



Impacts of an invasive grass on soil organic matter pools vary across a tree-mycorrhizal gradient

Matthew E. Craig · Nadia Lovko · S. Luke Flory · Justin P. Wright · Richard P. Phillips

Received: 7 June 2018 / Accepted: 4 June 2019
© Springer Nature Switzerland AG 2019

Abstract Increases in carbon (C) inputs can augment soil organic matter (SOM), or reduce SOM by accelerating decomposition. Thus, there is a need to understand how and why ecosystems differ in their sensitivity to C inputs. Invasive plants that invade wide-ranging habitats, accumulate biomass rapidly, and contribute copious amounts of C to soil can be ideal for addressing this gap. We quantified the effects of the invasive C4 grass, *Microstegium vimineum*, on SOM in three temperate forests across plots varying in their relative abundance of arbuscular mycorrhizal (AM) versus ectomycorrhizal (ECM) trees. We hypothesized that invasion would differentially affect SOM along the mycorrhizal gradient owing to

recognized patterns in nitrogen availability (AM > ECM) and the proportion of unprotected SOM (ECM > AM). Across all sites, *M. vimineum* was associated with lower particulate organic matter (POM) in ECM-dominated plots, consistent with our hypothesis that invader-derived C inputs should stimulate decomposers to acquire nitrogen from unprotected SOM in soils with low nitrogen availability. However, the pattern of lower POM in the ECM-dominated soils was offset by greater mineral-associated organic matter (MAOM)—and isotopic data suggest this was largely driven by native- rather than invader-derived SOM—implying an invasion-associated transfer of native-derived POM into MAOM. Our results demonstrate a context-dependent shift in the form of SOM in a system with presumably enhanced C inputs. This finding suggests a need to look beyond changes in total SOM stocks, as intrinsic SOM changes could lead to important long-term feedbacks on invasion or priming effects.

Responsible Editor: Melany Fisk.

Electronic supplementary material The online version of this article (<https://doi.org/10.1007/s10533-019-00577-2>) contains supplementary material, which is available to authorized users.

M. E. Craig (✉) · N. Lovko · R. P. Phillips
Department of Biology, Indiana University, 1001 E Third
St, Bloomington, IN 47403, USA
e-mail: maecraig@indiana.edu

S. L. Flory
Agronomy Department, University of Florida,
Gainesville, FL, USA

J. P. Wright
Department of Biology, Duke University, Durham, NC,
USA

Keywords Plant invasion · *Microstegium* · Priming · Mycorrhizal fungi · Carbon · Nitrogen

Introduction

Global changes, including biological invasion, are predicted to enhance the rate and alter the chemical composition of carbon (C) inputs to soils (van

Groenigen et al. 2006; Liao et al. 2008; Phillips et al. 2011; Sistla et al. 2013). Such changes can alter the balance of soil organic matter (SOM) formation and decomposition, with implications for SOM stocks (e.g. Fontaine et al. 2004; Sulman et al. 2014) and the many ecological functions SOM provides (Schmidt et al. 2011). However, despite substantial research efforts (e.g. Bradford et al. 2008; Chen et al. 2014), it remains unclear where plant community- or productivity-driven alterations to C inputs should lead to increases versus decreases in SOM (Zhang et al. 2013; Luo et al. 2016).

Soil microbes mediate the effect of altered C inputs on SOM. High-quality C inputs (i.e. those that are rapidly metabolized by soil microbes) can favor microbial growth (Bradford et al. 2013; Frey et al. 2013; Chen et al. 2014), a pre-requisite for stable mineral-associated SOM formation (Bradford et al. 2013), and reduce the necessity for microbes to decompose SOM to acquire carbon (Cardon et al. 2001). In this case, C inputs should lead to enhanced SOM stocks. However, C inputs are also often found to cause “priming effects” (sensu Kuzyakov et al. 2000) by stimulating the catabolic activity of microbes (Phillips et al. 2011; Rousk et al. 2016; Meier et al. 2017), or by inducing microbial community shifts (Fontaine and Barot 2005; Kuzyakov 2010), leading to enhanced SOM decomposition and, ultimately, reduced SOM stocks (Fontaine et al. 2004). Indeed, such effects may explain why plant-derived SOM pools often are unchanged by long-term experimental augmentation of litter inputs (Lajtha et al. 2018). Thus, the effect of altered C inputs on SOM is likely determined by the balance between microbial biosynthesis and catabolism (Liang et al. 2017).

Soil factors (e.g. nutrient availability, texture, moisture, or pH), in addition to having their own effects on SOM, may strongly determine whether C inputs lead to enhanced or reduced SOM stocks (Kuzyakov et al. 2010). For example, in systems with low inorganic N availability, high-quality organic inputs may alleviate microbial C limitation and stimulate microbes to decompose SOM in order to acquire N (Craine et al. 2007; Fontaine et al. 2011; Phillips et al. 2011; Moorhead and Sinsabaugh 2006). In contrast, added C inputs in areas with high inorganic N may lead to SOM gains (Bradford et al. 2008) by repressing the production of extracellular enzymes (Geisseler et al. 2010) or by enhancing

microbial growth (Bradford et al. 2013; Manzoni et al. 2012). The properties of the SOM itself could also modulate the effect of C inputs on SOM stocks. In general, the extent to which SOM is protected from microbial activity (e.g. through chemical interactions with mineral surfaces) is an important factor controlling the resistance of SOM stocks to environmental change. For example, SOM losses following changes such as plant invasion are often driven by the accelerated decay of unprotected SOM pools (Garten and Wullschlegel 2000; Six et al. 2002; Strickland et al. 2010). Taken together, a reasonable hypothesis is that high-quality C inputs should lead to losses of SOM in areas where inorganic N availability is low and where SOM is unprotected from microbial decay. To date, most attempts to test this hypothesis have focused on short-term (i.e. weeks to months) laboratory experiments (Bradford et al. 2008; Di Lonardo et al. 2017; Luo et al. 2016) and therefore exclude factors—like plant nutrient uptake, microbial community differences, or soil properties—that may covary with C inputs and modulate SOM decomposition and formation in natural systems.

Plant invasions provide a way to study the context-dependent effects of altered C inputs in a field setting. Globally, invasive plants enhance the production and input of high-quality C compounds (e.g. low-lignin litters) compared to the native plants they displace (Liao et al. 2008). Moreover, some invasive plants can enhance high-quality belowground C inputs directly via root exudation (Bradford et al. 2012; Sokol et al. 2018). Invaders can also alter soil factors, such as nutrient availability, soil pH, and water content (Vilà et al. 2011), that may independently or interactively affect SOM. Yet, despite these general patterns, invader impacts on SOM dynamics can vary substantially across space (Hughes and Uowolo 2006; Koutika et al. 2007; Strayer 2012). A common hypothesis for explaining the context-dependence of invader effects is that the pre-invasion conditions of the invaded site can modulate the direction and magnitude of invader impacts (Dassonville et al. 2008; Scharfy et al. 2009; Craig et al. 2015). If true, a framework for predicting pre-invasion site conditions would substantially improve our ability to predict where and to what extent plant invasion will alter SOM properties.

In temperate forests, the mycorrhizal association of dominant trees has been shown to predict soil nutrient

availability and SOM properties (Phillips et al. 2013). Specifically, ectomycorrhizal (ECM)-associated tree dominance is associated with low inorganic N availability (Phillips et al. 2013) and a lower amount of SOM stored in mineral-associated compared to unprotected particulate forms (Craig et al. 2018). Arbuscular mycorrhizal (AM)-associated tree dominance, on the other hand, is associated with high inorganic N availability (Phillips et al. 2013) and a greater amount of SOM stored in mineral-associated SOM pools (Craig et al. 2018). Accordingly, we hypothesize that invasion and its associated increases in high-quality C inputs should lead to decreases in SOM stocks in ECM-dominated areas (“ECM plots”), where N-limited microbial decomposers may decompose unprotected SOM in order to enhance inorganic N availability. However, in AM-dominated forests (“AM plots”), where there is evidence of greater SOM protection and less demand to break down SOM to acquire N, we hypothesize that invader-derived high-quality C inputs should be allocated more toward microbial growth, leading to an accumulation of microbial-derived mineral-associated SOM.

Here, we quantified the effects of a well-studied invasive grass, *Microstegium vimineum*, on SOM properties across gradients of ECM-associated tree dominance (hereafter “mycorrhizal gradients”) in a field study. We worked in three widely-distributed deciduous forests to assess the generality or site-specificity of observed patterns. *M. vimineum* is a widespread and problematic invader that is an ideal organism for studying the effects of C inputs on SOM dynamics because it is a C4 grass that invades C3-dominated forests. Thus, its contribution to soil C can be determined based on its distinct isotopic signature. Moreover, *M. vimineum* is known to have context-dependent effects on SOM (Kramer et al. 2012; Craig et al. 2015; Sokol et al. 2017) and is known to enhance belowground C inputs via root exudation (Strickland et al. 2010; Bradford et al. 2012; Sokol et al. 2018). Our goal was to determine whether the effects of *M. vimineum* on total, native-derived, or invader-derived SOM pools depend on the mycorrhizal dominance of invaded sites.

Methods

Study sites

We conducted this work in three forests, each containing a gradient of ECM- to AM-dominated forest stands. Moore’s Creek (MC; 39°05’N, 86°28’W) is an ~ 80-year-old temperate hardwood forest in South-Central Indiana, USA dominated by ECM-associated *Fagus grandifolia*, *Quercus*, and *Carya* species, and AM-associated *Acer saccharum*, *Liriodendron tulipifera*, *Fraxinus americana*, and *Sassafras albidum*. Soils at MC are silty loams classified as Hapludalfs, Hapludults, and Dystrudepts (Soil Survey Staff 1999). Duke Forest (DF; 36°01’N, 78°59’W) is a ~ 70-year-old temperate mixed forest in Central North Carolina, USA dominated by ECM-associated *Pinus taeda* and *Quercus phellos*, and AM-associated *Liquidambar styraciflua*, *Liriodendron tulipifera*, *Fraxinus pennsylvanica*, *Acer* species, *Ulmus* species, and *Platanus occidentalis*. Soils at DF are loams classified as Hapludalfs. Whitehall Forest (WF; 33°53’N, 83°22’) is an ~ 80-year-old forest in Northern Georgia, USA dominated by ECM-associated *Quercus* species, *Pinus taeda*, *Carya* species, and *Ostrya virginiana*, and AM-associated *Liriodendron tulipifera*, *Liquidambar styraciflua*, and *Ulmus* species. Soils at WF are loams classified as Hapludults. Further site details are reported in Table 1.

Established invasions of *M. vimineum* were located in upland areas in Fall 2013 and 30 plots were set up in areas containing *M. vimineum* (hereafter “invaded”) and in nearby uninvaded, “reference” areas (60 plots total; 18 at MC, 22 at DF, and 20 at WF). Plots were comprised of circular subplots (10 m radius) where all trees (diam. breast height > 5 cm) were identified, measured (dbh), and classified as ECM-associated or AM-associated based on published records (Phillips et al. 2013). Mycorrhizal dominance was then determined for each plot based on the relative abundance of AM versus ECM trees (see below). Each plot contained three subplots except for two plots at MC that were constrained by the extent of *M. vimineum* invasion (i.e. 1 plot had 2 subplots and 1 plot had subplot; 174 total subplots). AM- and ECM-dominated plots were intermixed throughout each site to avoid sampling along a confounding spatial gradient.

Table 1 Average soil characteristics and (SE) in invaded and reference plots at Whitehall Forest, Georgia, USA; Moore's Creek, Indiana, USA; and Duke Forest, North Carolina, USA

Site	Invader biomass (g m ⁻²)	Soil moisture (%)	Bulk density (g cm ⁻³)	pH	Sand (%)	Clay (%)	C stock (kg m ⁻²) ^a	N stock (kg m ⁻²) ^a
Whitehall forest								
Reference	1 (1)	25.9 (2.1)	0.92 (0.07)	5.0 (0.1)	54 (4)	11 (2)	3.09 (0.13)	0.23 (0.01)
Invaded	123 (14)	29.3 (1.7)	0.76 (0.05)	5.2 (0.1)	42 (5)	10 (1)	3.20 (0.18)	0.25 (0.02)
Moore's Creek								
Reference	0 (0)	16.0 (1.9)	0.64 (0.05)	4.6 (0.2)	16 (1)	7 (1)	3.15 (0.22)	0.23 (0.02)
Invaded	109 (26)	18.1 (1.7)	0.66 (0.04)	4.8 (0.1)	19 (2)	7 (1)	3.33 (0.33)	0.24 (0.02)
Duke forest								
Reference	4 (3)	17.8 (1.9)	0.93 (0.05)	4.3 (0.1)	46 (7)	11 (2)	3.71 (0.64)	0.12 (0.02)
Invaded	86 (15)	20.2 (1.5)	0.97 (0.06)	4.8 (0.1)	49 (6)	9 (2)	3.33 (0.34)	0.24 (0.04)

Each study site has substantial invasion by *M. vimineum*. *M. vimineum* was first recorded at DF in 1948 and is still spreading within the site (R. Peet, personal communication). At WF, *M. vimineum* was recorded in abundance prior to 2001 (Strickland et al. 2010; K. Miller, personal communication). *M. vimineum* was observed at MC between 2003 and 2006, however, anecdotal evidence and vegetation surveys suggest that it was initially constrained to floodplain areas and a lake shoreline (M. Chitwood, K. Clay, and A. Shelton, personal communication). Given the continual spread of *M. vimineum* at these sites, it is not possible to determine the specific age of *M. vimineum* populations in our study plots. However, based on the available information, it is likely that the DF populations are the oldest and the MC populations are the youngest.

Soil and vegetation sampling

In August and September 2014, soil cores (5.08-cm diam.) were collected from each subplot at 0–5 cm (including a thin O horizon where present) and 5–15 cm depth. Cores from the same plot and depth were composited ($n = 60$ samples for each depth; 120 total samples), sieved to 2 mm, subsampled for gravimetric moisture (105 °C), and air-dried until soil organic matter characterization. Moisture was also determined on a set of samples collected near peak biomass in 2015 and values from 2014 and 2015 were averaged. To determine soil bulk density and texture,

additional samples were collected from each subplot in June 2016 and composited by plot and depth. Samples were then dried (105 °C), sieved, and the mass of the fine (< 2 mm) fraction was used to determine soil bulk density (g soil cm⁻³ sample volume). These samples were then used to determine soil texture via the hydrometer method (Ulmer et al. 1994). Understory aboveground biomass was determined near peak *M. vimineum* biomass (MC: August, DF and WF: September) in 2015 by clipping and collecting all plant material within a 25 × 25-cm square in each subplot. Biomass was then separated into *M. vimineum* and non-*M. vimineum* materials, dried (55 °C), and weighed.

Soil organic matter characterization

Soil C and N content was determined by grinding samples to a powder and analyzing on an elemental combustion system (Costech ECS 4010, Costech Analytical Technologies, Valencia, CA, USA). Total C is considered equivalent to organic C given that all soils were below a pH of 5.8. To understand the effects of *M. vimineum* on protected versus unprotected SOM pools, we separated SOM into mineral-associated organic matter (MAOM) and particulate organic matter (POM) using a size fractionation procedure (Cambardella and Elliott 1992) as modified by Bradford et al. (2008). Briefly, we dispersed soil samples in 5% (w/v) sodium hexametaphosphate for 20 h on a reciprocal shaker and washed each sample through a

53- μm sieve. The fraction retained on the sieve was considered POM while the finer, clay and silt fraction that passed through the sieve was considered MAOM. Because SOM in the clay and silt fraction tends to have a longer residence time due to the chemical interactions with microbial-derived compounds (Anderson and Paul 1984; Grandy and Neff 2008), this method separates a putatively protected SOM pool (i.e. MAOM) from a putatively unprotected SOM pool (i.e. POM). Carbon and nitrogen concentrations as well as $\delta^{13}\text{C}$ values of the POM and MAOM fractions were determined by drying (55 °C), grinding, and analyzing samples using an elemental combustion system (Costech ECS 4010, Costech Analytical Technologies, Valencia, CA, USA) as an inlet to a ThermoFinnigan DELTA plus XP isotope ratio mass spectrometer (Thermo Fisher Scientific, San Jose, CA).

Soil inorganic nitrogen

In each plot, inorganic N availability was quantified using ion exchange resin bags (sensu Craig et al. 2015). This technique provides an integrated measure of inorganic N availability across the growing season. Briefly, mesh bags (150 μm) were filled with 5 g of a mixed-bed ion exchange resin (Rexyn R208, Thermo Fisher Scientific), and one bag was installed at 5-cm in each subplot and left in situ from June to November, May to November, and April to December in MC, DF, and WF, respectively, during the 2015 growing season. Upon removal, resin bags were sealed in separate plastic bags and refrigerated until extraction in 2 M KCl. Extracts were analyzed for NH_4^+ -N via the salicylate method and NO_3^- using a cadmium column reduction on a Lachat QuikChem 8500 (Hach Company, Loveland, Colorado, USA).

Data analysis

ECM dominance was calculated as the percentage of ECM-associated basal area relative to the total basal area. Tree species known to associate with both AM- and ECM-fungi and tree species with unknown mycorrhizal associations accounted for 1% or less of the basal area. Thus, low values of ECM dominance indicate AM-dominated plots. ECM gradients were comparable among the three sites as ECM dominance

ranged from 8 to 83%, 0 to 83%, and 13 to 76% at MC, DF, and WF, respectively.

The amount of C derived from *M. vimineum* in each invaded plot was determined as follows:

$$C_{MV} = C_{\text{soil}} \left(\frac{\delta^{13}\text{C}_i - \delta^{13}\text{C}_r}{\delta^{13}\text{C}_{mv} - \delta^{13}\text{C}_r} \right)$$

where C_{soil} is the total amount of soil C in the soil pool, $\delta^{13}\text{C}_i$ is the soil $\delta^{13}\text{C}$ value in invaded plots, $\delta^{13}\text{C}_{mv}$ is the $\delta^{13}\text{C}$ value for *M. vimineum* tissues (-14.31‰ ; Strickland et al. 2010), and $\delta^{13}\text{C}_r$ is the soil $\delta^{13}\text{C}$ value in reference plots. At WF and DF, we used the $\delta^{13}\text{C}$ value in the nearest reference plot (within 50 m) as our measure of $\delta^{13}\text{C}_r$. At MC, we observed a strong negative relationship between ECM dominance and $\delta^{13}\text{C}$ of the POM ($R^2 = 0.55$) and MAOM ($R^2 = 0.73$; Fig S1). Because the nearest reference plot sometimes differed in tree community composition at MC, we estimated $\delta^{13}\text{C}_r$ by fitting a site specific linear relationship between ECM dominance and $\delta^{13}\text{C}$ in reference plots and then interpolating $\delta^{13}\text{C}_r$ based on the ECM dominance of each invaded plot. Once determined, the *M. vimineum*-derived pool was used to estimate the native-derived pool ($C_{\text{native}} = C_{\text{soil}} - C_{MV}$) and the percentage of *M. vimineum*-derived C ($C_{\%MV} = C_{MV}/C_{\text{soil}} \times 100$). Given the methodological nuance in the determination of the *M. vimineum*-derived pool at MC, we also analyzed the raw $\delta^{13}\text{C}$ values (below).

To evaluate the relationship between *M. vimineum* presence and soil C and N dynamics, we fit general linear mixed models to soil C and N (i.e. MAOM-N, MAOM-C, POM-N, POM-C, MAOM- $\delta^{13}\text{C}$, POM- $\delta^{13}\text{C}$). Invasion status (invaded or reference plot), ECM dominance, site, and sample depth were included as fixed factors, with plot included as a random factor to account for non-independence between shallow and deep soils from the same plot. To test our hypothesis that the effect of *M. vimineum* on soil C and N pools would depend on the mycorrhizal status of the plot, we evaluated the interaction between invasion status and ECM dominance. We also included the three-way interaction of this term with site and with depth and all their nested two-way interactions, to determine whether hypothesized interactive effects between ECM dominance and invasion depend on site or soil depth, and we included % clay to account for potential differences in underlying soil

factors—though we acknowledge that % clay is an imperfect predictor of soil organic matter dynamics (Rasmussen et al. 2018). These additional terms were subjected to removal via backwards selection, and the most parsimonious model was selected based on AIC. These models were also run for soil pH and moisture to determine whether mycorrhizal associations or invasion status co-varied with other potentially important predictors of soil C and N pools. For response variables that did not have a depth component (e.g. resin N and plant biomass), general linear models were fit with a similar approach. Finally, we used general linear mixed models to determine whether the performance of *M. vimineum* or its contribution to soil C pools depended on ECM dominance. These models were run as above, but just for the invaded subset of plots (i.e. without invasion status or its interactions as a factor). For all models, we tested whether model residuals met assumptions of normality (Shapiro–Wilk test) and homoscedasticity (Levene’s test). When necessary, data were natural log transformed to improve normality. Mixed model analyses were performed in R 3.3.1 (R development Core Team) using the nlme package (Pinheiro et al. 2014) and results of the models were visualized using partial residual plots created with the visreg package to examine bivariate relationships while holding other fixed effects constant (Breheny and Burchett 2017).

Results

Understory plant biomass did not vary with ECM dominance ($P = 0.66$), and was six times greater in invaded than in reference plots ($P < 0.001$; Table 2). This difference was mostly driven by the presence of *M. vimineum* biomass. *M. vimineum* biomass was $105 \pm 11 \text{ g m}^{-2}$ (mean, SE) and did not vary with ECM dominance ($F_{1,26} = 0.8$, $P = 0.39$) or with site ($F_{2,26} = 1.2$, $P = 0.32$; Table 1). Total basal area was explained by the interaction between invasion and %ECM ($F_{1,52} = 8.6$, $P = 0.01$) such that overstory biomass tended to be greater in reference plots as %ECM increases. Soil moisture and soil pH varied across sites, soil depth, and with ECM dominance and invasion status (Table 2). In general, ECM dominance was negatively associated with moisture and pH. In addition, ECM dominance and invasion status were interactively related to soil moisture ($P < 0.001$) and

soil pH ($P = 0.01$) such that invasion was associated with wetter, less acidic soils in ECM plots, but not in AM plots.

Ectomycorrhizal-dominated soils tended to have lower resin-available inorganic N than AM-dominated soils (Fig. 1), however this pattern depended on site and invasion status (Invasion \times %ECM \times Site: $P = 0.04$; Table 2) and was driven by differences in the resin-available NO_3^- (Invasion \times %ECM \times Site: $P = 0.01$; Table S1) which accounted for ca. 85% of total resin N. Invasion was associated with greater resin-available N pools, but only in ECM-dominated plots in MC (Fig. 1).

Invasion effects on SOM pools

As hypothesized, the relationship between invasion status and SOM pools depended on ECM dominance. ECM plots had the largest invasion-associated SOM differences, while invaded and reference SOM pools were similar in AM plots. These general effects were consistent across the sites, even though SOM and soil properties differed among the three sites (Tables 1, 3). However, the relationships of ECM dominance and invasion with total C and N were weaker than relationships with individual SOM pools due to the opposing patterns of different SOM pools (Table 3; Fig. S2). Total C was not related to invasion status or ECM dominance. Total N was negatively related to ECM dominance ($P = 0.03$), but this effect depended on invasion status as invasion was associated with lower total N in AM plots and greater total N in ECM plots (Invasion \times %ECM: $P = 0.02$).

To examine relationships of invasion status and ECM dominance with different SOM pools, we separated SOM into MAOM and POM pools (Table 3; Fig. S2). ECM dominance was negatively related to MAOM-N ($P = 0.002$) and MAOM-C ($P = 0.02$), but positively interacted with invasion status such that invasion was associated with greater MAOM-N ($P = 0.002$) and MAOM-C ($P = 0.01$) in ECM plots, but not AM plots. For POM pools, soil depth modulated the interaction between ECM dominance and invasion status; the three-way interaction was retained in N ($P = 0.05$) and C ($P = 0.03$) models. In shallow soils, ECM dominance was positively associated with POM-N and POM-C pools, and invasion was associated with lower POM in ECM plots, but not AM plots (Fig. S2). Because the interactions between

Table 2 Linear mixed model (soil moisture and pH) and general linear model (Resin N, plant biomass) results for resin-available inorganic nitrogen (resin N; $\mu\text{g N g resin}^{-1} \text{d}^{-1}$), soil moisture (%), soil pH, and total understory biomass (plant biomass; g m^{-2}) with invasion status, ectomycorrhizal-associated tree dominance (%ECM), soil depth (soil moisture and pH), site, and clay content (%) as predictors

Response	Predictor	Coeff.	SE	df	F	P
Resin N	Invasion	0.332	0.493	1,47	0.5	0.50
	%ECM	- 0.002	0.010	1,47	0.1	0.81
	Invasion \times %ECM	- 0.005	0.013	1,47	0.2	0.69
	Invasion \times %ECM \times site			2,47	3.6	0.04
	Invasion \times site			2,47	1.4	0.25
	%ECM \times site			2,47	0.3	0.76
	Site			2,47	0.5	0.61
Soil moisture	Invasion	- 5.799	2.455	1,49	5.6	0.02
	%ECM	- 0.324	0.062	1,49	27.3	< 0.001
	Depth	- 6.837	0.925	1,54	54.7	< 0.001
	%Clay	0.356	0.115	1,49	9.6	0.003
	Invasion \times %ECM	0.258	0.051	1,49	25.9	< 0.001
	%ECM \times depth	0.039	0.019	1,54	4.1	0.05
	Invasion \times site			2,49	3.6	0.04
	%ECM \times site			2,49	3.1	0.05
	Site			2,49	4.3	0.02
	pH	Invasion	- 0.189	0.187	1,54	1.0
%ECM		- 0.007	0.003	1,54	6.5	0.01
Depth		- 0.247	0.039	1,55	39.2	< 0.001
Invasion \times %ECM		0.010	0.004	1,54	6.6	0.01
Site				2,54	11.0	< 0.001
Plant biomass	Invasion	151	33	1,51	21.3	< 0.001
	%ECM	0.217	0.491	1,51	0.2	0.66
	Invasion \times %ECM	- 0.633	0.670	1,51	0.9	0.35
	Invasion \times site			2,51	2.5	0.09
	Site			2,51	1.5	0.24

Resin N was natural log transformed

invasion and ECM dominance differed in direction for POM and MAOM (invasion was associated with greater MAOM, but less POM, with greater ECM dominance), the MAOM:POM ratio differed in invaded and reference plots across the gradient (Fig. 2; Table S2). While MAOM:POM ratios tended to decrease with increasing ECM dominance, there was a mycorrhizal- and depth-dependent invasion effect. In ECM plots, but not in AM plots, invasion was associated with increased MAOM-N:POM-N (Invasion \times %ECM: $P = 0.01$) and MAOM-C:POM-C (Invasion \times %ECM: $P = 0.04$). While this interactive effect was consistent across all sites, it depended on soil depth and was greater in shallow soils for N (Invasion \times %ECM \times Depth: $P = 0.03$) and, to a lesser extent, C (Invasion \times %ECM \times Depth: $P = 0.12$). Patterns in SOM pools were driven by patterns in native-derived

SOM, as the analysis of native-derived C pools yielded qualitatively similar results to that of the total (*M. vimineum*-derived + native-derived) SOM pools (Table S3).

Invader-derived carbon

Invaded soils were characterized by less negative $\delta^{13}\text{C}$ values for POM-C ($P = 0.003$; Table S4), reflecting *M. vimineum*'s C4 isotopic signature. For MAOM-C, the invasion effect on $\delta^{13}\text{C}$ depended on its three-way interaction with ECM dominance and site ($P = 0.006$), such that invasion was associated with a larger effect on $\delta^{13}\text{C}$ in AM plots in DF and WF, but in ECM plots in MC. This was driven, in part, by the strong negative relationship between $\delta^{13}\text{C}$ and %ECM in reference plots at MC (Fig. S1). Using these $\delta^{13}\text{C}$ values, we estimated the size of *M. vimineum* C

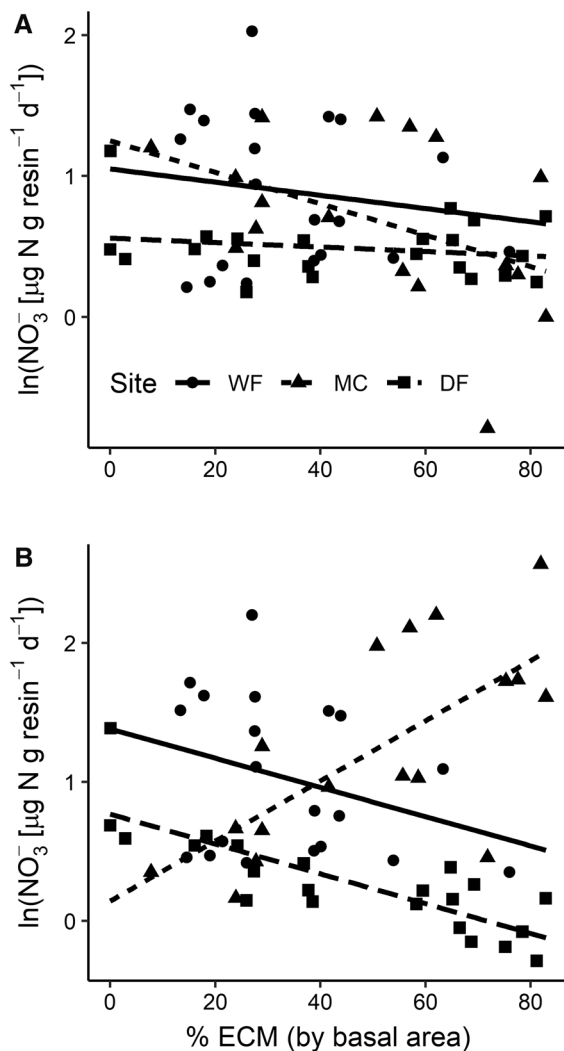


Fig. 1 Partial residual plot showing the relationship between ectomycorrhizal dominance and natural log transformed resin-available nitrate in reference (a) and invaded (b) plots in Whitehall Forest, Georgia, USA (WF; solid line); Moore's Creek, Indiana, USA (MC; dotted line); and Duke Forest, North Carolina, USA (DF; dashed line). Partial residual plots enable visualization of the effect of individual predictors in a linear model while holding other predictors constant. Statistical output from the full model is described in Table S1

pools. Carbon derived from *M. vimineum* accounted for only $2.77 \pm 0.43\%$ and $5.01 \pm 0.62\%$ (mean, SE) of MAOM-C and POM-C pools, respectively, but this contribution ranged from 0 to 13% for MAOM-C and 0 to 19% for POM-C, and varied with ECM dominance, sample depth, site, and soil texture (Table S5). *M. vimineum* contributed more C to shallow than to deep MAOM-C—by mass ($P = 0.004$) and by

percentage of total MAOM C ($P = 0.02$)—and POM-C pools by mass ($P = 0.04$) and percentage ($P = 0.06$). The effect of ECM dominance on the percentage of *M. vimineum*-derived C in the MAOM-C pool varied by site (Site \times %ECM: $P = 0.05$). Invasion of AM plots was associated with greater *M. vimineum*-derived C in DF and WF, but invasion of ECM plots was associated with greater *M. vimineum*-derived C in MC (Fig. 3). However, *M. vimineum*-derived C was insufficient to account for the greater overall MAOM-C in invaded ECM plots at MC as this pattern was mostly driven by changes in the native-derived MAOM-C pool (Table S3).

Discussion

We sought to determine whether soil conditions, which differ under distinct tree communities, modulate the response of SOM pools to invasion and associated increases in high-quality C inputs. To do this, we quantified total and invader-derived SOM pools in invaded and reference plots spanning gradients of ECM-associated tree dominance, because mycorrhizal gradients are known to predict differences in nitrogen availability and SOM stability in temperate hardwood forests. Given that *M. vimineum* has a C4 isotopic signature and is known to enhance belowground C inputs via root exudates (Bradford et al. 2012), our study system provided a unique opportunity to investigate the context-dependent effects C inputs in a natural setting. While we found only minor changes in total C, our results suggest that invasion of ECM-dominated soils, but not AM-dominated soils, led to a substantial flush of native-derived organic matter from the POM into the MAOM pool. Notably, this effect was observed across three sites that differed in their climatic and edaphic properties. These endogenous changes to SOM could have important consequences for ecosystem functioning and long-term feedbacks on invasion or priming effects.

Effects of invasion on SOM pools depend on tree community

We find support for our hypothesis that invasion should decrease SOM in soils with low inorganic N availability and high amounts of “unprotected”

Table 3 Linear mixed model results for total soil organic matter, particulate organic matter (POM), and mineral-associated organic matter (MAOM) nitrogen (N), and carbon (C) pools with invasion status, ectomycorrhizal-associated tree dominance (%ECM), soil depth, site, and clay content (%) as predictors

Response	Predictor	Coeff.	SE	<i>df</i>	<i>F</i>	<i>P</i>
Total N	Invasion	- 0.185	0.110	1,53	2.8	0.10
	%ECM	- 0.004	0.002	1,53	4.8	0.03
	Depth	- 0.385	0.046	1,55	68.8	< 0.001
	%Clay	0.015	0.005	1,53	7.9	0.01
	Invasion × %ECM	0.005	0.002	1,53	5.6	0.02
	Site			2,53	8.9	< 0.001
Total C	Invasion	- 0.325	0.208	1,53	2.4	0.12
	%ECM	- 0.002	0.003	1,53	0.8	0.37
	Depth	- 0.858	0.117	1,54	53.7	< 0.001
	%Clay	0.022	0.009	1,53	5.6	0.02
	Invasion × %ECM	0.006	0.004	1,53	2.3	0.13
	Invasion × depth	0.251	0.166	1,54	2.3	0.14
	Site			2,53	6.9	0.002
POM-N	Invasion	- 0.001	0.085	1,54	< 0.01	0.99
	%ECM	0.002	0.001	1,54	2.9	0.10
	Depth	- 0.321	0.084	1,52	14.8	< 0.001
	Invasion × %ECM	- 0.003	0.002	1,54	2.6	0.11
	Invasion × depth	- 0.045	0.106	1,52	0.2	0.67
	%ECM × depth	- 0.002	0.002	1,52	1.9	0.18
	Invasion × %ECM × depth	0.004	0.002	1,52	4.0	0.05
	Site			2,54	18.5	< 0.001
POM-C	Invasion	0.020	0.263	1,54	< 0.01	0.94
	%ECM	0.007	0.004	1,54	3.8	0.06
	Depth	- 1.098	0.242	1,52	20.6	< 0.001
	Invasion × %ECM	- 0.008	0.005	1,54	2.4	0.13
	Invasion × depth	- 0.204	0.306	1,52	0.4	0.51
	%ECM × depth	- 0.005	0.004	1,52	1.3	0.27
	Invasion × %ECM × depth	0.015	0.006	1,52	5.2	0.03
	Site			2,54	8.5	< 0.001
MAOM-N	Invasion	- 0.067	0.089	1,51	0.6	0.45
	%ECM	- 0.004	0.001	1,51	11.3	0.002
	Depth	- 0.328	0.024	1,55	194	< 0.001
	%Clay	0.009	0.004	1,51	4.9	0.03
	Invasion × %ECM	0.006	0.002	1,51	11.3	0.002
	Invasion × site			2,51	2.4	0.10
	Site			2,51	1.4	0.26
MAOM-C	Invasion	- 0.092	0.178	1,51	0.3	0.61
	%ECM	- 0.006	0.003	1,51	5.6	0.02
	Depth	- 0.741	0.052	1,55	205	< 0.001
	%Clay	0.012	0.008	1,51	2.0	0.16
	Invasion × %ECM	0.010	0.004	1,51	6.9	0.01
	Invasion × site			2,51	2.1	0.13
	Site			2,51	0.2	0.79

In each case, the response variable in mg C or N mg soil⁻¹ was natural log transformed

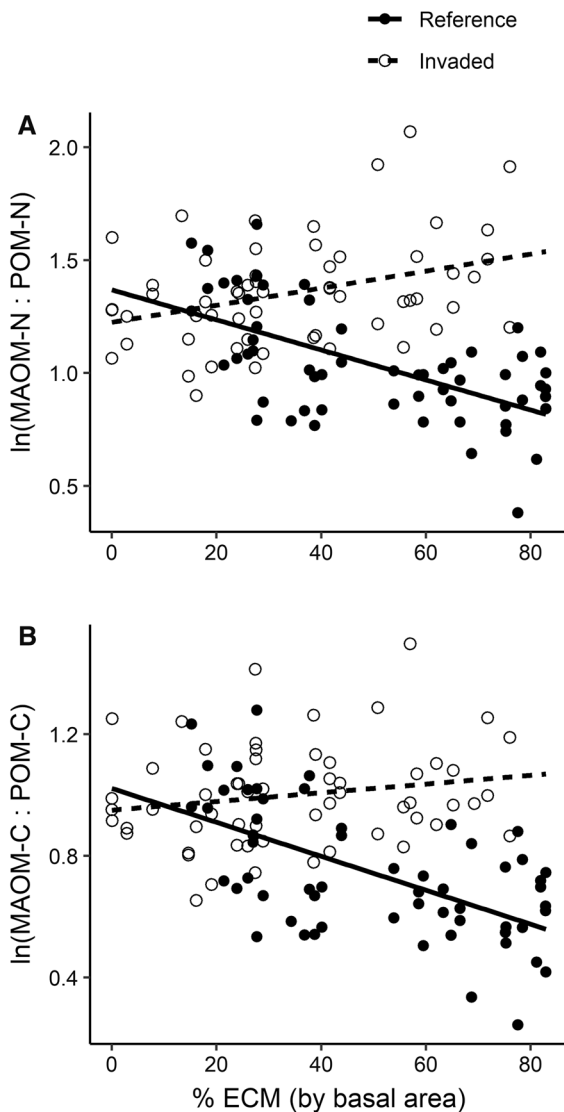


Fig. 2 Partial residual plot showing the variation in the natural log transformed ratio of mineral-associated organic matter (MAOM) to particulate organic matter (POM) nitrogen (N; **a**) and carbon (C; **b**) explained by ectomycorrhizal dominance in reference and invaded plots for 0–5 cm soils. Statistical output from the full model is described in Table S2

particulate organic N. Consistent with previous work (Phillips et al. 2013; Lin et al. 2016; Craig et al. 2018), we observed these conditions in reference ECM plots. In ECM plots, but not AM plots, we found that invasion was associated with less POM—a pool primarily comprised of recalcitrant plant inputs. We note that this effect was limited to the top 5 cm of soil, likely due to the greater abundance of POM at this depth and due to the shallow rooting depth of *M.*

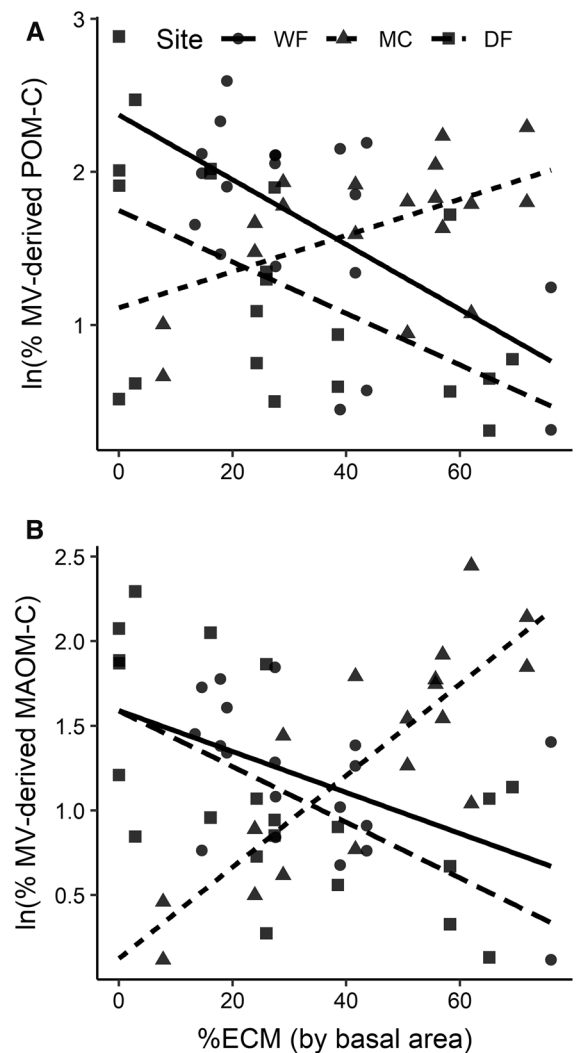


Fig. 3 Partial residual plot showing the relationship between ectomycorrhizal dominance and the natural log transformed percentage of *Microstegium vimineum*-derived particulate organic matter carbon (POM-C; **a**) and mineral-associated organic matter carbon (MAOM-C; **b**) for Whitehall Forest, Georgia, USA (WF; solid line); Moore's Creek, Indiana, USA (MC; dotted line); and Duke Forest, North Carolina, USA (DF; dashed line) for 0–5 cm soils

vimineum. We infer that a smaller POM pool in invaded ECM plots is driven by increased decay rather than decreased inputs, a key assumption given that POM is strongly influenced by plant litter inputs (Lajtha et al. 2014). We cannot rule out the influence of input differences as tree basal area tended to be lower in invaded plots as ECM dominance increased. However, understory biomass was much higher in invaded plots, previous work demonstrates

accelerated decay under *M. vimineum* (Strickland et al. 2010), and ongoing work at one of our sites confirms faster decay of the native organic matter with invasion of ECM plots (Kumar et al. unpublished). Thus, invasion-accelerated decay in ECM plots is a likely explanation for our findings, though future work characterizing invader effects on decay should also explicitly consider potential effects on inputs.

Previously reported *M. vimineum*-driven decreases in POM have been observed along with increased decay rates (Strickland et al. 2010) and are hypothesized to result from microbial priming effects stimulated by the greater quantity of high-quality belowground C inputs (Strickland et al. 2010, 2011; Bradford et al. 2012), though co-occurring changes in soil pH, moisture, or N availability may also be important. For example, *M. vimineum*-driven decreases in soil C may be greatest in soils with low inorganic N availability (Craig et al. 2015) due to enhanced plant-microbial competition for available inorganic N (Craig and Fraterrigo 2017). Yet, other studies have reported that *M. vimineum* may have little to no impact on POM pools (Kramer et al. 2012; Sokol et al. 2017). We propose that these variable impacts on the POM pool are explained by the N mining hypothesis (Moorhead and Sinsabaugh 2006; Craine et al. 2007), which proposes that high-quality C inputs should favor decomposition in soils with low inorganic N availability by lifting energetic constraints on decomposers capable of acquiring N from the SOM. While previous support for this hypothesis comes from short-term, lab-based C-addition experiments (Kuz'yakov 2010; Chen et al. 2014), our results indicate that N mining owing to enhanced C inputs could be an important constraint on SOM storage under realistic field conditions. Although there is evidence from other systems that plants can also stimulate decay of the MAOM pool (e.g. Keiluweit et al. 2015), here we only noted invasion-associated decreases in the unprotected POM pool. Thus, our results suggest that invasion effects depend on the extent to which SOM is protected against microbial decay.

We also hypothesized that invasion-associated increases in belowground C inputs to soils with high inorganic N availability (i.e. AM plots) would favor microbial growth and therefore an accumulation of invader-derived C. This, we predicted, would lead to a buildup of MAOM, which is primarily composed of microbial products (Grandy and Neff 2008). However,

while our observation of greater *M. vimineum*-derived C in AM plots at two of the three sites provides partial support for this hypothesis, we found no evidence of MAOM buildup in AM plots. On the contrary, invasion was associated with greater MAOM pools in ECM plots, a pattern that persisted at both soil depths. Thus, our data suggest that invasion simultaneously decreased the POM pool and increased the MAOM pool in ECM plots. Though *M. vimineum*-derived C did accumulate to a greater degree in ECM plots at one site (MC), *M. vimineum* contributed only small amounts of C to total soil C and patterns in total C pools were explained by native-derived rather than invader-derived C. Therefore, our results suggest that invasion of ECM-dominated soils led to a flush of native SOM from POM into MAOM pools. We hypothesize the following mechanism to explain this pattern. In N-limited soils, high-quality C inputs stimulate microbial decomposers to break down unprotected POM pools to acquire N. The resulting increase in the growth and turnover of microbes growing on POM substrates enhances the amount of POM-derived C in microbial necromass, which can then be stabilized on mineral surfaces. However, as this was an observational study, there is a need to consider the role of other covarying factors in mediating our observed patterns.

Covarying factors

Similar to the patterns we observed for SOM pools, we found that *M. vimineum* was associated with altered soil pH and soil moisture in ECM-, but not AM-dominated plots—two factors that could alter SOM decay and formation, or modulate the effect of enhanced C inputs on SOM. Consistent with previous work (e.g. Ehrenfeld et al. 2001; Kourtev et al. 2003; Craig and Fraterrigo 2017), we found that *M. vimineum* was associated with higher soil pH. But we only observed this pattern in ECM plots where we, and others (e.g. Phillips et al. 2013), observed a lower pH in reference plots. Given that soil acidity can inhibit the decay of plant-derived organic matter (Baath et al. 1980), this pH increase could have been an additional factor that promoted the decay of the POM pool in invaded, ECM-dominated soils. Alternatively, given previous evidence that priming effects increase with soil pH (Blagodatskaya and Kuzyakov 2011), the effect of invader-derived inputs on SOM

pools could have been amplified in ECM-dominated soils. Lastly, soil pH is a key determinant of mineral-organic association mechanisms (Rasmussen et al. 2018), so differences in pH could have led to changes in SOM association with clay minerals or metal oxides in invaded soils.

Soil moisture also could have played a role in our observed SOM patterns. *M. vimineum*-dominated soils are often associated with greater soil moisture than paired uninvaded soils (e.g. Strickland et al. 2010; Craig and Fraterrigo 2017)—an effect which could be driven by shading under *M. vimineum* and accumulated thatch—and pre-invasion soil moisture has been found to predict *M. vimineum* impacts on soil C pools (Craig et al. 2015). We observed greater soil moisture under *M. vimineum*, but only in ECM-dominated soils where reference soils were drier than in AM-dominated soils. This pattern of greater soil moisture in invaded areas could promote the decay of the POM pool by lifting water limitation on decomposition or by facilitating the diffusion of C inputs to microbial decomposers. Supporting this idea, previous research has found that priming effects tend to increase with soil moisture (Niklaus and Falloon, 2006; Dijkstra and Cheng, 2007). Moreover, given that the formation of mineral-organic associations is greatest in wet soils (Kleber et al. 2015), greater moisture in invaded, ECM-dominated soils may have facilitated a buildup of the MAOM pool in these same plots. This covariance of ECM dominance and invasion with soil moisture may also explain why Craig et al. (2015) did not similarly observe an invasion-associated MAOM increase in soils with low inorganic N availability. Nevertheless, as our results were only based on two sample points of a dynamic variable, future work should more rigorously evaluate how moisture and soil pH might mediate the effects of invasion or enhanced C inputs on SOM pools. Given that *M. vimineum* associates with arbuscular mycorrhizal fungi, future work might also consider how invasion-driven changes in the mycorrhizal community affects ecosystem processes across an ECM-dominance gradient.

Implications for SOM studies

Whatever the underlying mechanism, our finding that *M. vimineum* invasion differentially affected individual SOM pools has important implications for our understanding of invasion and other global change

effects on SOM. For example, priming effects are rarely determined by directly measuring SOM pools, due to the short-term nature of most C addition experiments, and are instead inferred based on CO₂ efflux (Blagodatskaya and Kuzyakov 2011). In our study, this approach would have underestimated the full impact of invasion as the contrasting responses of the POM and MAOM pools led to smaller invasion-associated differences in total soil C. By directly measuring SOM pools, we found evidence of an invasion-associated flush of C from the POM pool into the MAOM pool resulting in a dramatic increase in the amount of SOM stored in MAOM versus POM pools in ECM-dominated soils. Given the substantial differences in the stoichiometry, structure, and accessibility of MAOM versus POM pools, these endogenous changes to SOM could have important consequences for microbial communities (Sessitsch et al. 2001), nutrient cycling (Bingham and Cotrufo 2016), or C storage (Kleber et al. 2015). For example, to the extent that mineral-organic associations reduce microbial C availability (Schneider et al. 2010) and impair enzyme function (Bayan and Eivazi 1999), the concomitant buildup of the MAOM pool with POM losses could represent a negative feedback to priming effects in the long term. Indeed, this pattern is predicted by a recent theoretical simulation of AM-associated vegetation invading ECM-conditioned soil (Sulman et al. 2017). Such feedbacks could explain the lack of priming effects observed in some long-term studies (e.g. Lajtha et al. 2014; Cardinael et al. 2015; Luo et al. 2016). In sum, our results highlight the importance of considering intrinsic changes to SOM as well as bulk SOM stocks in investigations of priming effects.

Isotopic patterns and invader-derived carbon vary by site

Despite the consistent patterns in total SOM, the relationship of ECM dominance with $\delta^{13}\text{C}$ and estimated invader-derived C accumulation varied by site. Though we note that invader C accounted for a very small fraction of SOM, which makes sense given the dominance of tree inputs in *M. vimineum*-invaded forests (Strickland et al. 2010). Invader C accumulation was greatest in AM plots at WF and DF, as hypothesized, but was greatest in ECM plots at MC. We hypothesize that this relates to differences in invasion age or soil traits among the three sites. First,

we note that MC is likely the site with the youngest invasion (discussed in “[Methods](#)”). This may drive our observed patterns if the rates of inputs or outputs of *M. vimineum*-derived C in ECM plots change over the course of invasion. Though *M. vimineum* biomass did not vary predictably, there could be differences in belowground allocation within or among sites. For example, plants may allocate more C belowground in response to low inorganic N availability (Phillips et al. 2011) in ECM-dominated plots, leading to greater microbial activity and faster turnover of organic N. These traits may be favored for early generations of *M. vimineum* (e.g. at MC) in ECM plots, but may become less favored for later generations (e.g. at WF and DF) after unprotected N has been depleted which would explain our observation of greater inorganic N in ECM plots at MC. Such generational shifts have been reported for secondary compound production in *Alliaria petiolata* (Lankau et al. 2009). Alternatively, in newly invaded ECM plots, conditions and microbial communities may not be optimal for decomposition of the *M. vimineum* litter, but this may attenuate over time (Kramer et al. 2012). These patterns reinforce the need to understand how invasion and priming effects change over time (Strayer 2012; Sokol et al. 2017; Zhang et al. 2017).

Second, it is possible that the above pattern did not result from invader inputs per se, but from invader-mediated changes in the $\delta^{13}\text{C}$ of the native SOM. We found a negative relationship between ECM-dominance and soil $\delta^{13}\text{C}$ in reference plots, but only at MC. This pattern may reflect differences in the tree community (e.g. through differences in input $\delta^{13}\text{C}$) or decay rates among sites. Moreover, given that $\delta^{13}\text{C}$ values increase as organic materials are processed by decomposers (Tiunov 2007), *M. vimineum*-driven increases in decomposition could have caused a $\delta^{13}\text{C}$ increase that was most notable in ECM plots at MC where $\delta^{13}\text{C}$ was initially lowest. If true, this would suggest a need for isotopic tracking studies to consider that factors other than the isotopic signature of inputs could cause soil $\delta^{13}\text{C}$ differences.

Summary

Our analysis of invasion-associated changes in SOM across a mycorrhizal gradient represents one of few attempts to characterize context-dependent effects of

soil C inputs in a natural setting. In partial support of our hypothesis that invasion should lead to SOM decreases in low inorganic N systems and increases in high inorganic N systems, we found that the faster cycling POM pool tended to decrease to a greater degree in ECM-dominated forest plots. However, despite the observation of greater invader-derived C accumulation in AM forests at two of three study sites, we did not find evidence that the accumulation of C inputs leads to increases in the MAOM pool in systems with high inorganic N. Overall SOM concentrations in AM plots were unresponsive to invasion. Instead, we observed much greater MAOM in invaded ECM plots, driven by an apparent flush of the native SOM from POM into MAOM pools. Our results suggest that C inputs and biological invasion may alter the form and, therefore, the function and long-term stability of soil C, even where differences in respiration or total SOM stocks are not apparent. Finally, our results emphasize the importance of resolving the long-term effects of enhanced C inputs, or indeed any global change, in natural systems.

Acknowledgements This work was funded by the US National Science Foundation Ecosystem Studies Program (Grant Nos. 1353296, 1354879, and 1353211). Moore’s Creek is part of Indiana University’s Research and Teaching preserve. Marissa Lee and Cathy Fahey assisted with study design and plot setup and collected most of the samples from DF and WF, respectively. Mark Sheehan assisted with plot setup at MC. Laura Podzikowski contributed to the laboratory analysis of soil covariates, and Robin Johnson and Eric Ungberg helped with sample processing. We thank Steve Kannenberg, Adrienne Keller, and two anonymous reviewers for feedback on this paper; and Mark Bradford for input on the design of this project.

Compliance with ethical standards

Conflict of interest The authors declare no conflict of interest.

References

- Anderson DW, Paul EA (1984) Organo-mineral complexes and their study by radiocarbon dating. *Soil Sci Soc Am J* 48:298–301
- Baath E, Berg B, Lundgren B et al (1980) Effects of experimental acidification and liming on soil organisms and decomposition in a Scots pine forest. *Pedobiologia* 20:85–100
- Bayan MR, Eivazi F (1999) Selected enzyme activities as affected by free iron oxides and clay particle size. *Commun Soil Sci Plant Anal* 30:1561–1571

- Bingham AH, Cotrufo MF (2016) Organic nitrogen storage in mineral soil: implications for policy and management. *Sci Total Environ* 551:116–126
- Blagodatskaya E, Kuzyakov Y (2011) Priming effects in relation to soil conditions—mechanisms. In: Gliński J, Horabik J, Lipiec J (eds) *Encyclopedia of agrophysics*. Encyclopedia of earth sciences series. Springer, Dordrecht, pp 657–667
- Bradford MA, Fierer N, Reynolds JF (2008) Soil carbon stocks in experimental mesocosms are dependent on the rate of labile carbon, nitrogen and phosphorus inputs to soils. *Funct Ecol* 22:964–974. <https://doi.org/10.1111/j.1365-2435.2008.01404.x>
- Bradford MA, Strickland MS, DeVore JL, Maerz JC (2012) Root carbon flow from an invasive plant to belowground foodwebs. *Plant Soil* 359:233–244. <https://doi.org/10.1007/s11104-012-1210-y>
- Bradford MA, Keiser AD, Davies C et al (2013) Empirical evidence that soil carbon formation from plant inputs is positively related to microbial growth. *Biogeochemistry* 113:271–281. <https://doi.org/10.1007/s10533-012-9822-0>
- Breheeny P, Burchett W (2017) Visualization of regression models using visreg. *R J* 9:56–71
- Cambardella CA, Elliott ET (1992) Particulate soil organic matter changes across a grassland cultivation sequence. *Soil Sci Soc Am J* 56:777–783
- Cardinael R, Eglin T, Guenet B et al (2015) Is priming effect a significant process for long-term SOC dynamics? Analysis of a 52-years old experiment. *Biogeochemistry* 123:203–219. <https://doi.org/10.1007/s10533-014-0063-2>
- Cardon ZG, Hungate BA, Cambardella CA et al (2001) Contrasting effects of elevated CO₂ on old and new soil carbon pools. *Soil Biol Biochem* 33:365–373
- Chen R, Senbayram M, Blagodatsky S et al (2014) Soil C and N availability determine the priming effect: microbial N mining and stoichiometric decomposition theories. *Glob Chang Biol* 20:2356–2367. <https://doi.org/10.1111/gcb.12475>
- Craig ME, Fraterrigo JM (2017) Plant–microbial competition for nitrogen increases microbial activities and carbon loss in invaded soils. *Oecologia* 184:583–596. <https://doi.org/10.1007/s00442-017-3861-0>
- Craig ME, Pearson SM, Fraterrigo JM (2015) Grass invasion effects on forest soil carbon depend on landscape-level land use patterns. *Ecology* 96:2265–2279. <https://doi.org/10.1890/14-1770.1>
- Craig ME, Turner BL, Liang C et al (2018) Tree mycorrhizal type predicts within-site variability in the storage and distribution of soil organic matter. *Glob Chang Biol*. <https://doi.org/10.1111/gcb.14132>
- Craine JM, Morrow C, Fierer N (2007) Microbial nitrogen limitation increases decomposition. *Ecology* 88:2105–2113
- Dassonville N, Vanderhoeven S, Vanparys V et al (2008) Impacts of alien invasive plants on soil nutrients are correlated with initial site conditions in NW Europe. *Oecologia* 157:131–140. <https://doi.org/10.1007/s00442-008-1054-6>
- Di Lonardo DP, De Boer W, Gunnewiek PJAK et al (2017) Priming of soil organic matter: chemical structure of added compounds is more important than the energy content. *Soil Biol Biochem* 108:41–54. <https://doi.org/10.1016/j.soilbio.2017.01.017>
- Dijkstra FA, Cheng W (2007) Moisture modulates rhizosphere effects on C decomposition in two different soil types. *Soil Biol Biochem* 39:2264–2274. <https://doi.org/10.1016/j.soilbio.2007.03.026>
- Ehrenfeld JG, Kourtev P, Huang W (2001) Changes in soil functions following invasions of exoctic understory indigenous forests. *Ecol Appl* 11:1287–1300. <https://doi.org/10.2307/3060920>
- Fontaine S, Barot S (2005) Size and functional diversity of microbe populations control plant persistence and long-term soil carbon accumulation. *Ecol Lett* 8:1075–1087. <https://doi.org/10.1111/j.1461-0248.2005.00813.x>
- Fontaine S, Bardoux G, Abbadie L, Mariotti A (2004) Carbon input to soil may decrease soil carbon content. *Ecol Lett* 7:314–320. <https://doi.org/10.1111/j.1461-0248.2004.00579.x>
- Fontaine S, Henault C, Aamor A et al (2011) Fungi mediate long term sequestration of carbon and nitrogen in soil through their priming effect. *Soil Biol Biochem* 43:86–96. <https://doi.org/10.1016/j.soilbio.2010.09.017>
- Frey SD, Lee J, Melillo JM, Six J (2013) The temperature response of soil microbial efficiency and its feedback to climate. *Nat Clim Chang* 3:395–398. <https://doi.org/10.1038/nclimate1796>
- Garten CTJ, Wulfschlegler SD (2000) Soil carbon dynamics beneath switchgrass as indicated by stable isotope analysis. *J Environ Qual* 29:645–653
- Geisseler D, Horwath WR, Georg R, Ludwig B (2010) Pathways of nitrogen utilization by soil microorganisms—a review. *Soil Biol Biochem* 42:2058–2067. <https://doi.org/10.1016/j.soilbio.2010.08.021>
- Grandy AS, Neff JC (2008) Molecular C dynamics downstream: the biochemical decomposition sequence and its impact on soil organic matter structure and function. *Sci Total Environ* 404:297–307. <https://doi.org/10.1016/j.scitotenv.2007.11.013>
- Hughes RF, Uowolo A (2006) Impacts of *Falcataria moluccana* invasion on decomposition in Hawaiian lowland wet forests: the importance of stand-level controls. *Ecosystems* 9:977–991. <https://doi.org/10.1007/S10021-005-0083-9>
- Keiluweit M, Bougoure JJ, Nico PS et al (2015) Mineral protection of soil carbon counteracted by root exudates. *Nat Clim Chang* 5:588–595. <https://doi.org/10.1038/NCLIMATE2580>
- Kleber M, Eusterhues K, Keiluweit M et al (2015) Mineral-organic associations: formation, properties, and relevance in soil environments. *Adv Agron* 130:1–140. <https://doi.org/10.1016/bs.agron.2014.10.005>
- Kourtev PS, Ehrenfeld JG, Haggblom M (2003) Experimental analysis of the effect of exotic and native plant species on the structure and function of soil microbial communities. *Soil Biol Biochem* 35:895–905. [https://doi.org/10.1016/S0038-0717\(03\)00120-2](https://doi.org/10.1016/S0038-0717(03)00120-2)
- Koutika L, Vanderhoeven S, Chapuis-lardy L et al (2007) Assessment of changes in soil organic matter after invasion by exotic plant species. *Biol Fertil Soils* 44:331–341. <https://doi.org/10.1007/s00374-007-0210-1>
- Kramer TD, Warren RJ, Tang Y, Bradford MA (2012) Grass invasions across a regional gradient are associated with

- declines in belowground carbon pools. *Ecosystems* 15:1271–1282. <https://doi.org/10.1007/s10021-012-9583-6>
- Kuzyakov Y (2010) Priming effects: interactions between living and dead organic matter. *Soil Biol Biochem* 42:1363–1371
- Kuzyakov Y, Friedel JK, Stahr K (2000) Review of mechanisms and quantification of priming effects. *Soil Biol Biochem* 32:1485–1498
- Lajtha K, Townsend KL, Kramer MG et al (2014) Changes to particulate versus mineral-associated soil carbon after 50 years of litter manipulation in forest and prairie experimental ecosystems. *Biogeochemistry* 119:341–360. <https://doi.org/10.1007/s10533-014-9970-5>
- Lajtha K, Bowden RD, Crow S et al (2018) Science of the Total Environment The detrital input and removal treatment (DIRT) network: insights into soil carbon stabilization. *Sci Total Environ* 640–641:1112–1120. <https://doi.org/10.1016/j.scitotenv.2018.05.388>
- Lankau RA, Nuzzo V, Spyreas G, Davis AS (2009) Evolutionary limits ameliorate the negative impact of an invasive plant. *Proc Natl Acad Sci USA* 106:15362–15367. <https://doi.org/10.1073/pnas.0913493107>
- Liang C, Schimel JP, Jastrow JD (2017) The importance of anabolism in microbial control over soil carbon storage. *Nat Microbiol* 2:17105. <https://doi.org/10.1038/nmicrobiol.2017.105>
- Liao C, Peng R, Luo Y et al (2008) Altered ecosystem carbon and nitrogen cycles by plant invasion: a meta-analysis. *New Phytol* 177:706–714
- Lin G, McCormack ML, Ma C, Guo D (2016) Similar belowground carbon cycling dynamics but contrasting modes of nitrogen cycling between arbuscular mycorrhizal and ectomycorrhizal forests. *New Phytol* 213:1440–1451. <https://doi.org/10.1111/nph.14206>
- Luo Z, Wang E, Sun OJ (2016) A meta-analysis of the temporal dynamics of priming soil carbon decomposition by fresh carbon inputs across ecosystems. *Soil Biol Biochem* 101:96–103. <https://doi.org/10.1016/j.soilbio.2016.07.011>
- Manzoni S, Taylor P, Richter A et al (2012) Environmental and stoichiometric controls on microbial carbon-use efficiency in soils. *New Phytol* 196:79–91
- Meier IC, Finzi AC, Phillips RP (2017) Root exudates increase N availability by stimulating microbial turnover of fast-cycling N pools. *Soil Biol Biochem* 106:119–128. <https://doi.org/10.1016/j.soilbio.2016.12.004>
- Moorhead DL, Sinsabaugh RL (2006) A theoretical model of litter decay and microbial interaction. *Ecol Monogr* 76:151–174
- Niklaus PA, Falloon P (2006) Estimating soil carbon sequestration under elevated CO₂ by combining carbon isotope labelling with soil carbon cycle modelling. *Glob Chang Biol* 12:1909–1921. <https://doi.org/10.1111/j.1365-2486.2006.01215.x>
- Phillips RP, Finzi AC, Bernhardt ES (2011) Enhanced root exudation induces microbial feedbacks to N cycling in a pine forest under long-term CO₂ fumigation. *Ecol Lett* 14:187–194
- Phillips RP, Brzostek E, Midgley MG (2013) The mycorrhizal-associated nutrient economy: a new framework for predicting carbon-nutrient couplings in temperate forests. *New Phytol* 199:41–51. <https://doi.org/10.1111/nph.12221>
- Pinheiro J, Bates D, DebRoy S, Sarkar D (2014) R Core Team (2014) nlme: linear and nonlinear mixed effects models. R package version 3.1-117. <http://CRAN.R-project.org/package=nlme>
- Rasmussen C, Heckman K, Wieder WR et al (2018) Beyond clay: towards an improved set of variables for predicting soil organic matter content. *Biogeochemistry* 137:297–306. <https://doi.org/10.1007/s10533-018-0424-3>
- Rousk K, Michelsen A, Rousk J (2016) Microbial control of soil organic matter mineralization responses to labile carbon in subarctic climate change treatments. *Glob Chang Biol* 22:4150–4161
- Scharfy D, Eggenschwiler H, Olde Venterink H et al (2009) The invasive alien plant species *Solidago gigantea* alters ecosystem properties across habitats with differing fertility. *J Veg Sci* 20:1072–1085
- Schmidt MWI, Torn MS, Abiven S et al (2011) Persistence of soil organic matter as an ecosystem property. *Nature* 478:49–56. <https://doi.org/10.1038/nature10386>
- Schneider MPW, Scheel T, Mikutta R et al (2010) Sorptive stabilization of organic matter by amorphous Al hydroxide. *Geochim Cosmochim Acta* 74:1606–1619. <https://doi.org/10.1016/j.gca.2009.12.017>
- Sessitsch A, Weilharter A, Gerzabek MH et al (2001) Microbial population structures in soil particle size fractions of a long-term fertilizer field experiment. *Appl Environ Microbiol* 67:4215–4224. <https://doi.org/10.1128/AEM.67.9.4215>
- Sistla SA, Moore JC, Simpson RT et al (2013) Long-term warming restructures Arctic tundra without changing net soil carbon storage. *Nature* 497:615–618. <https://doi.org/10.1038/nature12129>
- Six J, Conant RT, Paul EA, Paustian K (2002) Stabilization mechanisms of soil organic matter: implications for C-saturation of soils. *Plant Soil* 241:155–176
- Soil Survey Staff (1999) Soil taxonomy: a basic system of soil classification for making and interpreting soil surveys, 2nd edn. United States Department of Agriculture–Natural Resources Conservation Service
- Sokol NW, Kuebbing SE, Bradford MA (2017) Impacts of an invasive plant are fundamentally altered by a co-occurring forest disturbance. *Ecology* 98:2133–2144. <https://doi.org/10.1002/ecy.1906>
- Sokol NW, Kuebbing SE, Karlsen-Ayala E, Bradford MA (2018) Evidence for the primacy of living root inputs, not root or shoot litter, in forming soil organic carbon. *New Phytol* 221:233–246. <https://doi.org/10.1111/nph.15361>
- Strayer DL (2012) Eight questions about invasions and ecosystem functioning. *Ecol Lett* 15:1199–1210
- Strickland MS, Devore JL, Maerz JC, Bradford MA (2010) Grass invasion of a hardwood forest is associated with declines in belowground carbon pools. *Glob Chang Biol* 16:1338–1350. <https://doi.org/10.1111/j.1365-2486.2009.02042.x>
- Strickland MS, Devore JL, Maerz JC, Bradford MA (2011) Loss of faster-cycling soil carbon pools following grass invasion across multiple forest sites. *Soil Biol Biochem* 43:452–454. <https://doi.org/10.1016/j.soilbio.2010.10.006>
- Sulman BN, Phillips RP, Oishi AC et al (2014) Microbe-driven turnover offsets mineral-mediated storage of soil carbon

- under elevated CO₂. *Nat Clim Chang* 4:1099–1102. <https://doi.org/10.1038/NCLIMATE2436>
- Sulman BN, Brzostek ER, Medici C et al (2017) Feedbacks between plant N demand and rhizosphere priming depend on type of mycorrhizal association. *Ecol Lett* 20:1043–1053. <https://doi.org/10.1111/ele.12802>
- Tiunov AV (2007) Stable isotopes of carbon and nitrogen in soil ecological studies. *Biol Bull* 34:395–407. <https://doi.org/10.1134/S1062359007040127>
- Ulmer M, Knuteson J, Patterson D (1994) Particle size analysis by hydrometer a routine method for determining clay fraction. *Soil Surv Horizons* 35:11–17
- Van Groenigen K, Six J, Hungate BA et al (2006) Element interactions limit soil carbon storage. *Proc Natl Acad Sci USA* 103:6571–6574
- Vilà M, Espinar JL, Hejda M et al (2011) Ecological impacts of invasive alien plants: a meta-analysis of their effects on species, communities and ecosystems. *Ecol Lett* 14:702–708. <https://doi.org/10.1111/j.1461-0248.2011.01628.x>
- Zhang W, Wang X, Wang S (2013) Addition of external organic carbon and native soil organic carbon decomposition: a meta-analysis. *PLoS ONE* 8:e54779. <https://doi.org/10.1371/journal.pone.0054779>
- Zhang X, Han X, Yu W et al (2017) Priming effects on labile and stable soil organic carbon decomposition: pulse dynamics over two years. *PLoS ONE* 12:e0184978

Publisher's Note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.