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Grass invasion effects on forest soil carbon depend on landscape-level land use patterns

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Abstract. Plant invasions can alter the quality and quantity of detrital and root-derived inputs entering a system, thereby influencing the activities of microbial decomposers and affecting the soil carbon cycle. The effect of these inputs on soil carbon storage is often conflicting, suggesting strong context dependency in the plant–decomposer relationship. Whether there is a generalizable pattern that explains this dependency remains relatively unexplored. Here, we (1) examine how invasion by the exotic grass *Microstegium vimineum* affects carbon cycling across a land use gradient, and (2) evaluate the importance of inorganic nitrogen availability and other environmental variables for explaining patterns in soil carbon. Using paired invaded and uninvaded plots, we quantified invasion effects on belowground carbon pools, extracellular enzyme activities, and native leaf litter decomposition in forests embedded in an urban, agricultural, or forested landscape matrix. Compared to the urban matrix, invasion-associated declines in total soil organic carbon in the forested and agricultural landscapes were 3.5 and 2.5 times greater, respectively. Inorganic nitrogen availability and *M. vimineum* biomass interacted to explain these patterns: when both nitrogen availability and *M. vimineum* biomass were high, invaded soils exhibited higher total organic carbon, unchanged particulate organic matter carbon, and higher mineral-associated organic matter carbon compared to adjacent uninvaded soils. Consistent with these patterns, activities of carbon-mineralizing enzymes were lower in invaded than in uninvaded soils when both nitrogen availability and *M. vimineum* biomass were high. By contrast, decomposition of native leaf litter was faster when inorganic nitrogen availability and *M. vimineum* biomass were high. Our findings suggest that, although this invader may accelerate carbon cycling in forest soils, its effects on soil carbon storage largely depend on nitrogen availability and invader biomass, which can be altered by landscape-level patterns of land use. Additional research is needed to determine whether land use or other broad-scale processes such as atmospheric nitrogen deposition can explain context dependence in plant invasion effects on other ecosystem processes.

Key words: context dependency; exoenzymes; invasive plants; leaf litter decomposition; microbial nitrogen mining; nitrogen availability; priming; soil carbon; urban–rural.

Introduction

Invasions by nonnative plants not only threaten native biodiversity, but also affect ecosystem functioning (Vilà et al. 2011), potentially amplifying their role as drivers of global environmental change. The effects of invasive plants on soil carbon (C) storage are a major concern (Peltzer et al. 2010) because soils are the largest terrestrial organic C pool and widespread changes due to invasion could have important implications for atmospheric CO_2 concentrations. Although such effects are increasingly understood at local scales (Litton et al. 2008, Strickland et al. 2010, Tamura and Tharayil 2014), the regional effects of plant invasions on soil C storage remain difficult to predict. Effects on C cycling often vary substantially across space for the same species (Hughes and Uowolo 2006, Koutika et al. 2007, Kramer et al. 2012), supporting the idea that plant–decomposer relationships are context dependent (Wardle et al. 2004). Yet the processes that generate such variation are largely unknown. This limits our ability to anticipate the magnitude of invasion effects, and thus where plant invasions might appreciably alter ecosystem functioning. Understanding the context dependency of invasion effects is imperative for predicting how biogeochemical processes will change, particularly the loss or formation of soil carbon.

Changes in soil organic C (SOC) storage following nonnative plant invasion are thought to be mediated through changes in the quantity and quality of detrital and root inputs. Relative to natives, nonnative invasive species often have enhanced nutrient acquisition (Blumenthal 2006), high resource use efficiencies (Funk and Vitousek 2007), root exudation (Bradford et al. 2012),

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and greater biomass (Ehrenfeld 2003, 2010), leading to increases in the quantity and quality of organic inputs. "Preferential substrate utilization" theory predicts that these increases will have a negligible and in some cases positive effect on soil C because microbial decomposers preferentially use high-quality C sources (fresh, rapidly cycling C which is more readily available to microbes such as low C:N leaf litter and low molecular mass rhizodeposits) before lower-quality C sources (slowly cycling SOC [Cardon et al. 2001, Hagedorn et al. 2003]). Consistent with this mechanism, meta-analyses of plant invasion effects on C cycling show mean increases in both plant production and SOC stocks (Liao et al. 2008, Vilà et al. 2011). Increases in high-quality organic inputs also stimulate the metabolic activities of microbial decomposers, however, which can accelerate the mineralization of low-quality organic compounds in soils (Zyakun and Dilly 2005, Phillips et al. 2012) and the decomposition of recalcitrant litters (Fyles and Fyles 1993, Briones and Ineson 1996, McTiernan et al. 1997). This can result in the loss of SOC (positive "priming effects" [Fontaine et al. 2004, Kuzyakov 2010]), a pattern observed for several invaded ecosystems (Jackson et al. 2002, Strickland et al. 2010, Koteen et al. 2011). Moreover, positive priming effects are proportional to the amount of added C substrate (Paterson and Sim 2013), which may account for the observed positive relationship between invasive species biomass and SOC decline (Kramer et al. 2012). This pattern supports Grime's mass ratio hypothesis, which predicts that the effect of a species will scale with its relative contribution to community biomass (Grime 1998). At the same time, the microbial byproducts produced during biochemical decomposition of plant inputs are hypothesized to have a high mineral association (Cotrufo et al. 2013, Wieder et al. 2014), which favors the formation of stable SOC (Miltner et al. 2012). Thus, counterintuitively, the stimulation of microbial activities can result in the buildup of stable SOC even as SOC stocks are depleted (Prescott 2010). Supporting this idea, Tamura and Tharayil (2014) found that forest stands invaded by a nonnative species that produced large quantities of high-quality leaf litter had 28% less soil C overall, but 50% more soil C that was resistant to oxidation.

Nitrogen (N) availability can shift the balance between SOC decomposition and formation in the presence of high-quality C inputs. Experimental studies indicate that low inorganic N availability promotes litter (Craine et al. 2007) and SOC (Fontaine et al. 2011, Phillips et al. 2011, Chen et al. 2014, Chowdhury et al. 2014) decomposition as microbial decomposers use high-quality C inputs to acquire N from low-quality organic compounds (microbial N mining [Moorhead and Sinsabaugh 2006]). In contrast, high inorganic N availability reduces the decomposition of low-quality litters (Knorr et al. 2005, Hobbie et al. 2012) and SOC (Bradford et al. 2008, Du et al. 2014), either by attenuating microbial N demand (Schimel and Weintraub 2003), or repressing the production of lignolytic (Carreiro et al. 2000, DeForest et al. 2004, Piscitelli et al. 2011) or N-acquiring enzymes (Geisseler et al. 2010). High inorganic N availability combined with high-quality C inputs can also enhance SOC formation (Bradford et al. 2008), possibly by increasing the carbon-use efficiency of microbial decomposers (Manzoni et al. 2012). Despite these findings, the role of N availability in modulating the effects of plant invasion on soil C storage has not been investigated.

Human activities are a primary driver of differences in N availability at regional and global scales (Vitousek et al. 1997) and have significantly altered N cycling within and around urban areas (Kaye et al. 2006). Urban forests are subjected to higher rates of atmospheric N deposition (Rao et al. 2013) and thus have higher concentrations of inorganic N in their soils than forests embedded in a matrix of native land cover (Lovett et al. 2000, Pouyat et al. 2007). Such differences in N availability may account for variation in the magnitude of invasion effects via the mechanisms described above. For example, soil C loss following invasion may be reduced by high inorganic N availability in urban areas because of decreased microbial N mining of litters or SOC. Additionally, human activities may alter the magnitude of invasion effects on SOC by influencing invader density. Many invasive species achieve higher densities near urban areas because of dispersal facilitation (Parendes and Jones 2000) and an abundance of favorable microhabitats created by disturbance (Hobbs and Huenneke 1992). Consequently, invaded urban areas may have high availabilities of both inorganic N due to enhanced deposition, and high-quality C due to the greater biomass of invasive species, which could have a net positive effect on SOC because of reduced microbial N mining as well as accelerated SOC formation.

In this study, we compared belowground SOC content and leaf litter decomposition rates in invaded and uninvaded forests embedded within a regional landscape matrix of urban, agricultural, or forested lands to determine whether land use context (i.e., surrounding land use) modulates the effects of an invasive plant on SOC storage. We also quantified inorganic N availability, enzyme activities, abiotic characteristics, and invader biomass to investigate potential mechanisms driving variation in soil C storage. We chose to study the invasive grass *Microstegium vimineum* because it is an aggressive and widespread invader (see Plate 1), which, like many invasive plants, can have varying impacts on biogeochemical cycling (Ehrenfeld et al. 2001, Kramer et al. 2012). Though this species is well studied, the mechanisms underlying the context dependence of *M. vimineum* invasion effects are not understood. Moreover, its effects on the decomposition of native leaf litter, which comprises the majority of aboveground C inputs in temperate forests, are unknown. We expected that

TABLE 1. Characteristics of study sites and surrounding land cover in western North Carolina, USA.

Site type and number	Land cover within 2 km			Soil series†	Elevation (m)	Dominant tree genera (by basal area)
	Forest (%)	Agricultural (%)	Urban (%)			
Forest						
1	90.9	0.7	4.8	S-S	779	*Liriodendron*, *Acer*, *Juglans*
2	90.8	0.8	4.7	N-M	665	*Liriodendron*, *Robinia*, *Quercus*
3	93.3	0.5	3.8	Sy-S	692	*Quercus*, *Acer*, *Pinus*
4	90.4	0.2	4.6	Sy-S	712	*Quercus*, *Acer*, *Fraxinus*
Agricultural						
5	72.9	8.2	6.4	W-O-M	628	*Acer*, *Juglans*, *Liriodendron*
6	55.4	24.3	7.0	E-C	582	*Prunus*, *Juglans*, *Pinus*
7	64.8	12.1	9.3	E-C	581	*Carya*, *Juglans*, *Platanus*
8	64.2	15.5	8.2	Tate	647	*Liriodendron*, *Pinus*, *Cornus*
Urban						
9	24.8	2.7	68.9	Tate	620	*Betula*, *Platanus*, *Juglans*
10	42.5	6.4	45.2	Chestoa	662	*Quercus*, *Liriodendron*, *Oxydendron*
11	23.1	4.9	70.2	E-C	618	*Pinus*, *Liriodendron*
12	7.9	2.3	88.0	E-C	641	*Liriodendron*, *Quercus*, *Pinus*

Note: Sites are classified as forested, agricultural, or urban.
† S-S, Soco-Stechoah; N-M, Northcove-Mayhead; Sy-S, Sylco-Soco; E-C, Evard-Cowee; W-O-M, Walnut-Oteen-Mars Hill.

forests in an urban matrix would be characterized by higher N availability than those in an agricultural or forested matrix. We therefore hypothesized that invasion would result in less SOC loss in the urban matrix and more SOC loss in forests surrounded by other land use types because higher N availability should lead to (1) reduced microbial N mining of SOC and/or decomposing litters; and (2) greater SOC formation.

METHODS

Site selection

This study was conducted along a 45-km transect extending from Asheville, North Carolina, USA (35°35′ N, 82°33′ W) northwest to Hot Springs, North Carolina (35°55′ N, 82°47′ W). Using a map based on the National Land Cover Database for 2011 (*available online*),[4] we identified landscapes with the matrix dominated by either urban, agricultural, or forest land covers. Within each landscape type, we located four forested sites at least 1 km apart that contained established *M. vimineum* populations. Historically, most forests in this region were farmed or logged, but abandoned and reforested throughout the past century (Davis 2000). Based on our observations and previous work conducted in the region (Fraterrigo et al. 2005), we estimate that the secondary forests in which we worked were at least 50 years old. All sites were located in the French Broad River Basin, had low elevations (580–780 m), similar soil properties (well-drained loams or sandy loams classified as either Typic Hapludults or Typic Dystrudepts), and mixed hardwood–conifer canopies consisting mostly of *Liriodendron tulipifera*, *Pinus strobus*, *Quercus* species, *Juglans nigra*, and *Acer* species (Table 1). The percentage of land classified as forested, agricultural (row crop + pasture/hay), or urban (i.e., developed) was quantified for the area defined by a 2-km radius buffer centered on each site (12.6 km^2; Table 1). The land surrounding "forested" sites was dominated by forest (>90%) while the land surrounding "agricultural" sites contained less forest (<74%), and more agricultural land (8–25%). Land surrounding urban sites had >40% urban and <45% forest cover.

Populations of *M. vimineum* were located one growing season prior to sampling to ensure continuous invasion for at least one year. Individual patches of *M. vimineum* can be difficult to age because *M. vimineum* disperses in a hierarchical manner, with infrequent, long-distance dispersal events followed by intermediate- and short-distance dispersal events as the invader becomes more locally widespread (Anderson et al. 2013). However, observations and published records suggest that our study populations are probably much older than one year. *M. vimineum* was first collected in the study region in 1933 (Blomquist 1948, Fairbrothers and Gray 1972), was present near our urban sites before 1978 (B. Alexander, *personal communication*) and in more rural areas before the early 1990s (S. Pearson, *unpublished data*). In addition, some of the populations we studied, or nearby populations, were first observed 4–10 years before the initiation of this project (*available online*).[5]

At each site, four sets of 1 × 2.5 m paired invaded–uninvaded plots were established around *M. vimineum* fronts (four pairs at each site, $n = 48$ pairs and 96 total plots). Invaded plots were placed inside of *M. vimineum* patches, which covered an area of at least 5 m^2, regardless of density. Paired uninvaded plots were located between 1 and 5 m away so that they were not so close to the invaded plots that they would be invaded, but not so far that there would be obvious differences in light, moisture, or elevation. Over the course of the

[4] http://landcover.usgs.gov/

[5] http://www.eddmaps.org

study, we observed expansion of *M. vimineum* populations, suggesting that invaded–uninvaded boundaries were not due to *M. vimineum* niche boundaries. That is, there was the potential for uninvaded plots to become invaded.

Field sampling for soil properties

We collected soil samples in June and July 2012, corresponding with the period when *M. vimineum* biomass reaches its peak. Using a 2 cm diameter soil corer, we collected eight individual cores (0–10 cm depth) from mineral soils and composited them by plot. Samples collected in June were transported back to the laboratory and air dried before sieving to 2 mm. These samples were used to determine pH, texture, and total C and N by combustion (see laboratory analyses). Soils collected in July were immediately sieved to 4 mm, then placed on ice for transportation to the laboratory where a subsample was stored at −80°C until analysis for enzyme activities. The remaining soil was stored at 5°C until analysis (within 10 days) for microbial biomass (see *Laboratory analyses*). Bulk density (in grams of soil per cubic centimeter) of both coarse fragment and <2-mm fractions was determined for each site by averaging values obtained from four 5.08 cm diameter soil cores per site. Finally, one 10.16 cm diameter core was collected from each plot in July 2012 and thoroughly picked for roots. All roots (<5 mm diameter) were gently rinsed with deionized water, dried (55°C), massed, ground in a coffee grinder, and analyzed for C and N by combustion.

We also characterized soil moisture and temperature, and N availability at each site. To characterize site-level differences in ambient soil moisture and temperature, we deployed data loggers (HOBO data loggers, Onset Computer Corporation, Bourne, Massachusetts, USA) at one uninvaded area in each site and monitored moisture and temperature continuously for one year, recording twice daily at 5-cm depth. To detect within-site differences between invaded and uninvaded areas, we determined gravimetric moisture (105°C) on samples collected in July and August. Temperature loggers (iButton, Maxim Integrated, San Jose, California, USA) were deployed in pairs adjacent to one invaded and one uninvaded plot at each site. We quantified inorganic N availability in each plot using ion-exchange resin bags. Nylon bags were filled with 10 g of a mixed-bed ion exchange resin (Rexyn R208, Thermo Fisher Scientific, Waltham, Massachusetts, USA), and one bag was installed at 5-cm depth at the center of each plot and left in situ for two months (June–August). Upon removal, resin bags were sealed in separate plastic bags and refrigerated until extraction in 2 mol/L KCl. Following correction for laboratory and field blanks, we determined the mass of N in the resin by multiplying extract concentration (see *Laboratory analyses*) by the volume of KCl used for extraction.

Laboratory analyses

We determined soil texture using a standard hydrometer analysis as described in Ulmer et al. (1994). Soil pH (2:1 mL H_2O : g soil) was determined using a bench-top pH meter. To determine the effects of *M. vimineum* on SOC pools of differing stability, we fractionated SOC using a modification of the method described in Marriott and Wander (2006). This method separates SOC into slow-cycling, mineral-associated, microbe-derived pools; and fast-cycling, particulate, plant-derived pools. Briefly, 10 g soil was added to a 30-mL Nalgene plastic bottle containing 5% (mass/volume) sodium hexametaphosphate as a dispersant. The bottle was covered with a 53-μm mesh fabric, and the slurry was left undisturbed for 12 hours to facilitate dispersion. The 30-mL bottle was then placed in a 250-mL centrifuge bottle which contained an additional 120 mL dispersant. The bottles were placed on a reciprocal shaker at 180 rpm for one hour to facilitate the separation of the particulate organic matter (POM; operationally defined as organic particles having diameters >53 μm) from the mineral-associated organic matter (MAOM). After the initial rinse, the fine particles and dispersant that collected in the larger bottle were discarded and replaced with 150 mL of distilled water. Samples were shaken for 15 minutes to rinse the fine particles and dispersant into the larger bottle. This rinsing was repeated seven times to ensure isolation of the POM. The material remaining in the 30-mL bottle was dried at 55°C and ground with a mortar and pestle for analysis of C and N by combustion (Costech ECS 4010, Costech Analytical Technologies Incorported, Valencia, California, USA). We also determined C and N concentrations of the total soil sample. Mineral-associated organic matter C was determined by mass balance as the difference between total and POM C concentrations (Salvo et al. 2010, Viaud et al. 2011, Leifeld et al. 2013).

We measured the activities of four extracellular enzymes involved in the breakdown of SOM constituents of varying turnover times. The hydrolytic enzymes β-glucosidase (BG) and β-1,4-*N*-acetylglucosaminidase (NAG) are associated with the breakdown of fast- to moderate-cycling SOM pools, with the latter also involved in N acquisition; phenol oxidase (PPO), and peroxidase (PER) are lignolytic enzymes associated with the breakdown of recalcitrant SOM pools. Enzyme assays are described in Finzi et al. (2006). Briefly, soil slurries consisting of 1 g fresh soil suspended in 125 mL of 50 mmol/L, pH 5.0 acetate buffer (soil pH was 4.2–5.7) were dispensed in 24 replicate, 200-μL aliquots to 96-well microplates. For the hydrolytic enzyme assays, eight replicates received 50 μL of 200 μmol/L 4-methylumbelliferone (MUB), and eight replicates received a MUB substrate so that there were eight replicate wells for each blank, quench control, standard, and substrate assay. PPO and PER were measured together (i.e., PPO + PER) using L-DOPA + 10 μL of

0.3% hydrogen peroxide. Microplates were incubated in the dark at 20°C for two hours (BG and NAG) or four hours (PPO and PER). BG and NAG microplates were read at 360-nm excitation and 460-nm emission after adding 10 μL of 1 mol/L NaOH. PPO and PER assays were read at 460-nm absorbance after transferring the supernatant to a fresh microplate to avoid absorbance interference by soil particles. Enzyme activity was calculated as the amount of substrate cleaved during the incubation.

We quantified microbial biomass C using a simultaneous chloroform fumigation-extraction (CFE) procedure (Fierer and Schimel 2003). Two 3–10 g (dry mass equivalent) soil subsamples were shaken for four hours at 150 revolutions/m with 40 mL 0.5 mol/L K_2SO_4. Before shaking, 0.5 mL of ethanol-free chloroform was added to one K_2SO_4 mixture. The top 20–30 mL of each sample was gravity filtered through a Whatman No. 1 paper filter (Whatman Incorporated, Florham Park, New Jersey, USA) and the filtrate was bubbled with house air for 20 minutes. Microbial biomass C was determined as the difference in dissolved organic C between the fumigated and non-fumigated samples. No correction factor was applied.

All KCl slurries were filtered through 0.7-μm Whatman filter paper and frozen (−20°C) until analysis. Extracts were analyzed for NH_4^+-N using the phenolate method and NO_3^- plus NO_2^--N (hereafter referred to as NO_3^-) using a cadmium column reduction on a Lachat QuikChem 8500 (Hach Company, Loveland, Colorado, USA).

Litterbag study

To characterize leaf litter decomposition in invaded and uninvaded plots, we conducted a litterbag study from November 2011 until December 2012 following the protocol described by Harmon and Lajtha (1999). Recently senesced *Liriodendron tulipifera*, *Quercus prinus*, and *Acer rubrum* leaves were collected from one location in October 2011 and air-dried for two weeks. Litterbags (20 × 20 cm) were constructed out of fiberglass window screening with a mesh size of 1 mm, large enough to allow passage of most soil mesofauna (Swift et al. 1979), and filled with 1.5 g of each species for a total of 4.5 g of leaf mass in each. By using a standard mixture of litter from common trees, we were able to isolate the effects of invasion and site rather than litter chemistry on decomposition dynamics. A subsample of air-dry leaves was oven-dried (55°C) for 72 hours to calculate the air dry-to-oven dry conversion factor. Eight litterbags were deployed in each plot and one was collected immediately to quantify initial C and N concentrations and amount of mass lost during travel. One bag was collected after 1, 2, 4, 6, and 9 months and the remaining two bags were collected after 13 months of incubation in the field. Upon collection, litter was kept cool until it was oven-dried to determine mass loss through time. The dried litter was then ground to a powder and ashed for four hours at 450°C to determine ash-free dry mass (AFDM). Total C and N were determined by combustion. To account for potential soil contamination, mass loss is corrected following Blair (1988).

Data analysis

We evaluated the effects of land use context on inorganic N availability with linear mixed models. We used the values for NO_3^- and NH_4^+ from uninvaded plots as response variables (with site as a random effect) because we were interested in the ambient (i.e., preinvasion) differences in inorganic N availability. To test for differences in belowground C content between invaded and uninvaded plots with respect to landscape matrix, we used linear mixed models with landscape matrix, invasion, and the interaction of these terms as fixed factors, and site as a random factor. To further examine how the effects of plant invasion on various C pools differed with land use context, we constructed linear mixed models using the values for SOC (corrected for variation in soil bulk density), microbial biomass C, and root C content as response variables; landscape matrix, *M. vimineum* biomass, and the interaction of these terms as fixed factors; and site as a random factor. If the interaction was statistically significant at $\alpha = 0.10$ (indicating unequal slopes), we conducted post hoc analyses to compare the effects of *M. vimineum* biomass on carbon pools in each individual landscape type. One outlying data point (from site No. 6) was discarded from analyses of SOC pools, as its inclusion resulted in non-normally distributed residuals and unequal variances between treatment groups. Total C in this uninvaded plot was almost six times greater than in its invaded pair, an unrealistic difference compared to the other 47 pairs. Based on inspection of a Natural Resources Conservation Service soil map (*available online*),[6] this pair may have occurred along the boundary of a well-drained and poorly drained soil series, suggesting a violation of the assumptions of the paired plot approach.

For the litterbags, we used linear mixed models, treating mass loss and litter chemistry as repeated measures to account for nonindependence between bags collected from the same site, invasion treatment, landscape matrix, date, and their interactions as fixed factors, and site as a random factor. For all analyses, we tested assumptions of normality (Kolomogrov-Smirnov test) and homogeneity of variance (Levene's test). When necessary, we ln- or square root- transformed data to meet assumptions of normality.

We used linear mixed models and an information-theoretic approach (Burnham and Anderson 2002) to determine the ability of N availability, aboveground *M. vimineum* biomass, root biomass, or other site characteristics to explain the magnitude of invasion effects on

[6] http://www.nrcs.usda.gov/

SOC pools and litter decomposition. We also used this approach to investigate differences in microbial investment in the breakdown of different SOC pools by modeling enzyme activities scaled to microbial biomass (McFarland et al. 2013). For C pools and enzymes, the magnitude of invasion effects were characterized by computing the differences in C content (ΔTOC, ΔPOMC, ΔMAOMC, ΔCFE biomass) and scaled enzyme activities (ΔPPO + PER, ΔBG, and ΔNAG) between paired invaded and uninvaded plots. For litter decomposition, the magnitude of invasion effects were characterized as the mass remaining in litterbags in invaded plots at the sample date corresponding with *M. vimineum* peak biomass. Candidate models representing our a priori hypotheses contained the following variables: *M. vimineum* aboveground biomass; ambient pH, NO_3^-, and soil moisture; and interactions among these terms. Ambient values for pH, NO_3^-, and soil moisture were determined from adjacent uninvaded plots and were used to represent pre-invasion site conditions. We focus on NO_3^- rather than total inorganic N because it directly influences the fitness of *M. vimineum* (Kourtev et al. 1999, Lee et al. 2012). To determine whether root biomass influenced SOC pools, we also included the difference in root C content between invaded and uninvaded plots in models for ΔTOC, ΔPOMC, and ΔMAOMC. We considered models to have competitive support when the difference between the value of Akaike's information criterion corrected for small sample size (AIC_c) of a given model and the AIC_c value of the most-supported model (ΔAIC_c) was ≤ 2 (Burnham and Anderson 2002). We quantified support for competing models by calculating Akaike weights (ω_i). To assess the relative importance of individual predictor variables, we calculated $\Sigma\omega_i$ for all supported models containing the variable of interest. The larger the $\Sigma\omega_i$ for a given variable, the more important it is relative to the other variables. Parameter estimates, reported for the top model containing that parameter, were calculated using restricted maximum likelihood estimation. However, because fixed effects varied between models, maximum likelihood estimates were used for model selection.

To further assess effects of N on C pools and enzyme activities, we created interaction plots by splitting the data for each response variable around the median value for N availability and *M. vimineum* biomass, calculating the mean difference in C stocks and litter mass remaining for each of these groups. We also examined how the magnitude of effects at a given level of *M. vimineum* biomass changed continuously by plotting Pearson's correlation coefficients relating *M. vimineum* biomass and our measures of effect magnitude (ΔTOC, ΔPOMC and ΔMAOMC, ΔCFE biomass, and litter mass remaining) against average ambient NO_3^- availability for each site. All statistical analyses were performed with SAS 9.4 (SAS Institute Inc., Cary, NC, USA).

Results

N availability, aboveground biomass, and belowground C content

Overall, inorganic N ranged from 0.01–2.57 mg N/(10 g resin)$^{-1}$ for the 60-d sampling period. NO_3^- accounted for 54% of the available inorganic N pool and was highest at sites in the urban matrix and lowest at sites in the forested matrix (Table 2). This trend was not statistically significant, however, due to substantial variation among sites ($P = 0.19$). NH_4^+ availability did not vary with landscape matrix ($P = 0.89$).

Microstegium vimineum biomass ranged from 4 to 144 g/m^2 and was highest at sites in the urban matrix, but this trend was not statistically significant ($P = 0.15$). Average *M. vimineum* biomass was 68.8 ± 29.6 g/m^2 (mean ± SE), 43.7 ± 37.8 g/m^2, and 47.1 ± 39.7 g/m^2 for the urban, agricultural, and forested matrix, respectively.

Invasion effects on belowground C content varied with land use context (Appendix: Table A1). Compared to uninvaded soils, invaded soils in the forested matrix had 21% less TOC ($F_{1,80} = 4.66$, $P = 0.03$), 32% less POMC ($F_{1,80} = 8.40$, $P = 0.01$), 41% less microbial biomass C ($F_{1,81} = 10.9$, $P = 0.001$), and 48% less root C ($F_{1,81} = 11.8$, $P < 0.001$). In the agricultural matrix, invaded soils had 34% less microbial biomass C than uninvaded soils ($F_{1,81} = 3.8$, $P = 0.05$), but did not differ with respect to SOC ($P > 0.09$ for POMC and MAOMC) or root C content ($P = 0.40$). In the urban matrix, invaded and uninvaded soils had similar amounts of SOC ($P > 0.09$ for POMC and MAOMC) and microbial biomass C ($P = 0.15$), whereas root C content was 41% lower in invaded than uninvaded soils ($F_{1,81} = 7.3$, $P < 0.01$).

There was also an interaction between land use context and *M. vimineum* biomass (TOC, $F_{2,80} = 3.61$, $P = 0.02$; POM, $F_{2,80} = 2.70$, $P = 0.08$; MAOMC, $F_{2,80} = 3.31$, $P = 0.03$) driven by the differential effects of *M. vimineum* biomass on SOC in urban landscapes relative to agricultural and forested landscapes (Fig. 1 and Appendix: Fig. A1). In the urban matrix, we observed a significant positive relationship between *M. vimineum* biomass and C content for all SOC pools (TOC, $\beta = 16.8$, $P = 0.02$; POMC, $\beta = 11.0$, $P = 0.02$; MAOMC, $\beta = 6.25$, $P = 0.02$), whereas there was no such relationship in the agricultural or forested matrix ($P > 0.5$). For microbial C and root C content, landscape matrix did not influence invasion effects (interaction, $P > 0.5$). Rather, there was a nonsignificant trend for decreasing microbial C with increasing *M. vimineum* biomass ($P = 0.14$) and a significant negative relationship between *M. vimineum* biomass and root C content ($\beta = -0.006$, $P = 0.03$).

Litter decomposition

Invasion had a small but significant effect on the decomposition of native litters (Fig. 2). Across the three landscape types, litters in invaded plots decomposed

TABLE 2. Edaphic properties of study sites.

Site type and number	Clay (%)	Sand (%)	Soil temperature (°C)	Soil moisture (L/L)	ρb (g/cm^3)	[C] (mg/g)	Resin bag nitrogen		pH
							NO_3^-	NH_4^+	
Forest									
1	12	53	15.3	0.23	0.90 (0.05)	30.5 (7.5)	186 (84)	222 (79)	4.56 (0.08)
2	8	70	15.8	0.20	0.70 (0.09)	19.7 (1.7)	118 (55)	248 (98)	5.35 (0.15)
3	15	57	16.6	0.19	0.65 (0.05)	29.7 (3.3)	22 (14)	55 (36)	4.27 (0.01)
4	12	57	16.4	0.16	0.88 (0.10)	32.2 (5.3)	12 (6)	38 (15)	4.48 (0.30)
Agricultural									
5	26	43	16.0	0.37	1.00 (0.03)	26.9 (2.0)	1404 (910)	1351 (1007)	5.50 (0.27)
6	11	73	14.9	0.23	1.07 (0.03)	23.0 (5.4)	371 (130)	280 (180)	5.19 (0.17)
7	9	66	15.1	0.25	1.04 (0.10)	23.3 (2.4)	46 (21)	69 (9)	5.83 (0.05)
8	20	50	14.9	0.24	0.86 (0.06)	28.2 (3.3)	7 (3)	85 (31)	5.17 (0.10)
Urban									
9	11	60	15.7	0.17	1.16 (0.11)	14.9 (1.2)	762 (354)	86 (31)	5.49 (0.16)
10	16	56	15.8	0.20	0.91 (0.06)	32.5 (4.9)	1163 (282)	250 (140)	4.96 (0.06)
11	11	60	15.9	0.21	0.78 (0.07)	34.2 (2.9)	535 (456)	235 (207)	4.19 (0.13)
12	16	51	15.0	†	0.99 (0.06)	40.9 (1.4)	525 (271)	81 (6)	5.69 (0.10)

Notes: Soil temperature data are averaged from sensors left in situ from July through December 2012. Soil moisture data are averaged values from a moisture sensor left in situ for 13 months (November 2011–December 2012). Bulk density (ρb), soil carbon content ([C]), resin bag data, and pH are shown as means (±SE). Units for resin bag data are μg N·(10 g resin)$^{-1}$·(60 d^{-1}).

† Data logger destroyed.

more rapidly ($F_{1,510} = 7.84$, $P = 0.01$) than those in uninvaded plots, but did not differ with respect to N remaining ($F_{1,500} = 0.98$, $P = 0.32$). Land use context influenced invasion effects on decomposition (land use context × invasion, $F_{2,510} = 5.12$, $P = 0.01$) and N remaining (Fig. 2; land use context × invasion, $F_{2,500} = 2.43$, $P = 0.09$), such that effects were more pronounced in the urban matrix. At day 280, when *M. vimineum* reached peak biomass, invaded plots in the urban matrix had 15% less litter mass remaining (compared to uninvaded plots) compared to 2% less in the forested matrix and 8% more in the agricultural matrix. Similarly, litters in invaded plots in the urban matrix had 16% less nitrogen remaining than uninvaded plots compared to 4% less in the agricultural matrix and 9% more in the forested matrix. After 13 months of decomposition, litters in urban and agricultural invaded plots had lost 25% ($P = 0.19$) and 24% ($P = 0.15$) more mass, respectively, and 19% ($P = 0.40$) and 29% ($P = 0.11$) more N, than invaded plots in the forested matrix.

Factors explaining the magnitude of invasion effects

Variation in the magnitude of invasion effects on TOC and POMC based on differences between invaded and uninvaded soils (ΔTOC and ΔPOMC) was explained by ambient soil moisture, soil pH, and the NO_3^- × *M. vimineum* biomass interaction (Appendix: Table A2). The difference in root biomass C between invaded and uninvaded soils did not appear in any of the supported models, indicating that it lacked explanatory power (Appendix: Table A2). Based on the sum of Akaike weights across all models, soil moisture followed by the NO_3^- × *M. vimineum* biomass interaction were the most important parameters for explaining invasion effects on TOC and POMC (Appendix: Table A3). For MAOMC, the more stable C pool, the model containing soil moisture, NO_3^-, and the NO_3^- × *M. vimineum* biomass interaction was the only competitive model (Appendix: Table A2), and the most important parameters for explaining invasion effects on MAOMC were soil moisture followed by the NO_3^- × *M. vimineum* biomass interaction (Appendix: Table A3). For all supported models, the effect of soil moisture was negative (Appendix: Table A2), indicating that the greatest losses of SOC occurred in invaded plots with more moist soils. In contrast, the parameter estimate for the NO_3^- × *M. vimineum* biomass interaction was positive (Appendix: Table A2), such that high *M. vimineum* biomass was associated with increased TOC and MAOMC content at N-rich sites and decreased TOC and MAOMC content at N-poor sites (Fig. 3 and

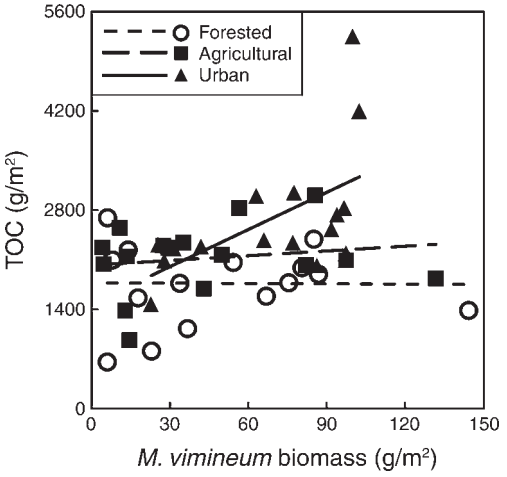

FIG. 1. Relationship between *M. vimineum* biomass and total organic carbon (TOC) for sites located in a forested, agricultural, and urban landscape matrix.

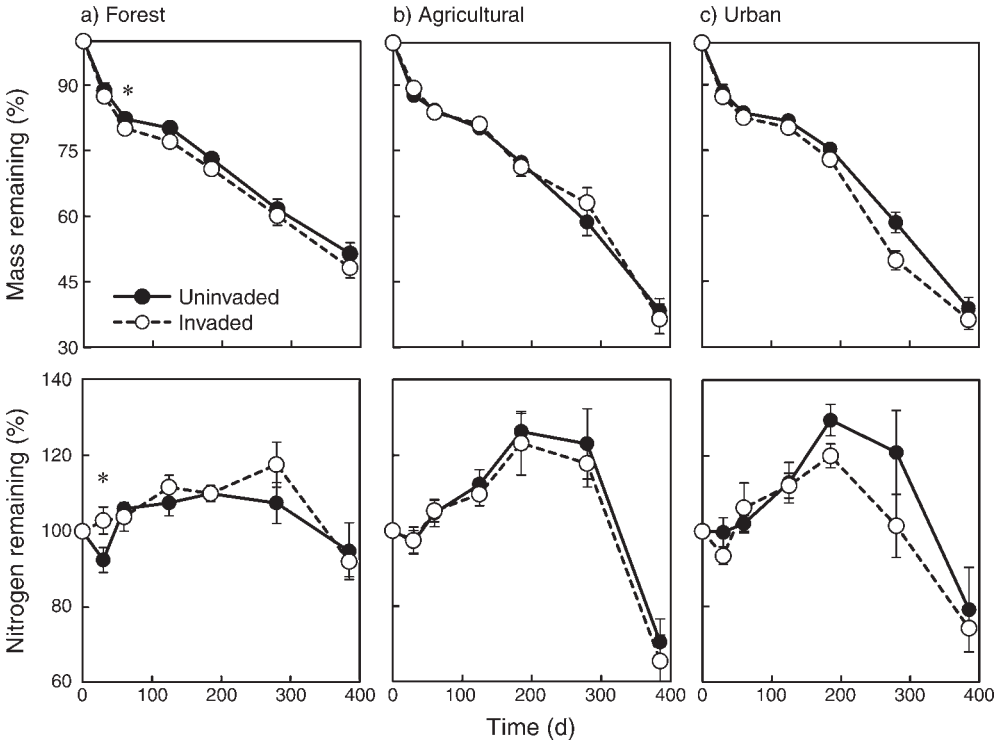

FIG. 2. Mass and nitrogen remaining in litter bags over time for (a) forest, (b) agricultural, and (c) urban landscapes. Nitrogen remaining will exceed 100% if nitrogen is immobilized during decomposition. Asterisks indicate a significant ($P < 0.05$) main effect of invasion for a given time period.

Appendix: Fig. A2). A similar pattern was evident for POMC, except that invaded plots always had less POMC than uninvaded plots (Fig. 3). The correlation coefficients relating *M. vimineum* biomass and differences in SOC content between invaded and uninvaded soils within a site were also significantly positively related to average site NO_3^- availability for TOC and POMC, and nonsignificantly, positively related for MAOMC (Fig. 3).

The magnitude of invasion effects on microbial biomass C (ΔCFE) and specific enzyme activities (ΔPPO + PER, ΔBG, ΔNAG) were explained by NO_3^- availability, *M. vimineum* biomass, soil pH, the interactions of these terms, and, to a lesser extent, soil moisture (Appendix: Table A2). For microbial biomass C, the most important parameters were *M. vimineum* biomass and the soil pH × *M. vimineum* biomass interaction, followed by the NO_3^- × *M. vimineum* biomass interaction (Appendix: Table A3). The effect of *M. vimineum* biomass was negative, indicating that the greatest losses of microbial C occurred in plots with more *M. vimineum* biomass (Appendix: Table A2). Similar to SOC pools, the NO_3^- × *M. vimineum* biomass interaction was positive (Appendix: Table A2), such that high *M. vimineum* biomass was associated with smaller losses of microbial C at N-rich sites than at N-poor sites (Fig. 3). The correlation coefficients relating *M. vimineum* biomass and differences in microbial biomass C content between invaded and uninvaded soils within a site were also positively related to average site NO_3^- availability (Fig. 3). For specific enzyme activities, *Microstegium vimineum* biomass was among the most important parameters (Appendix: Table A3) and had a positive effect (Appendix: Table A2), suggesting that the activities of PPO, PER, BG, and NAG increased with increasing invader biomass. However, the effects of *M. vimineum* biomass on specific enzyme activities, especially PPO and PER, were strongly contingent on NO_3^- availability, as evidenced by the negative NO_3^- × *M. vimineum* biomass interaction (Appendix: Tables A2 and A3). At N-rich sites, high *M. vimineum* biomass was associated with a decrease in specific enzyme activities (differences are <0), whereas at N-poor sites, high *M. vimineum* biomass was associated with an increase in specific enzyme activities (Fig. 4).

Litter mass remaining at peak *M. vimineum* biomass was best predicted by the model containing only the ambient NO_3^- × *M. vimineum* biomass interaction (Appendix: Table A4). For all models, the ambient NO_3^- × *M. vimineum* biomass interaction was the most important parameter ($\omega_i = 0.63$) and, in contrast to SOC pools, was negatively related to litter mass remaining (Appendix: Table A4). The correlation between *M. vimineum* biomass and litter mass remaining within a site was significantly, negatively related to average site NO_3^- availability (Fig. 5).

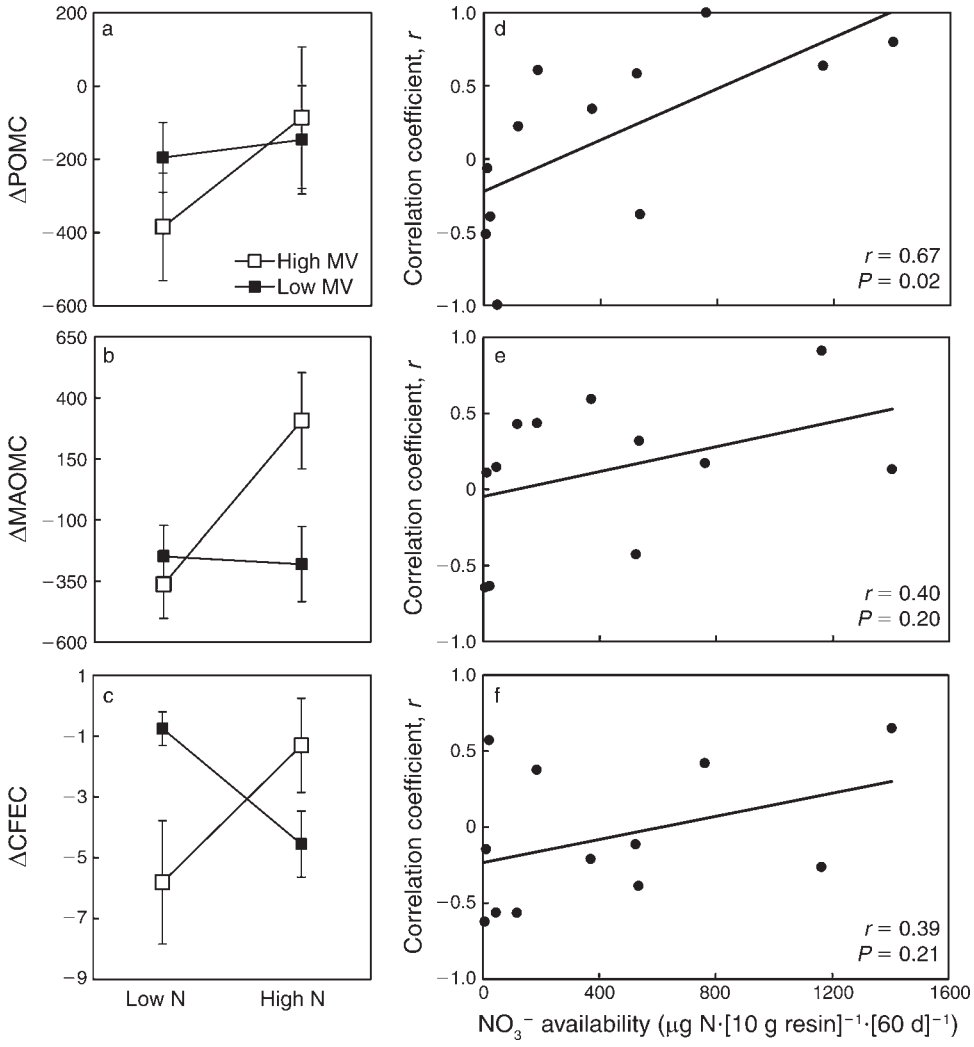

FIG. 3. Context dependence of the effects of high and low *M. vimineum* biomass (MV in the graph) on belowground carbon pools. (a–c) Interaction plots showing the effects of high and low invader biomass on the changes in carbon content at sites with high and low ambient NO_3^-. Error bars show ±SE. (d–f) Regression plots showing the dependence of the relationship between *M. vimineum* biomass and C impacts on inorganic N availability. Each data point is a within-site Pearson correlation between *M. vimineum* biomass and change in (d) particulate organic matter carbon (POMC), (e) mineral-associated organic matter carbon (MAOMC), and (f) microbial carbon pools. CFEC is chloroform fumigation-extraction carbon.

DISCUSSION

Previous research demonstrates that the effects of invasive plants can vary across space (Hughes and Uowolo 2006, Dassonville et al. 2008), but few studies have investigated whether broad-scale factors such as land use patterns can account for this variation. Here, we found that *M. vimineum*-invaded plots embedded in an urban matrix had higher SOC content than those embedded in a forested matrix. Additionally, rates of leaf litter decomposition and litter N loss were greatest in urban invaded plots. Ambient NO_3^- availability and *M. vimineum* biomass interacted to explain these patterns. Specifically, high NO_3^- availability and high *M. vimineum* biomass were associated with higher SOC content, faster litter decomposition, and greater litter N release, whereas low NO_3^- availability and high *M. vimineum* biomass were associated with the opposite patterns.

Grime's mass ratio hypothesis proposes that a species' effects on ecological processes should scale with its biomass (Grime 1998). This idea has been used to explain variability in the magnitude of invasion effects for several nonnative species (Bobbink and Willems 1987, Standish et al. 2001), including *M. vimineum* (Kramer et al. 2012, Lee et al. 2012). Our findings provide partial support for the mass ratio hypothesis in that *M. vimineum* biomass was positively related to SOC content in the urban matrix. One possible explanation for this pattern is that plant detritus, an important source of soil C, may have increased with increasing

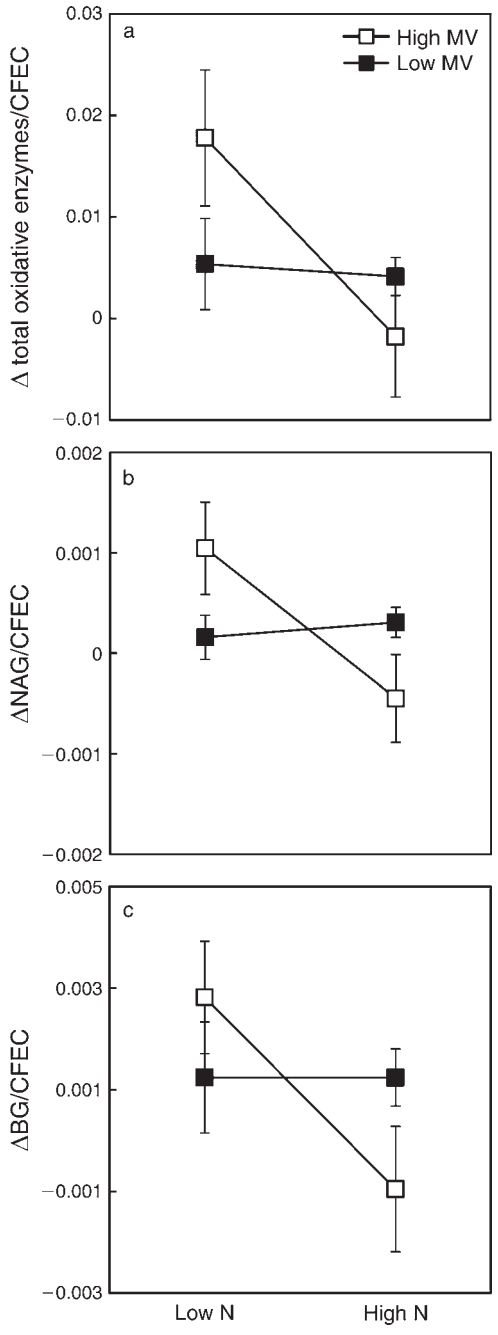

FIG. 4. Interaction plots showing the effects of high and low *M. vimineum* biomass (MV) on the changes in enzyme activities scaled to microbial biomass at sites with high and low ambient NO_3^-. Scaled enzyme activities are the ratios of the various enzyme activities relative to the total microbial biomass (represented by CFEC). (a) Phenol oxidase + peroxidase (total oxidative enzymes), (b) β-1,4-*N*-acetylglucosaminidase (NAG), and (c) β-glucosidase (BG). Error bars show ±SE.

biomass and accumulated as SOC over time. Koteen et al. (2011) invoked this mechanism to explain why SOC was lower under an invasive annual grass that had low productivity relative to the native perennials that it replaced. Likewise, Liao et al. (2008) suggested that higher soil C under N-fixing invasive species may be due to the positive effects of increased N availability on plant productivity. However, if increased detrital inputs were driving the accrual of SOC in the urban matrix, we would expect most of this C to accumulate in the POMC pool, which primarily consists of recently plant-derived C (Denef et al. 2009). Instead, we found that the POMC pool was consistently lower (25% on average) under *M. vimineum*, and higher SOC was mainly attributable to the MAOMC, or microbe-derived, pool. Moreover, higher invader biomass was unrelated to SOC in the agricultural and forested matrix (Fig. 1). Collectively, these results suggest that a different mechanism underpins the relationship between *M. vimineum* biomass and SOC.

We hypothesize that aboveground biomass determines the amount of C exuded belowground via roots, which in turn influences microbial activities and SOC. In forest ecosystems, a surprisingly high amount of C enters the soil through root exudation of low molecular mass compounds. Girdling and pulse-labeling studies show that as much as 50% of soil respiration is fueled by the exudation of recently fixed carbon (Hogberg et al. 2001, 2008, van Hees et al. 2005). Assuming that roots exude a consistent fraction of C fixed in photosynthesis (Pinton et al. 2001), plants that invest more in aboveground production, such as *M. vimineum*, should have high rates of root exudation (Dijkstra et al. 2006, but see Fu and Cheng 2002). Supporting this hypothesis, Bradford et al. (2012) pulse-labeled patches of *M. vimineum* and found that 15% of fixed C was recovered in the soil microbial biomass after one week. Using stable isotopes, Strickland et al. (2010) further determined that the microbial biomass derived substantially

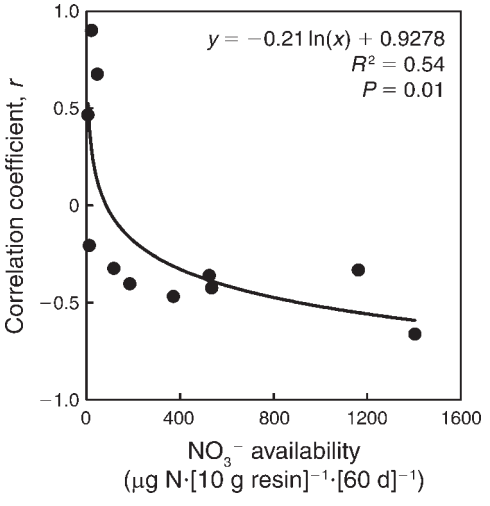

FIG. 5. Regression plot showing the dependence of the relationship between *M. vimineum* biomass and litter mass remaining on inorganic N availability. Each data point is a within-site Pearson correlation between *M. vimineum* biomass and litter mass determined at peak *M. vimineum* biomass.

PLATE 1. Invasion of a forest understory by *Microstegium vimineum*. Photo credit: M. E. Craig.

more C from *M. vimineum* pre-senescence (~30%) than post-senescence (~5%). Taken together, these findings suggest that root exudates under *M. vimineum* are an important source of C for soil microbes and are related to aboveground biomass.

High inputs of labile C can prime the decomposition of soil organic matter by fueling microbial decomposers (Dalenberg and Jager 1989, Kuzyakov 2010). Strickland et al. (2010) suggested that this mechanism is what leads to reduced POMC under *M. vimineum*; citing increased rates of glucose mineralization and higher active : total microbial biomass ratios as evidence for enhanced microbial activity. However, field and laboratory experiments demonstrate that priming effects can be smaller when N availability is high (Fontaine et al. 2004, 2011, Phillips et al. 2011). Consistent with this effect of N fertilization and with evidence that priming effects scale with plant biomass (Dijkstra et al. 2006), we found that the strength of the relationship between invader biomass and POMC depended on N availability (Fig. 3), with the greatest decline in POMC (32%) observed at sites with low N availability and high invader biomass. In addition, we found that these sites had the greatest microbial biomass-specific enzyme activities (Fig. 4), indicating that soil decomposers in these sites were more active in breaking down SOC.

Typically, the increase in microbial activity observed in C-addition studies and associated with priming is attributed to an increase in microbial biomass (Kuzyakov 2010). However, like others (Strickland et al. 2010, Kramer et al. 2012), we found that microbial biomass (but not microbial activity) was lower under *M. vimineum*. Microbial growth in temperate forest soils is often limited by the availability of N (Hart and Stark 1997, Allen and Schlesinger 2004), and therefore plant alterations of N availability could lead to changes in microbial biomass. Previous work suggests that *M. vimineum* can enhance plot-level N demand by sequestering N in aboveground biomass (Fraterrigo et al. 2011). Thus, low microbial N availability under *M. vimineum* may explain the negative relationship between aboveground and microbial biomass observed by Kramer et al. (2012) and may favor a microbial community that allocates energy acquired from root exudates towards N acquisition (i.e., enzyme production) rather than growth (Moorhead and Sinsabaugh 2006). Because we did not directly measure priming effects or microbial N limitation, we cannot be certain that this mechanism explains our observations. Future work should address how plant N uptake may modulate the effects of root exudates on microbial biomass and activity.

Regardless, the patterns in microbial biomass may be important for explaining the observed patterns in SOC. Recent literature suggests that microbial biomass is a major agent of SOC formation (Bradford et al. 2013, Cotrufo et al. 2013). Thus, lower microbial biomass under *M. vimineum* is another hypothesized mechanism of reduced SOC in invaded areas (Kramer et al. 2012). We found that differences in microbial biomass were greatest at sites with low N and high invader biomass where microbial biomass was 48% lower compared to sites with high N and high invader biomass where microbial biomass was only 18% lower. This may be why we observed a 12% increase, rather than a decrease in MAOMC (microbe-derived C), at sites with high N and high invader biomass.

In addition to the interaction between N availability and invader biomass, we also found soil moisture to be an important predictor of *M. vimineum* invasion effects on SOC. The greatest decreases in SOC occurred at the wettest sites. Though *M. vimineum* is known to prefer moist sites, it can survive in a range of moisture conditions (Warren et al. 2011). As such, future studies and management efforts should consider that moisture and N availability as well as invader biomass may all contribute to the context dependence of *M. vimineum* impacts (Fraterrigo et al. 2014).

Root inputs are another important source of SOC formation (Rasse et al. 2005). However, the effect of invasion on inputs of root C is often overlooked. Here, we found that invaded areas contained 32% less root biomass than uninvaded areas. The most likely explanation for this is that *M. vimineum*, similar to many annual species, has a lower root : shoot ratio than the perennial species it displaces (Fraterrigo et al. 2011). Although root C did not explain differences in SOC stocks in our study (Appendix: Table A2), lower root biomass may contribute to reduced SOC stocks in invaded areas over longer time scales, especially in forests with productive understories.

We quantified leaf litter decomposition to assess the relative importance of aboveground vs. belowground factors for invader effects on SOC, and found significant but small differences between invaded and uninvaded areas. Decomposition rates were greatest in the urban matrix where N availability and *M. vimineum* biomass were high, suggesting a synergistic interaction between these factors. While it is known that both N availability and invasion can alter decomposer communities, the interaction between these two effects has rarely been observed, and because we did not assess the composition of microbial or mesofaunal communities, we do not know the mechanism underlying these patterns. Moreover, the effect of altered litter decomposition rates on SOC stocks has not yet been resolved. SOC could accumulate from either slower litter decomposition through selective preservation (Zak et al. 2008, Tamura and Tharayil 2014) or from faster decomposition which may lead to greater stable C formation by enhancing microbial growth efficiency (Cotrufo et al. 2013, Tamura and Tharayil 2014). Regardless, our observation of small effects of invasion on native litter decomposition coupled with previous observations that *M. vimineum* litter has a small contribution to SOC (Strickland et al. 2010, Kramer et al. 2012) suggests that differences in SOC content between invaded and uninvaded areas are largely driven by belowground rather than aboveground factors.

Our results add to a growing body of evidence suggesting that the impacts of invasive plants are often inconsistent between sites (Ehrenfeld 2010). Similar to our findings, a multi-site survey of the impacts of *M. vimineum* on SOC found that, even though SOC pools were depleted on average across a regional climate and elevation gradient, these impacts were not evident in 15 of 31 sites (Kramer et al. 2012). Such findings have generated interest in the reasons for spatial variability in invader impacts (Dassonville et al. 2008, Scharfy et al. 2009, 2010). We show that the magnitude and direction of invader impacts are related to N availability and invader biomass. We propose some hypotheses for the observed patterns, but suggest that caution be used when making inferences about the context dependence of *M. vimineum* impacts due to the short-term, observational nature of this study. Specifically, we suggest that future studies take an experimental approach to demonstrate causal mechanisms linking invasion to altered SOC. Additionally, the effects of invasion could change through time for several reasons, such as evolution (Lankau et al. 2009), "boom-and-bust" dynamics (Simberloff and Gibbons 2004), or positive or negative plant–soil feedbacks (Levine et al. 2006, Diez et al. 2010). As a result, temporal variability could be as or more important than spatial variability, suggesting a need for long-term or chronosequence studies. Finally, we show that invader performance (biomass) may relate to invader impacts, but do not fully investigate the climatic and edaphic factors that led to differences in performance. Future work could combine our findings with spatial models of *M. vimineum* performance to make predictions about effects at broader scales.

Despite extensive research, many gaps exist in our understanding of the ecosystem-level consequences of plant invasion. One question that remains largely unanswered is how invasion will interact with other global changes to affect ecosystem functioning (Strayer 2012). To date, most investigations have focused on whether other anthropogenic changes may affect invader success and therefore invader impacts. However, we provide evidence that the effects of plant invasion on SOC and litter decomposition depend not only on invader performance (biomass), but also on other factors that are sensitive to modification by human activities. Impacts on soil C and litter decomposition varied with land use context. Whether the interaction between invasion and land use context is a general phenomenon and whether the abiotic factors studied

here modulate other impacts of invasive plants (e.g., reductions of native diversity) are questions for future research, but our results suggest that the impacts of biological invasion need to be understood in the context of other global change drivers that act to both facilitate invasions and modulate their effects.

Acknowledgments

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Supplemental Material

Ecological Archives

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