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Short Communication

Loss of faster-cycling soil carbon pools following grass invasion across multiple forest sites

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ABSTRACT

It is established that invasive plant species can alter soil carbon cycling, although data are rare for late successional ecosystems. We examined effects of a grass invader (*Microstegium vimineum*) on soil carbon across eight sites in southeastern U.S. forests to establish which factors are related to these effects, by coupling isotopic and soil carbon fractionation approaches. Invasion was associated with declines in mass of faster-cycling, particulate organic matter (POM) carbon pools. This led to a significant decline (11% on average) in native-derived carbon in the surface 10 cm of the soil profile. Formation of soil carbon from the invader-derived inputs partially mitigated these losses (total carbon loss 6% on average). Our data suggest that *Microstegium* invasion of forest understories may accelerate carbon cycling and could result in a net loss of soil carbon from eastern U.S. forests.

Invasive plants alter a range of ecosystem properties, including soil carbon (C) cycling (Mack and D'antonio, 2003; Liao et al., 2008). Whilst research into these effects has been directed towards early successional habitats, the impacts of invaders in late successional forests have been under-represented (Martin et al., 2009). For example, a meta-analysis by Liao et al. (2008) on invasive species and soil C included only two studies that assessed effects of grass invasion on forest soil C. This shortage of studies contributes to the uncertain pattern of grass invasion effects on soil C, with a variety of increases, decreases and no apparent change in C observed (Litton et al., 2008; Strickland et al., 2010a; Wolkovich et al., 2010).

Microstegium vimineum (Trin.) A. Camus (hereafter *Microstegium*) is an annual grass widely distributed throughout the eastern U.S., having invaded 25 states (Warren et al., 2010). *Microstegium* alters soil properties related to C cycling (Kourtev et al., 1998, 2002; Ehrenfield et al., 2001), with concomitant reductions in soil C stocks (Strickland et al., 2010a). The objective of this study is to determine whether this reduction in soil C is an isolated or general effect, and if general to elucidate potential environmental drivers.

We examined effects of *Microstegium* on soil C across eight bottomland forest sites (composed of *Quercus* sp., *Carya* sp., *Liquidambar styraciflua* (L.), and *Pinus taeda* (L.)). Sites were located <1 to ~80 km apart throughout the Georgia Piedmont physiographic region in the southeastern U.S. and were specifically located in Whitehall Forest (N33.89° W83.37°), Hard Labor Creek State Park (N33.67°, W83.60°), and Oconee National Forest (N33.20°, W83.49°). At each site we established two 7.6 × 7.6 m plots, one where *Microstegium* was present and the second ahead of the invasion. Importantly for an invasive-species impact study, *Microstegium* colonized our non-invaded plots (see Strickland et al., 2010a) and we weeded *Microstegium* from the controls. When present, *Microstegium* accounted for >90% cover, and other understory plants <5% (Strickland et al., 2010a). From each plot we randomly sampled and combined three 8 cm dia. × 10 cm deep soil cores, which were sieved (4 mm) and either air-dried for carbon analysis or stored fresh (5 °C). Using fresh soil we determined mineralizable C (a measure of microbially-available C), pH, and substrate induced respiration (SIR; a measure of active microbial biomass). We also measured soil moisture and temperature across

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the growing season, and the contribution of *Microstegium* to forest floor litter using its unique δ^{13}C value (see below).

Soil C responses to *Microstegium* were determined by coupling soil C fractionation and stable isotope approaches (described in Bradford et al., 2008; Strickland et al., 2010a). For the fractions, mineral-associated C turns over more slowly than particulate organic matter (POM) C (Schlesinger and Lichter, 2001; Grandy and Robertson, 2007). Using *Microstegium*'s unique δ^{13}C value (it is the sole C4-photosynthesizer at our sites), we resolved soil C formed from native C3 species and from *Microstegium* (Strickland et al., 2010a), permitting a detailed picture of soil C dynamics under invasion.

Microstegium invasion was associated with decreased native-derived C stocks. Specifically, significant mean decreases in native POM (29%) and total C (11%) were observed (Table 1, Fig. 1). Soil C derived from *Microstegium* did not compensate for these decreases in native-derived C, meaning the total mass (i.e. native-derived + *Microstegium* C) of POM and total C also declined, by 25% and 6%, respectively (Table 1, Fig. 1). The 6% decline in total C was not significant ($P = 0.12$), although this may be due to lack of statistical power (power = 0.15; 70 replicates needed for power of 0.80; see Carney et al., 2007; Strickland et al., 2010a). There was a 13% decline in microbially-available C, but this was not significant ($P = 0.10$) and again lacked power (power = 0.18; 50 replicates needed for power of 0.80 using the variability found in this study and $\alpha = 0.05$). Our results suggest Strickland et al.'s (2010a) observation, in a single forest, that *Microstegium* is associated with declines in soil C pools extends to other forests where *Microstegium* invades.

Marked variation was observed across sites in the response of soil C to invasion. For example, declines in POM C ranged from 4 to 39%, and changes in mineral-associated C ranged from 9% loss to 58% gain. To elucidate factors related to this variation, we used an information-theoretic approach to compare multiple linear models simultaneously (Burnham and Anderson, 1998; Strickland et al., 2010b). None of the top models (i.e. models within 2 AICc of the model with the lowest AICc [AICc is Akaike's information criterion corrected for small sample size; Burnham and Anderson, 1998]) had >40% probability of being the best model at describing change in soil carbon pools, although some were statistically significant (see below), suggesting high uncertainty in model selection and possibly meaning that unmeasured environmental factors may be better predictors (Burnham and Anderson, 1998). However, of the top models we did find that the additive combination of change in SIR biomass and soil temperature were positively related to change in total C ($F_{2,5} = 6.10, P < 0.05, r^2 = 0.82$), mineral C ($F_{2,5} = 7.73, P < 0.05, r^2 = 0.76$), and native-mineral C ($F_{2,5} = 5.88, P < 0.05, r^2 = 0.70$). This suggests that a greater increase in SIR biomass, an estimate of active microbial biomass, and factors like temperature that promote activity, then the more positive an impact *Microstegium* has on longer-term C pools. Supporting this inference there was a marginally significant ($P < 0.10$), negative relationship between relative change in POM and mineral-associated C with invasion ($F_{1,6} = 4.27, P = 0.08, r^2 = 0.41$). That is, the greater the relative percent decrease in POM C the more positive the change in mineral-associated C. These observations might be explained by faster C-cycling associated with *Microstegium* – i.e. if POM C decomposes more rapidly (Bradford et al., 2008; Strickland et al., 2010a) it will increase formation of microbial-derived products, which themselves comprise the bulk of the mineral-associated C pool (Grandy and Robertson, 2007; Bradford et al., 2008; Grandy and Neff, 2008). It is uncertain in the long-term whether this will lead to greater C storage in invaded forests, and certainly our data show that gains in mineral-associated C do not offset losses of total soil C.

Table 1
Results from analysis of variance testing for differences in soil C pools in the presence/absence of *Microstegium vimineum* ($n = 8$). The top three parameters (POM C, Mineral C, and Total C) show the analysis results of the total pools (*Microstegium* + native-derived soil C). The bottom three parameters (Native POM C, Native-mineral C, and Native total C) show the analysis results for the native-derived C only. All plots were blocked by site. Significant *P*-values are in bold.

Parameter	Source of variance	d.f.	MS	*F*-value	*P*-value
POM C	*Microstegium*	1	3944	19.6	**<0.01**
	Site	7	2537	12.6	**<0.01**
	Residuals	7	200.8		
Mineral C	*Microstegium*	1	251.7	0.28	0.62
	Site	7	2661	2.93	0.09
	Residuals	7	907.3		
Total C	*Microstegium*	1	2203	3.24	0.12
	Site	7	3842	5.66	**<0.05**
	Residuals	7	679.3		
Native POMC	*Microstegium*	1	5192	22.8	**<0.01**
	Site	7	2388	10.5	**<0.01**
	Residuals	7	227.8		
Native-mineral C	*Microstegium*	1	13.4	0.01	0.91
	Site	7	2561	2.37	0.14
	Residuals	7	1081		
Native total C	*Microstegium*	1	5734	6.56	**<0.05**
	Site	7	3671	4.20	**<0.05**
	Residuals	7	874.5		

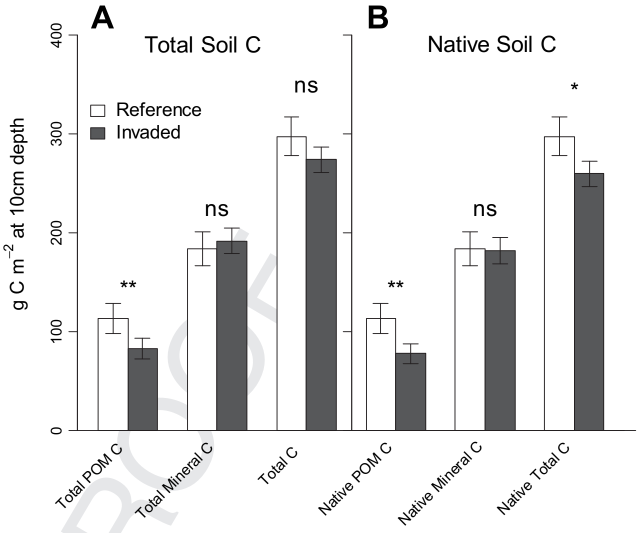

Fig. 1. Amount of C (g m^{-2}) to 10 cm depth found in reference (white bars) or *Microstegium vimineum* invaded sites (black bars) across eight southeastern U.S. forest sites. A) Total (*Microstegium* + native-derived) amount of C found in particulate organic matter (POM) C, mineral C, and total (POM + mineral) C. B) Native-derived C found in the same three pools. Notably, total- and native-derived C pools in the presence of *Microstegium* are very similar. This is likely because these pools are dominated by native tree inputs and turn over slowly. Shown are means ± 1 S.E. ($n = 8$). Symbols above the bars denote the level of statistical significance between C pools in the presence/absence of *Microstegium* (** = $P < 0.01$; * = $P < 0.05$; ns = not significant).

We selected advancing invasions to ensure our non-invaded plots did not differ fundamentally from adjacent invaded plots. In four of our sites the invasions are <15 y old, and for the other sites the advancing fronts suggest the invasions are also young. Yet we observed marked variation across sites in the relative effects of *Microstegium* on POM and mineral-associated C pools. We found that for total, mineral, and native-mineral C that this variation may be related to changes in soil temperature and SIR biomass. Yet reliable predictions of *Microstegium* effects on forest soil C require investigations into other habitat characteristics (Grandy et al., 2009), and

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such investigations should be conducted across its entire geographic range. Given the difficulties in identifying early stages of understory invasions (Martin et al., 2009), this may require experimental invasions. What is certain from our work is that *Microstegium* is consistently associated with declines in faster-cycling C pools across eight, distinct forest sites, translating to net declines in the total, native-derived soil C. Notably, *Microstegium* appeared to be associated with more rapid C cycling, shifting the proportion of C found in pools that cycle faster (POM C) to those cycling more slowly (mineral-associated C). This means that detailed analyses of soil C fractions across time are needed to predict long-term impacts of *Microstegium* on ecosystem C storage.

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