successful invasion across varied habitat conditions make it a useful species to investigate whether its impacts can be generalized across a broad range of environmental conditions. Notably, most reports suggest that arthropod herbivory on *M. vimineum* is low (Sanders et al. 2004; Morrison et al. 2007), and its impact on arthropod diversity and abundance is equivocal with effects reported as negative (McGrath and Binkley 2009; Simao et al. 2010) to negligible (Carroll 2003; Marshall and Buckley 2009). However, Bradford et al. (2010) showed considerable flow of *M. vimineum*-derived carbon into herbivorous arthropods at a single invasion site in a southeastern U.S. hardwood forest. The southeastern U.S. is of particular interest because *M. vimineum* was first recorded there in the early 1900s (Fairbrothers and Gray 1972). In addition, *M. vimineum* occurs across marked gradients in climate, elevation, topography and habitat type in the southeast (Warren et al. 2011a). It also has a unique $\delta^{13}\text{C}$ value because it employs the C_4 -photosynthetic pathway in habitats dominated by C_3 -plants (Horton and Neufeld 1998; Warren et al. 2011b). Use of the C_4 -pathway provides an isotopic tracer by which *M. vimineum*-derived carbon can be resolved from native plant carbon in recipient food webs.

As with understanding impacts of plant invasion on arthropod diversity and abundance, multi-site regional studies that capture environmental variation may reveal general patterns of invasive plant-carbon flow through arthropod feeding groups. We investigated arthropod communities at 36 *M. vimineum*-invaded sites arrayed equally across three general locations positioned along a 100-km geographic and environmental gradient in the southeastern U.S. The spatial design captures a wide range of environmental gradients created by broad-scale shifts in elevation and latitude (piedmont, foothills and mountains) corresponding with regional differences in climate (temperature and precipitation). Our intention was to investigate whether the invader’s impacts were generalizable within its long-established invasive range. Although our results may not apply to newer parts of *M. vimineum*’s range, they may suggest the eventual

impacts in those locations. We collected arthropod abundance, taxonomic diversity, leaf damage, and carbon isotope composition data across 36 microhabitat invasion fronts to test (1) how *M. vimineum* invasion corresponds with changes in arthropod abundance and diversity across broad-scale environmental gradients; (2) how much *M. vimineum*-derived carbon contributes to the biomass of different arthropod trophic levels; and (3) whether environmental variation across sites modifies invasion effects on arthropod community abundance, composition and feeding.

Methods

Study sites

We conducted investigations at three locations spanning a 100-km climate gradient from the northern piedmont of Georgia to the foothills of north Georgia to the southern Appalachian Mountains of North Carolina, USA (Fig. 1). The three locations were: (1) Whitehall Experimental Forest (WHF), Athens-Clarke County, GA (33°53'N, 83°21'W; 150–240 m elevation, 122 cm MAP, 17 °C MAT), (2) Chattahoochee National Forest (CNF), Habersham County, GA (34°30'N, 83°29'W, 315–450 m elevation, 153 cm MAP, 14 °C MAT) and Coweeta Hydrologic

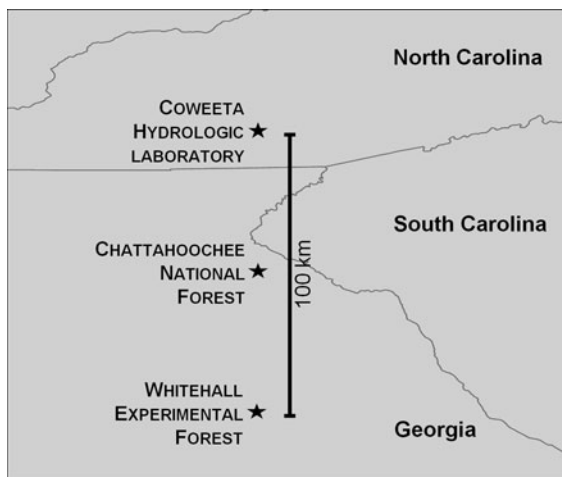


Fig. 1 Twelve transects bisecting *Microstegium vimineum* invasion fronts were established at three locations ($n = 36$ total) along a 100-km climate gradient in southeastern U.S. forests and forest edges

Laboratory (CWT), Macon County, NC, USA (35°03'N, 83°25'W; 750–1,025 m elevation, 183 cm MAP, 13 °C MAT). Four plots considered part of the CWT location were located nearby in the Little Tennessee Valley (35°04'03.57"N; 83°23'00.53"W, 612–622 m elevation) on land managed by the Land Trust for the Little Tennessee.

Plot sampling

Paired invaded and uninvaded plots were established at WHF, CNF and CWT (12 pairs at each location, $n = 72$ plots total) in May 2009 (see Warren et al. 2011a for more information on study design). The plots intersected the edge of *M. vimineum* patches in a straight 6-m line so that three 0.25 × 0.25 m quadrats fell in adjacent invaded (1, 2 and 3 m from invasion edge) and uninvaded (−1, −2 and −3 m from invasion edge) patches. The plot locations were selected for discrete invasion boundaries within apparently similar habitats (i.e., not crossing roads). Most of these occurred at or near, but did not span, forest edges. Plant subsamples consisting of 15 stems of standing aboveground biomass from each quadrat were collected and pooled for leaf damage and isotopic analyses. Subsamples were stored in plastic bags with a wet paper towel and sprayed with water to preserve freshness and to prevent the leaves from wilting. Remaining above ground plant matter was collected for plot level estimates of site productivity (see Warren et al. 2011a). *Microstegium vimineum* cover (%) and biomass (g) were measured per quadrat and pooled by plot in invaded and uninvaded samples. The *M. vimineum* vegetative biomass was collected in June–July 2009, dried at 65 °C and weighed. The biomass of all other herbaceous species, leaf litter and its coverage (%), as well as shrub coverage, also were measured, with samples collected and pooled across the three quadrats on the invaded and uninvaded sides.

Arthropods found within the aboveground plant biomass and leaf litter of each quadrat were collected by hand, and the first 10 cm of the soil were removed and sifted to collect any invertebrates in the top soil level. These samples were pooled with those collected following 40 person minutes catching aboveground invertebrates by hand and by sweep net in the area immediately surrounding each plot (delimited by the invasion edge and 3 m in all directions from the quadrats). We identified all arthropods to order for

M. vimineum-derived carbon analysis. We chose the ordinal as opposed to species level for our work because functional arthropod richness is high at the level of order but typically redundant at the species level (Moulder and Reichle 1972; Post 2002; Singer and Parmesan 2010; Hof et al. 2011).

As changes in arthropods and *M. vimineum* presence may reflect correlated responses to covarying habitat variables, we also measured diffuse light, soil moisture and temperature within each plot. All abiotic measurements were taken in the three permanent quadrats per plot and averaged. Volumetric soil moisture (%) was measured within each plot with a handheld Hydrosense Soil Water Content Measurement System (Campbell Scientific Inc., Logan, Utah, USA) in May, July and September 2009. Percent photosynthetically active radiation (PAR, diffuse light) was calculated as the difference between plot-level PAR readings and a fully exposed PAR reference site. The understory measurements were taken in July 2009 with an LI-191 line quantum sensor and the open reference measurements were taken with an LI-200 spherical PAR sensor and logged with a LI-1400 datalogger (LiCor Inc., Lincoln, Nebraska, USA). Measurements were taken on cloudy days between 10 a.m. and 2 p.m. to minimize relative error in diffuse light. Ambient soil temperature was measured with a T-shaped digital thermometer inserted 8 cm into the soil in May and September 2009.

Each native plant and *M. vimineum* leaf was examined for evidence of herbivory damage, and scored by type. The categories for damage type were: center (e.g., gastropod chewing), edge (e.g., adult Lepidoptera and Orthoptera chewing), mining (e.g., within-leaf chewing by larval Lepidoptera, Hymenoptera, Coleoptera and Diptera), and fungal disease spots (e.g., *Bipolaris* sp. Kleczewski and Flory 2010). Damaged and total leaves were counted for each plant type in each plot. Plant subsamples were then dried with remaining plant and litter samples at 65 °C and weighed. Arthropods were freeze-killed, dried at 65 °C and weighed. Plant and arthropod samples were ball milled into a fine powder and analyzed for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ ratios using continuous-flow isotope-ratio mass spectrometry (Thermo Scientific, San Jose, CA, USA).

The C_4 photosynthetic pathway creates a distinct carbon isotope ratio that can distinguish C_3 and C_4 plant biomass, and the ^{13}C signal persists in organisms

that consume the biomass (Fry 2006) enabling discrimination between *M. vimineum*- and native-derived carbon (Bradford et al. 2010). We calculated the proportion of *M. vimineum*-derived carbon in leaf litter and arthropods using a mixing model with two carbon sources (Fry 2006):

$$\% M. \textit{vimineum} \text{ derived carbon} = \frac{\delta^{13}\text{C}_{\text{sample}} - \delta^{13}\text{C}_{\text{source1}}}{\delta^{13}\text{C}_{\text{source2}} - \delta^{13}\text{C}_{\text{source1}}},$$

where $\delta^{13}\text{C}_{\text{sample}}$ is the $\delta^{13}\text{C}$ value of the biomass of the sample, $\delta^{13}\text{C}_{\text{source1}}$ is the $\delta^{13}\text{C}$ value of the native carbon source and $\delta^{13}\text{C}_{\text{source2}}$ is the $\delta^{13}\text{C}$ value of the *M. vimineum* carbon source. Given that variation in plant water-use efficiencies and photosynthetic fixation of soil-derived CO_2 can influence plant $\delta^{13}\text{C}$ values (Fry 2006), values used in the mixing models were site specific (i.e. unique to each of the 36 sites) as opposed to averaged by location or across sites.

We used a subset of all arthropods collected for isotope analysis and sorted by orders to detritivore (*Haplotaxida*, earthworms; which are not arthropods), herbivore (Orthoptera, grasshoppers, families *Tettigoniidae* and *Acrididae*) and predator (Aranae, spiders). Because herbivore (grasshopper and katydid) carbon values closely resemble their food source (Fry et al. 1978), we used the isotope values of *M. vimineum* biomass as $\delta^{13}\text{C}_{\text{source2}}$ and native biomass as $\delta^{13}\text{C}_{\text{source1}}$ to establish the proportion of *M. vimineum*-C assimilated as biomass. This approach is robust, given the direct relationship between food and body-tissue $\delta^{13}\text{C}$, whether or not the mobile herbivores foraged only within or across the invasion boundaries. Native plant biomass $\delta^{13}\text{C}$ values were typical for C_3 plants (mean \pm SE: -31.73 ± 0.49 ; $n = 36$) and those for *M. vimineum* typical for C_4 plants (-15.32 ± 0.29 ; $n = 36$). In contrast to herbivores, the food source for detritivores and predators does not necessarily derive directly from green plant biomass, instead first being partially decomposed or assimilated by lower trophic levels, respectively. These processes enrich the food sources of detritivores and predators in ^{13}C relative to the original plant carbon source. Given that these trophic groups also often feed on food sources spanning multiple stages of decay and/or trophic levels, green plant $\delta^{13}\text{C}$ values are poor tools for determining their feeding ecology (Ponsard and Arditi 2000; Scheu and Falca 2000). Instead, to

discern reliably the *M. vimineum*-C assimilated as biomass in their tissues, we used the arthropod values from uninvaded plots as $\delta^{13}\text{C}_{\text{source1}}$. Individual predators (spiders) and detritivores (earthworms) are capable of movement distances that would cross our invasion boundaries, but it is more likely that in the summer months they forage at local scales (<1 m; Ahrens and Kraus 2007; Eijsackers 2011). If foraging across our boundaries occurred, it would lead to underestimates of the amount of *M. vimineum*-derived C they assimilated. Note that soil carbonate was not a concern in our mixing model calculations because all of our sites were underlain by acidic, low-base status, Ultisols, which have no inorganic carbon accumulation. For leaf litter carbon, we used litter values from uninvaded plots as $\delta^{13}\text{C}_{\text{source1}}$ and *M. vimineum* biomass as $\delta^{13}\text{C}_{\text{source2}}$.

Data analysis

Arthropod diversity and abundance measures were calculated per plot ($n = 36$) for statistical replication: (1) abundance = total arthropods, (2) richness = arthropods by Order, (3) evenness = Pielou's evenness index (Pielou 1966) and (4) diversity = expected richness in random subsamples from the community. We included the last analysis because diversity indices are not independent of counts due to the probability of detecting additional taxa increases with sample size (Gotelli and Colwell 2001). For this reason, we used the 'rarefy' function in the Vegan package (Oksanen et al. 2011) in the R statistical Package (R Development Core Team 2009). This approach is based on Hurlbert (1971), and it is equivalent to Simpson's index while accounting for sample size bias (Smith and Grassle 1977).

We used generalized linear and linear mixed models (G/LMM) to evaluate arthropod abundance and diversity as functions of *M. vimineum* invasion, herbaceous, shrub and litter percent coverage (%), *M. vimineum* herbaceous and litter biomass (g), temperature (°C), diffuse light (%) and soil moisture (%). We employed a mixed model structure with location as a random effect to account for potential autocorrelation arising from the clustering of plots at three locations along the 100-km gradient. Because the coverage and biomass measurements were highly collinear (variance inflation factors >10), we used

Akaike's Information Criterion (AIC) values (Akaike 1973) to select the best plant fixed effects and then evaluated them with an invasion factor, abiotic effects and potential interactions. We used GLMMs assuming Poisson distributed error for arthropod abundance and species richness. Because overdispersion was high in the arthropod abundance model ($\phi > 8$), we used a lognormal Poisson model with individual-level random effects (e.g., Elston et al. 2001). We used LMMs assuming Gaussian distributed error for arthropod evenness and diversity. We also used LMMs to evaluate *M. vimineum*-derived carbon flow to detritivores, herbivores and predators from putative trophic sources: *M. vimineum*:total leaf litter carbon, *M. vimineum*:total herbaceous biomass and *M. vimineum*:total carbon in detritivores and herbivores. We included additional environmental factors as fixed effects to account for the context of the interactions. The fixed effects were: *M. vimineum*:total herbaceous cover (%), leaf litter biomass (g), invertebrate abundance, invertebrate biomass (g), soil clay content (%), temperature (°C), diffuse light (%) and soil moisture (%). Note that texture was measured on pooled soil samples from 10-cm deep, 8-cm dia. cores from each of the three quadrats per site within invaded and uninvaded plots, using a simplified version of the hydrometer method (Gee and Or 2002). The LMMs included site as a random effect assuming a Gaussian error distribution. We used AIC to select the best fixed effects and interaction terms. Because the F-statistic is not considered accurate in mixed models, making p values anticonservative, we used Markov Chain Monte Carlo sampling in the "language" package (Baayen 2007) for the R statistical programming environment (R Development Core Team 2009) to estimate the coefficients and p values for retained parameters in LMMs.

We calculated leaf damage as the binomial proportion of leaves damaged (of all leaves in a plot) by each category and used generalized linear models (GLM) to evaluate the difference in leaf damage type (center, edge, mining, spot) between *M. vimineum* and native plant leaves. Because the models were overdispersed ($\phi > 6$), we used GLMs assuming a quasiPoisson error distribution. We evaluated the slope value of the fixed effects and considered coefficients with p value <0.05 significant and coefficients with p value <0.10 marginally significant (sensu Hurlbert and Lombardi 2009).

Results

The three study sites comprise a broad-scale, annual gradient in climate (temperature and precipitation) with WHF the hottest and driest, CWT the coolest and wettest and CNF falling in between (NOAA 2009). During the 2009 growing season when data for the current study were collected, the sites generally followed a similar pattern. Mean (\pm SD) soil moisture was lowest at WHF (14.7 ± 9.1 %) but similar between CNF (21.1 ± 19.0 %) and CWT (20.4 ± 12.6 %). CWT was the shadiest site (2.0 ± 2.6 %), followed by WHF (12.5 ± 11.0 %) and CNF (19.2 ± 15.0 %). Temperature was lowest at CWT (21.0 ± 0.8 °C) but similar between CNF (24.2 ± 0.9 °C) and WHF (24.9 ± 1.7 °C).

We collected 1,696 invertebrates representing 17 orders (0.5 % unidentified spp.) across all sites. The most common orders were Orthoptera (44 %, grasshoppers, crickets), Haplotaxida (24 %, earthworms), Araneae (9 %, spiders) and Opiliones (7 %, harvestmen), and no other order accounted for >3 % of the total. Model selection (based on AIC) indicated that temperature, soil moisture, diffuse light and *M. vimineum* cover were the best predictors of arthropod abundance and diversity, but only the increase with diffuse light ($coefficient = 0.013$, $SE = 0.006$, t value = 2.432, p value = 0.015) and increase with *M. vimineum* cover ($coeff. = 0.004$, $SE = 0.002$, t value = 1.928, p value = 0.054) differed from zero (at $p < 0.1$, Fig. 2a). The effects of temperature

($coeff. = 0.055$, $SE = 0.035$, t value = 1.573, p value = 0.12) and soil moisture ($coeff. = -0.005$, $SE = 0.006$, t value = -0.927 , p value = 0.354) were not significant, and there were no interaction effects. Whereas overall arthropod abundance was higher in *M. vimineum*-invaded plots, trophic types were found in similar numbers in *M. vimineum*-invaded and uninvaded plots (detritivore, uninvaded: 6.91 ± 6.7 , invaded: 7.27 ± 5.4 ; herbivore, uninvaded: 4.71 ± 7.0 , invaded: 4.29 ± 6.0 ; predator, uninvaded: 2.75 ± 2.1 , invaded: 3.48 ± 3.2). Notable for the abundance data, and other data reported below, was the fact that *M. vimineum* effects were not dependent on other environmental variables such as temperature and moisture (i.e. there were no significant interactions), suggesting *M. vimineum* impacts were independent of environment.

Arthropod taxon richness increased with temperature ($coeff. = 0.049$, $SE = 0.026$, z value = 1.883, p value = 0.059) and decreased with litter cover ($coeff. = -0.003$, $SE = 0.002$, z value = -1.679 , p value = 0.093), and there were no interaction effects (Fig. 2b). *Microstegium vimineum* invasion was the only factor that influenced species evenness, however, and it was significantly lower in *M. vimineum*-invaded plots with no interaction effects ($coeff. = -0.035$, $pMCMC = 0.023$; Fig. 2c). Conversely, arthropod diversity was significantly higher in *M. vimineum*-invaded plots with no interaction effects ($coeff. = 0.941$, $pMCMC < 0.001$; Fig. 2d).

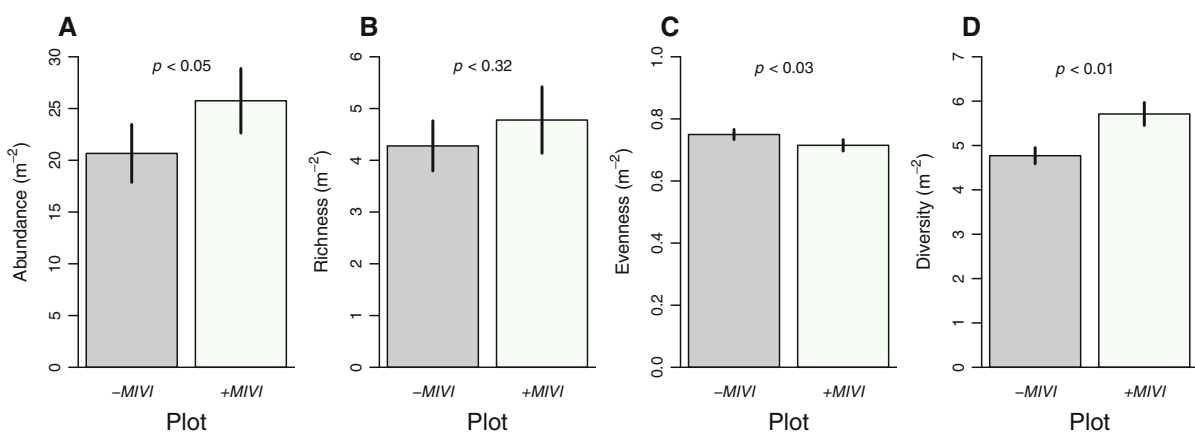


Fig. 2 Arthropod **a** abundance, **b** richness, **c** evenness and **d** diversity in *Microstegium vimineum* uninvaded ($-MIVI$) and invaded ($+MIVI$) plots ($n = 36$). Note that in some models other variables (e.g., diffuse light) also contributed significantly

to arthropod abundance and diversity, but shown here is the effect of *M. vimineum* invasion for taxon comparisons. Values are mean \pm 95 % CI

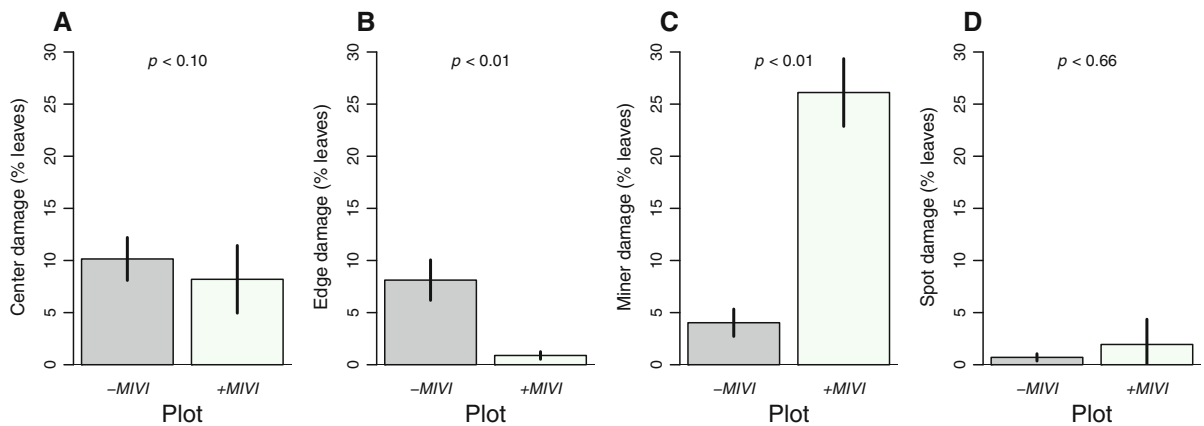


Fig. 3 Leaf herbivory scored as the percent of leaves with different damage types: **a** center (e.g., gastropod chewing), **b** edge (e.g., adult Lepidoptera and Orthoptera chewing),

c miner (e.g., within-leaf chewing by larval Lepidoptera, Hymenoptera, Coleoptera and Diptera), and **d** spot (e.g., fungal spot disease). Values are plot mean \pm 95 % CI, $n = 36$

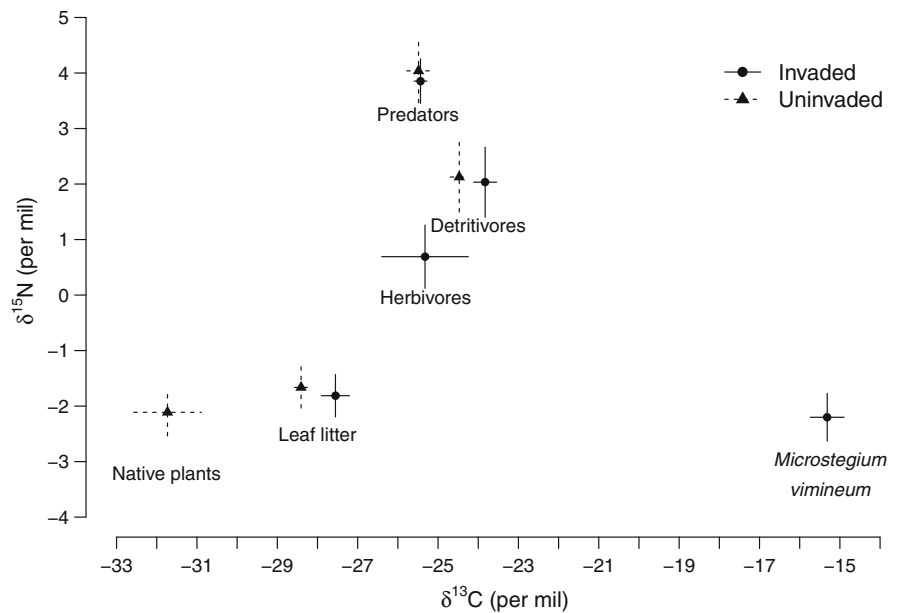
The overall number of leaves damaged by herbivory and disease was similar between *M. vimineum* (23.2 %) and native herbaceous plants (20.2 %), but the types of damage differed. *M. vimineum* plants had a significantly lower proportion of leaves damaged by center ($coeff. = -0.594$, $SE = 0.354$, t value = -1.678 , p value = 0.098) and edge ($coeff. = -2.62$, $SE = 0.466$, t value = -5.622 , p value < 0.001) chewing than native plants (Fig. 3). Conversely, *M. vimineum* plants had a significantly higher proportion of leaves damaged by mining ($coeff. = 1.67$, $SE = 0.291$, t value = 5.754 , p value = 0.001) than native plants, whereas there was no difference in leaf spot disease ($coeff. = 0.680$, $SE = 1.56$, t value = 0.437 , p value = 0.664).

As a species using the C_4 -photosynthetic pathway, *M. vimineum* had higher $\delta^{13}C$ values than co-occurring native plants (all C_3 ; Fig. 4). Significant shifts in leaf litter $\delta^{13}C$ values between uninvaded and invaded plots, with corresponding shifts in detritivore values, indicated *M. vimineum* carbon had entered detrital food webs (Fig. 4). Mixing model analysis indicated that mean (\pm SD) percent *M. vimineum* carbon in the leaf litter was 6.7 ± 6.8 %. The intermediate herbivore $\delta^{13}C$ values between native plants and *M. vimineum* values indicated that the invasive plant carbon also was incorporated into the plant-based food webs (Fig. 4). Herbivores had the highest mean (\pm SD) percentage of *M. vimineum*-derived carbon (37.2 ± 25.1 %); detritivores contained only approximately a quarter of this amount (9.1 ± 9.7 %); and predators

contained about half that (4.0 ± 4.7 %). The large errors around each of the mean estimates reflected the marked variation across the 36 sites in the extent to which the recipient food webs were incorporating *M. vimineum*-derived carbon into animal body tissues. For example, within the herbivore families *Tettigoniidae* and *Acrididae*, mean $\delta^{13}C$ values across individuals within invaded plots ranged from -31.7 to -19.7 , and -31.9 to -13.3 , respectively. That is, in some invaded plots the herbivores were deriving their carbon almost exclusively from native plants (i.e. $\delta^{13}C$ values more negative than -30) and in others almost exclusively from *M. vimineum* (i.e. $\delta^{13}C$ values between -12 and -18).

The best fitting model (based on AIC selection) for *M. vimineum*-derived carbon in detritivores only included the proportion of *M. vimineum* carbon in leaf litter (Fig. 5a). *Microstegium vimineum*-derived carbon increased significantly ($coeff. = 1.105$, $pMCMC < 0.001$) in detritivores with the amount of *M. vimineum* carbon in the proximate leaf litter. For herbivores, only the proportion of *M. vimineum* biomass in overall plant biomass corresponded with significant increases ($coeff. = 34.69$, $pMCMC < 0.048$) in *M. vimineum*-derived carbon in herbivore biomass (Fig. 5b). The best fitting model for *M. vimineum*-derived carbon in predators only included the proportion of *M. vimineum*-derived carbon in herbivores, where the amount in predators decreased significantly ($coeff. = -0.179$, $pMCMC < 0.030$) with the proportion of *M. vimineum* carbon in

Fig. 4 $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for native and *M. vimineum* plants, leaf litter, predators and detritivores in invaded and uninvaded plots, and herbivores. Note that herbivore $\delta^{13}\text{C}$ values are indicative of their proportional feeding on native plants and *M. vimineum*. Given isotopic fractionation, for other predator and detritivore feeding groups and leaf litter, incorporation of *M. vimineum* carbon into these pools is represented by a positive shift in $\delta^{13}\text{C}$ values from uninvaded plots. Values are mean \pm 95 % CI, $n = 36$



herbivores (Fig. 5c). The $\delta^{15}\text{N}$ values revealed the isotopic enrichment and hence trophic positioning expected for the plants, herbivores and predators (see Post 2002). However, although $\delta^{13}\text{C}$ is a reliable metric for revealing food sources, the reticulate nature of soil food webs means that natural abundance $\delta^{15}\text{N}$ values are unreliable for revealing trophic position of detritivores (Ponsard and Ardit 2000; Scheu and Falca 2000), which explains their enriched values (Fig. 4).

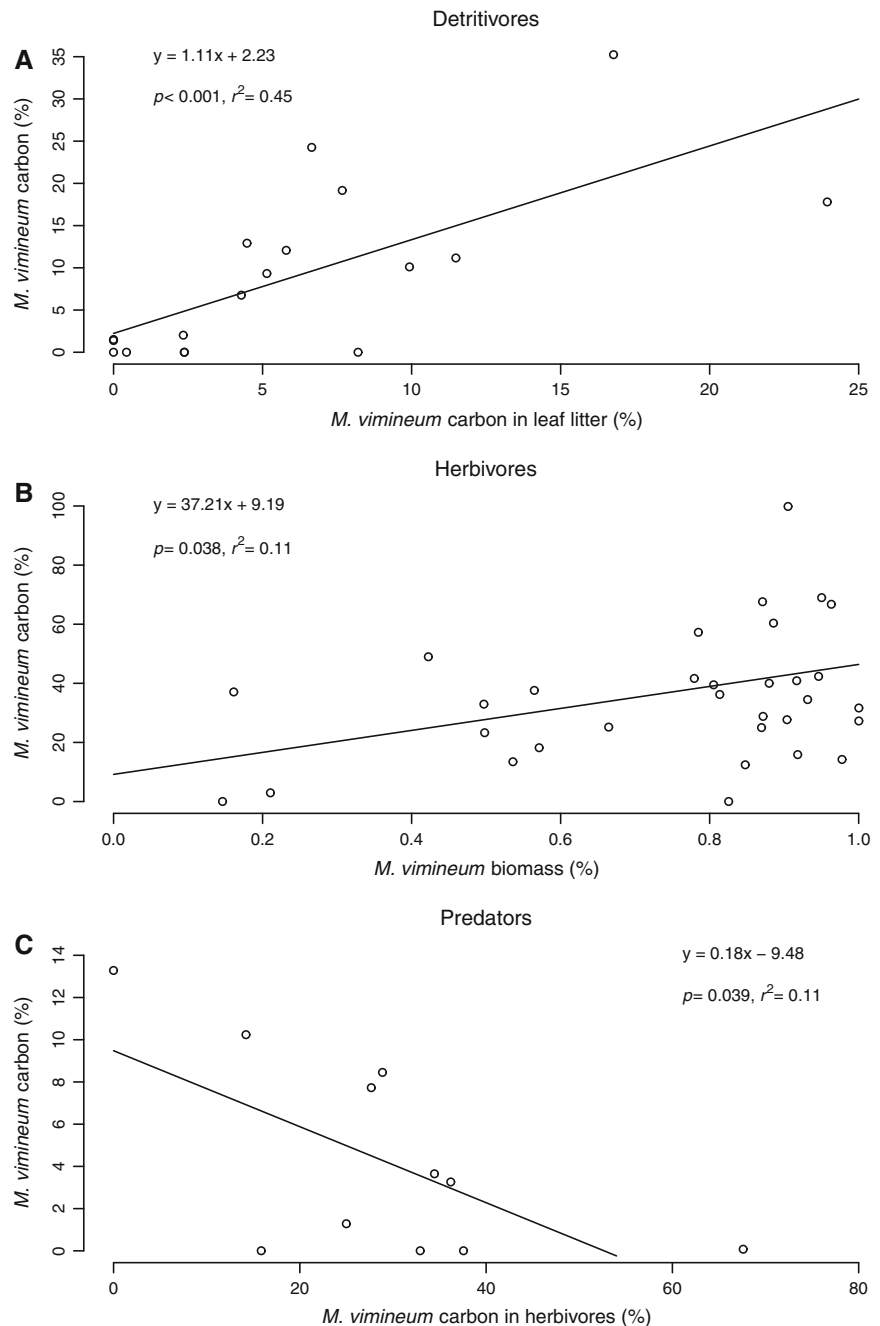
Discussion

Exotic plant invasion not only changes native plant communities, it also alters associated arthropod community diversity and structure. *Microstegium vimineum* invasion corresponds with considerable changes in arthropod abundance and diversity and shifts in herbivore damage. As a new and often dominant addition to plant communities, *M. vimineum* contributes substantial carbon into the arthropod food web, particularly through herbivores. Despite that reported exotic plant impacts on arthropod communities seem somewhat idiosyncratic (e.g., Sax 2002; Derraik et al. 2005; Bartomeus and Santamaria 2008; Wu et al. 2009; Litt and Steidl 2010; Simao et al. 2010; Yoshioka et al. 2010), we find no evidence that environmental variation modifies the invasion effects of *M. vimineum* on arthropod communities. The

consistency suggests that, in the longer-term, impacts of a specific invasive plant might be generalizable. These consistent effects seem surprising given that our study design includes heterogeneous habitats and covers a relatively broad geographic scale (see Warren et al. 2011a for greater detail on site characteristics). This heterogeneity probably also explains why, when we collect relatively fewer individuals than similar studies of arthropod communities, we also observe relatively more orders (e.g., Marshall and Buckley 2009; Litt and Steidl 2010; Simao et al. 2010).

A general effect of exotic plants on arthropods is unknown as plant invasion corresponds with both increases (e.g., Sax 2002; Derraik et al. 2005; Bartomeus and Santamaria 2008; Pearson 2009) and decreases (e.g., Mgobozi et al. 2008; Wu et al. 2009; Litt and Steidl 2010; Yoshioka et al. 2010) in arthropod community abundance, composition and diversity. Similarly, the outcomes from *M. vimineum* invasion are mixed, from no effect (Carroll 2003) to a shift in community composition (Marshall and Buckley 2009) to an overall decrease in arthropod abundance and diversity (Simao et al. 2010). We find that *M. vimineum* invasion corresponds with increased arthropod diversity and abundance, but reduced evenness (Fig. 2). Whereas species diversity can increase with abundance because greater numbers increase the probability of detecting new species, we used an unbiased estimate of Simpson's Index that accounts

Fig. 5 Linear regressions showing the correspondence between **a** the percent *Microstegium vimineum*-derived carbon in detritivores and the percent *Microstegium vimineum*-derived carbon in corresponding leaf litter, **b** the percent *M. vimineum*-derived carbon in herbivores and the corresponding percent of *M. vimineum* biomass, and **c** the percent *Microstegium vimineum*-derived carbon in predators and in corresponding herbivores



for sample size. These results suggest that *M. vimineum* invasion corresponds with larger, more diverse arthropod communities, but also that there is greater discrepancy between the relative abundance of uncommon and common species. That is, *M. vimineum* invasion may change the structure of arthropod communities by consistently favoring more taxa, but invasion also appears to favor the dominance of

common taxa in these communities. *Microstegium vimineum* often forms large, mono-specific stands (Barden 1987), and we find total vegetative biomass in *M. vimineum*-invaded plots ($27.4 \pm 29.9 \text{ g plot}^{-1}$) more than double the biomass in uninvaded plots ($12.5 \pm 19.1 \text{ g plot}^{-1}$). One explanation for the discrepancy between arthropod diversity and evenness in *M. vimineum* plots then is that the considerable

increase in biomass also increases vegetative homogeneity through the understory dominance of one plant species. Arthropod abundance and diversity increases with the greater vegetative biomass, but because it forms a homogenous *M. vimineum* layer, there is lower evenness among arthropod species.

We are the first to report increased arthropod abundance and diversity with *M. vimineum* invasion, but we found no difference in community composition by orders or trophic type. Whereas Marshall and Buckley (2009) found no overall difference in arthropod abundance or diversity with *M. vimineum* invasion, they found greater herbivore abundance in invaded plots, specifically Orthoptera and Hemiptera. Simao et al. (2010) found decreased abundance and diversity, and along with it decreases in predators and herbivores, but no change in detritivores. We find no change in detritivore abundance with invasion, similar to Simao et al. (2010), despite the fact *M. vimineum* invasions are associated with marked changes in soil chemistry (particularly pH), decomposition, moisture (see Warren et al. 2011b and references therein), soil carbon cycling (Strickland et al. 2011) and exotic earthworm invasion (Nuzzo et al. 2009).

In addition to changes in the abundance and diversity of arthropod communities, we also find that the type of arthropod damage on leaves differs between native plants and *M. vimineum* (Fig. 3). There is greater chewing on the center and edge of native plant leaves, consistent with gastropod and adult Lepidoptera and Orthoptera herbivory, and significantly more leaf mining on *M. vimineum* leaves, consistent with the larvae of arthropods such as Lepidoptera and Diptera. Interestingly, the proportion of leaves damaged was consistent (~20 %) between natives and *M. vimineum*, suggesting that in our study region the exotic plant has built-up herbivores. Whether these loads equate with similar total biomass/areal damage to native and *M. vimineum* foliage, and what the relative fitness consequences might be, merits further study given that *M. vimineum* is typically reported to have low herbivory (Sanders et al. 2004; Morrison et al. 2007). That is, based on our measurements of leaf proportion damage rather than leaf area damage, it remains possible that *M. vimineum* suffered less total damage than the natives and additional herbivory research is needed to get leaf area comparisons.

When associating plant invasion with community changes, it is difficult to determine whether the

correlation reflects a mechanistic link between *M. vimineum* and arthropods or a response by the plant and arthropod community to unmeasured factors (Palmer et al. 2004). Arthropods also might respond to changes in plant structure, such as height and cover but establishing a mechanistic link requires tracking carbon flow from *M. vimineum* through the arthropod food web. We accomplish this task by using *M. vimineum*'s C₄ carbon value in communities comprising only native C₃ plants (Fig. 4).

Our results indicate that *M. vimineum* contributes considerable carbon to the “green” food webs in the study habitats (Figs. 4,5). Herbivores in invaded plots derive ~40 % of their carbon from *M. vimineum*, and they are the most abundant arthropods in both invaded and uninvaded plots. Bradford et al. (2010) observed that foliar herbivores derive substantial carbon from *M. vimineum* at a single site in the southeastern U.S. (within our WHF location). That we observe this pattern across multiple sites, up to 100 km apart, suggests it can be generalized to well-established invasions. However, the large variance around the mean values for *M. vimineum*-derived carbon indicated that at a subset of sites the herbivores derived their carbon almost exclusively from native plants and in others almost exclusively from *M. vimineum*. Bradford et al. (2010) observed such striking variation for individuals of the same orthopteran species, at the same site, but our study was designed to assess variance across rather than within populations. Clearly, there is pronounced intra- and inter-population variation in the amount *M. vimineum* is incorporated into animal diets but further work is required to determine those factors influence these foraging choices.

We also found pronounced inter-population (i.e. across site) variation in the amount of *M. vimineum* carbon in detritivore and predator biomass, but the mean contribution of *M. vimineum* carbon to the detrital food web was less in our study than found previously. For example, Strickland et al. (2010) found that the soil microbial biomass in a bottomland hardwood forest derived almost 30 % of its carbon from *M. vimineum*; we did observe detritivores with similar proportions (Fig. 5a), but average incorporation of *M. vimineum* carbon into the “brown” food web is much less across our sites (i.e. ~9 % for detritivores). Consistent with the idea that detritivores often feed non-selectively and so in proportion to

what's available in the soil (Andren et al. 1999, but see Smith and Bradford 2003), there is a positive relationship between the relative amount of *M. vimineum* biomass in the litter layer and what is recovered in the earthworms (Fig. 5a). We find a similar positive relationship between *M. vimineum* aboveground biomass and *M. vimineum*-derived carbon in herbivores, although it explained much less variation (11 %) compared to the relationship between litter and detritivores (45 %). There is a weak (but significant) negative relationship between *M. vimineum*-carbon in predators and herbivores, but predators incorporate very little (~4 %) *M. vimineum* carbon. The predators we measure are wolf spiders and many of the Orthoptera herbivores are likely too large to function as prey. Indeed, wolf spiders incorporate many soil animals (detritivores) into their diet (Moulder and Reichle 1972; Sanders and Platner 2007), and so the relatively low proportion of *M. vimineum* carbon in the spiders might reflect the lower proportion of *M. vimineum* carbon recovered in the brown versus green food web components. Future work is required to disentangle the role this resource addition plays relative to other impacts of *M. vimineum* (e.g., changes in understory structure, altered soil pH) in shaping arthropod communities in invaded systems.

We demonstrate that *M. vimineum* acts as a carbon source for arthropods across multiple taxa and trophic levels. Most notable is the substantial fraction of *M. vimineum*-derived carbon in the herbivores. Indeed, current invasion theories posit that exotic species establishment rests on competitive advantage resulting from natural enemy escape (Blossey and Notzold 1995; Keane and Crawley 2002). *Microstegium vimineum*'s importance to the green food web highlights the need for research into how build-up of natural enemies might affect the persistence of an invasive plant once established. Further, given that arthropods are the most abundant and biomass-dense animals in most ecosystems (Wilson 1987; Losey and Vaughan 2006), the effects on arthropod abundance and diversity might well be indicative of cascading effects through the invaded communities (Price and Hunter 2005), but future research is required to disentangle the manner and mechanisms of these. Many investigations into *M. vimineum*, and plant invasions as a whole, reveal idiosyncratic and potentially context-dependent impacts on arthropod communities. Perhaps our most notable finding is that we

find the arthropod community responses to *M. vimineum* invasion are independent of the marked environmental variation across our sites.

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