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ORIGINAL PAPER

Woody invaders do not alter rhizosphere microbial activity in a temperate deciduous forest

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Abstract Non-native, invasive plants are often strong competitors that have large effects on ecosystem functioning. While limited experimental evidence suggests invasive species can change soil carbon (C) and nitrogen (N) processes, little is known about how they alter biogeochemistry in the field. We examined soils collected from beneath native and non-native, invasive woody plants in a temperate forest in central New York, USA, to test whether invaders change rhizospheric C and N processes compared to that of common native species. We hypothesized that a combination of high-quality leaf and root litter and greater rates of rhizospheric deposition of invaders would enhance the quality of soil organic matter, leading to greater measured rates of C and N mineralization. We removed soil cores from directly below the canopy of 105 individuals of 8 native and 3 invasive species of shrubs and small trees, each paired with an adjacent sample to account for site effects on soil properties. We measured inorganic N pools, percent soil C and N, and potential C and N mineralization rates with 10-day laboratory incubations. Contrary to our hypothesis, we found that invaders did not significantly alter any of the measured soil traits. Instead, root biomass per sample, which did not vary by nativity, was a better predictor of potential mineralized C and N. This suggests plant tissue quantity controls available C and N pools, and plants that produce more roots are able to better stimulate microbial activity. Thus, understory invaders do not appear to alter soil biogeochemistry in this forest unless they drive large changes in forest root mass.

Keywords Invasive plants · N mineralization · Soil C respiration · Soil incubations · Biogeochemistry

Introduction

Non-native, invasive plant species often reduce native plant diversity and abundance (Grotkopp and Rejmanek 2007; Vilà et al. 2011), but the long-term ecosystem impacts of non-native plant establishment remain poorly understood, particularly for ecosystems that remain dominated by native species. Belowground processes in forested ecosystems are a case in point. Although there are many studies of the effects of plant invaders on soil processes in communities where they dominate (e.g., Liao et al. 2008; Ehrenfeld 2010; Jo et al. 2017), it is less clear whether invaders

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significantly alter biogeochemical processes like carbon (C) cycling in communities where invaders are common but account for less biomass than native species. Most temperate forests, for example, remain dominated by native trees (but see Richardson and Rejmánek 2011), yet often have understories heavily invaded by non-native plant populations (Martin et al. 2009). If non-native understory species in such habitats alter soil processes despite their lower abundance, then their influence on soil C and nutrient dynamics may facilitate further invasion and ecosystem change (Tamura and Tharayil 2014; Kuebbing et al. 2015; Bennett and Klironomos 2019), including the facilitation of non-native trees (Essl et al. 2011).

Non-native species are typically resource-acquisitive plants that grow faster and are more productive than natives (Grotkopp and Rejmánek 2007; Leishman et al. 2007; van Kleunen et al. 2010; Vilà et al. 2011). Aboveground, they have leaf traits linked to high productivity and photosynthetic capacity, including high SLA and leaf N, and low leaf C:N (Leishman et al. 2007; van Kleunen et al. 2010; Heberling and Fridley 2016; Jo et al. 2017). Deciduous shrub invaders often exhibit later seasonal leaf senescence (Fridley 2012) and higher photosynthetic energy-use efficiency than native shrubs (Heberling and Fridley 2013), allowing them to maintain high levels of productivity over a longer growing season. Despite their high resource demand, invaders can maintain their competitive advantage even in ecosystems with low resource supply (Funk and Vitousek 2007; Funk 2013), including the light- and nitrogen (N)-limited understories of deciduous temperate forests (Dreiss and Violin 2013; Heberling and Fridley 2016). The greater rates of productivity aboveground need to be supported by greater rates of nutrient uptake by invaders compared to native species. However, comparatively little is known about differences in belowground resource uptake strategies between native and invasive species (Drenovsky et al. 2008; Jo et al. 2015). This is particularly true in northeastern forests of the USA where the canopy is dominated by native species.

Invasive plants can potentially influence the availability of soil nutrients by means of two pathways. The first involves changing the rate of litter decomposition by altering the quality of litter. Globally, invasive plants often increase litter quality by shedding leaves of more favorable chemistry for soil microbial activity, including lower CN ratios and lignin content (Liao et al. 2008; Castro-Díez et al. 2009; Zhang et al. 2019). In addition, invaders may facilitate soil nutrient availability by changing the rate of rhizodeposition. Rhizodeposition includes root exudation and turnover that provides new and labile soil organic material for soil microbes in the rhizosphere (Dijkstra and Cheng 2007; Tan 2009; Bardgett and Wardle 2010; Cheng et al. 2014). Rhizodeposition accelerates microbial metabolism and population growth, exoenzyme production (Cheng et al. 2014; Kuzyakov 2002), and the availability of N in the rhizosphere (Kuzyakov 2002; Hamilton et al. 2008; Bardgett and Wardle 2010). The rate of rhizodeposition is closely associated with plant production and leaf level photosynthetic rates (Henneron et al. 2019). Like many invaders, invasive shrubs of deciduous forests show higher photosynthetic and growth rates compared to native species (Liao et al. 2008; Heberling and Fridley 2013), suggesting rhizodeposition rates may also be higher for invaders. Thus invasive species may facilitate rhizospheric soil C and N processes by increasing the quality of decomposing litter and/or supporting greater rhizodeposition.

Our objective was to determine how woody invasive species in deciduous forests of Eastern North America (ENA) influence soil C and N mineralization. We were particularly interested in how invading species influence C and N mineralization rates in their rhizospheres, which, we reasoned, would be sensitive to invasive plant effects by means of both the litter and rhizodeposition pathways. We sampled rhizospheric soil from below and around non-native, invasive plants (hereafter referred to as "invaders") and native, non-invasive plants in a deciduous forest in central New York, USA. We measured soil total C and N pools, and used short-term laboratory soil incubations to determine how invasive species alter potential microbial respiration and N mineralization rates, which reflect the quantity (per soil mass) and quality of soil organic matter. We hypothesized that invaders would increase potential C and N mineralization rates compared to native species.

Methods

Study design and species selection

Our study was conducted in Pompey, New York, USA (42°55′ N, 76°02′ W) in a closed-canopy, secondary deciduous forest. Canopy composition across sample locations included native trees dominated by *Acer saccharum*, followed by secondary dominants *Fraxinus americana*, *Prunus serotina*, and *Ostrya virginiana*, with occasional *Carya cordiformis* and *Tilia americana*. Forest shrub and herbaceous layers in our sampling locations included both native and non-native species, with shrub cover from 30 to 60% and herbaceous cover typically < 50% after the senescence of spring ephemeral herbs. In the shrub layer, three non-native woody species were widespread and locally abundant, including the multi-stemmed shrub *Lonicera* x *bella*, the thicket-forming briar *Rosa multiflora*, and the single-stemmed shrub or small tree *Rhamnus cathartica*. Common native understory woody species in these stands included low-stature, multi-stemmed shrubs (e.g., *Ribes cynosbati*), single-stemmed shrubs or small trees (e.g., *Prunus virginiana*), and saplings of the above overstory species. We sampled roots of each of these 11 woody species, 8 native and 3 non-native (Table 1). Although there are several herbaceous invasive species in this forest stand, particularly *Alliaria petiolata*, we avoided sampling from areas of high herbaceous biomass, whether native or non-native.

We took soil samples from early-June 2017, after full closure of the canopy, to the end of August 2017 to determine the influence of plant identity on soil when plants were most physiologically active. We used spatial blocking to account for site effects with a total of 10 blocks, each sampled at unique times: blocks 1–6 were sampled from June 12 to 30, blocks 7–8 on July 19 and 25, block 9 on August 2, and block 10 August 12–25. We chose blocks as adjacent but nonoverlapping, contiguous areas of forest containing the target invasive species, and included the eight nearest neighboring individuals of target native species that met size criteria (see below). Block size was 1000–2000 m^2, and all blocks were dominated by the same canopy species. One individual of each species was sampled within each block, with the exception of *Acer saccharum* (n = 9), *Tilia americana* (n = 9), and *Carya cordiformis* (n = 7), for a total of 30 invader and 65 native plants sampled. We sampled plants 0.5–2 m tall to limit the effect of plant size on soil measurements, and at least 0.5 m from their nearest neighbor to isolate individual plant effects. We measured plant height, crown diameter, and stem diameter at 5 cm height for each individual, including multiple stems when present.

We extracted five soil cores (3.5 cm diameter, 5 cm depth) from directly beneath the base of each individual, and five cores 1–2 m outside each focal plant canopy. This paired sampling design for each individual allowed us to account for the effect of species identity on soil processes independent of site properties. Ground cover often included leaf litter on top of mineral soil, which was excluded from soil cores. We sampled to 5 cm depth because roots from the target plants were primarily in the top 5 cm of soil. We confirmed that roots in the cores were from the targeted plant by verifying the morphology of roots

Table 1 Study species

Species	Nativity	Species code	Growth form
Acer saccharum	Native	ACSA	Tree
Carya cordiformis	Native	CACO	Tree
Fraxinus americana	Native	FRAM	Tree
Lonicera x *bella*	Non-native	LOBE	Shrub
Ostrya virginiana	Native	OSVI	Tree/small tree
Prunus serotina	Native	PRSE	Tree
Prunus virginiana	Native	PRVI	Shrub/small tree
Rhamnus cathartica	Non-native	RHCA	Shrub/small tree
Ribes cynosbati	Native	RICY	Shrub
Rosa multiflora	Non-native	ROMU	Shrub/liana
Tilia americana	Native	TIAM	Tree

with roots traced back to the target plant species or that roots from the core originated from the target plant. The five cores were pooled into a single combined sample so each individual plant was represented by one soil sample from its base and one outside its rooting zone. The soil samples were immediately stored in an ice-filled cooler in the field and transferred to 4 °C storage at the end of the day.

Soil nutrient analysis

Within 2 days after collection, soil was sieved to remove rocks and other debris and forceps were used to remove roots. Herbaceous roots were discarded and woody roots were rinsed with DI water, dried at 60 °C for 48 h, and weighed. The soil pools of ammonium and nitrate were determined by extracting 10 g of soil with 50 mL 1 M KCl following the methods of Robertson et al. (1999). Each sample was shaken for 10 min, allowed to sit overnight, and then filtered through Whatman glass microfiber filter paper into scintillation vials. The vials were frozen at − 20 °C until ammonium and nitrate levels were assessed with a Seal Autoanalyzer3 colorimetric analyzer (Mequon, Wisconsin, United States). The remaining soil was dried at 60 °C for 48 h and stored until further analysis.

To measure potential rates of microbial respiration and net N mineralization, we followed the methods of Stanford et al. (1974). Two 20 g subsamples were collected from each pooled sample of dry soil and each was added to a 1 pint wide-mouth mason jar: one for the initial inorganic N measurements and one for the final inorganic N and C measurements after a 10 day incubation period. The samples were brought up to 50% water holding capacity and the jars were sealed and placed into an incubator at 25 °C. After a 24-hour pre-incubation period to allow the microbe populations to grow and stabilize, which was determined in a preliminary trial, 100 mL of 1 M KCl were added to the initial samples. These samples were shaken for 30 min at 200 rpm and then allowed to settle overnight. The KCl supernatant was filtered through Whatman glass microfiber filter paper into 20 mL scintillation vials, which were stored at − 20 °C until further analysis. While the initial samples were being processed, the second set of jars were opened and vented for five minutes. A 20 mL scintillation vial with 2 mL of 2 N NaOH was placed in each jar to trap the respired CO_2 (Robertson et al. 1999). The jars were resealed and placed back into the incubator for 10 days.

At the end of the incubation period the NaOH traps were removed and single end-point titrations were used to measure mineralized CO_2 (Robertson et al. 1999). Carbon absorbed in the NaOH was precipitated out with 2 mL of 1 N $BaCl_2$ and thymolphthalein was added as a pH indicator. NaOH samples were titrated with 0.5 N HCl until the solution turned clear. Respired CO_2 was then calculated as ([B − T] × 0.5 × 6 mg C), where B was a blank with fresh NaOH, T was the sample, and 0.5 was the molarity of the HCl in mol/L.

Ammonium and nitrate were extracted from the incubated soils with 100 mL of 1 M KCl. The samples were shaken for 30 min at 200 rpm and the KCl supernatant was filtered out into scintillation vials. Vials were kept frozen at − 20 °C until inorganic N analysis with a Seal Autoanalyzer3 colorimetric analyzer. The daily total mineralized inorganic N was calculated as $N_{mineralized} = [(nitrate_{final} + ammonium_{final}) - (nitrate_{initial} + ammonium_{initial})]/T_{days}$. This extractable N was reported on a dry soil mass basis (Robertson et al. 1999).

Total N and C were determined on finely ground dry soils using an NC-2100 Elemental Autoanalyzer (Milan, Italy).

Data analysis

Potential mineralizable N and C were calculated per g soil N and soil C, respectively, to determine the mineralizable N and C relative to soil N and C pools. Differences in soil measurements (i.e. soil C, soil N, potential mineralizable N per soil mass, potential mineralizable N per soil N, and potential mineralizable C per soil mass, potential mineralizable C per soil C) between native and invasive plants were assessed using linear mixed effects models (LME) with the "nlme" package (Pinheiro et al. 2019) in R 3.5.1 (R Core Team 2018). Response variables were log transformed. The above dependent variables (Y) were fitted in mixed models of the form:

$$Y \sim \text{nativity} * (\text{sample location}) + \text{plant height} + N\left(0, \sigma^2_{\text{Block}}\right) + N\left(0, \sigma^2_{\text{Species}}\right)$$

where "nativity" represents a native or invasive individual and "sample location" represents samples taken either below or around each individual. Differences between species in the above dependent variables (Y) were also assessed using LME with the model:

$$Y \sim \text{species} * (\text{sample location}) + \text{plant height} + N\left(0, \sigma^2_{\text{Block}}\right)$$

We also used principal component analysis (PCA) to examine how invasive and native plants differed based on the all the soil variables measured in the study. The relationships of potential mineralizable C and N (at both per soil mass and per element bases) versus root biomass were assessed using ordinary least squares regression. For the ordinary least squares regressions comparing root biomass to potential mineralizable N, the samples were first assessed together, and then split into two groups based on sampling date (pre-June 14th and post-June 14th) due to a dramatic seasonal difference in ammonium (Fig. S1).

Results

We found that the soil inorganic N pool was unaffected by nativity (Table S1, t = − 0.28, df = 41, $P = 0.78$). There also was no difference in extractable organic N between cores taken below versus beyond the rooting zone of individuals (t = 0.56, df = 47, $P = 0.58$), and no significant interaction of nativity and core location (t = 0.03, df = 47, $P = 0.98$) (Fig. 1). Patterns for the inorganic N pool were similar; although the log ratio of inorganic N below versus around individuals was highly variable, we found no systematic differences in this ratio across native and non-native species (Fig. S2).

We did not detect differences between natives and non-native species in rhizospheric soil %C and %N (Table S1; t = − 0.58, df = 93, $P = 0.57$; t = − 0.63, df = 93, $P = 0.53$, resp.), and there was no interaction between core sampling location and nativity on these

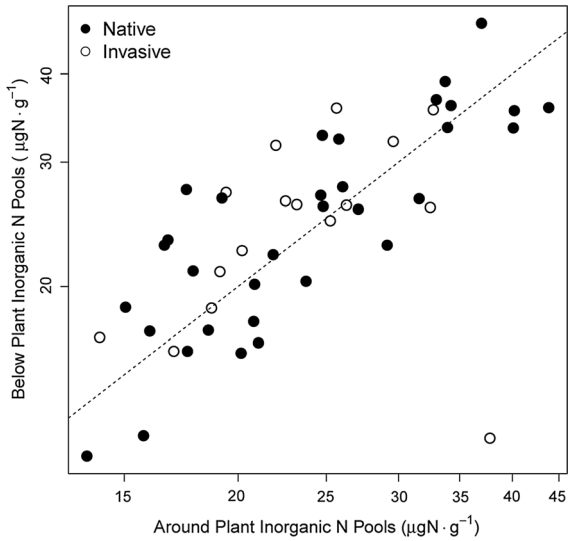

Fig. 1 Inorganic N pools in soil cores taken below versus around each individual, with 1:1 line

variables (Fig. 2; t = − 0.02, df = 93, $P = 0.98$; t = − 0.64, df = 93, $P = 0.53$, resp.). When C and N were analyzed together as soil C:N ratio, we found no nativity effect on overall soil C:N (t = − 0.26, df = 93, $P = 0.80$), although there was a marginal increase in soil C:N for non-native cores when considering core sampling location of below versus around individuals (t = 2.14, df = 103, $P = 0.06$; results not shown).

Nativity had no effect on potential respired C per mass soil (mg C g soil^{-1} day^{-1}) (Fig. 2c, Table S1; t = − 0.95 df = 93, $P = 0.35$) and did not interact with core sampling location (t = − 1.15, df = 103, $P = 0.25$). Nativity also had no effect on potential mineralizable C per soil C (mg C g soil C^{-1} day^{-1}) (Fig. 2d, Table S1; t = − 0.30, df = 93, $P = 0.77$). Neither potential mineralized N per mass soil (μg N g soil^{-1} day^{-1}) (Fig. 2e) nor potential mineralized N per soil N (μg N g soil N^{-1} day^{-1}) (Fig. 2f) differed between invaders and natives (t = − 0.70, df = 93, $P = 0.49$; t = − 0.16, df = 93, $P = 0.88$, resp.). Potential mineralizable N differed by season (Fig. S1); samples collected in the second week of June generally had more ammonium (1.28 ± 0.36 μg N g soil^{-1} day^{-1}) than blocks sampled in the third week of June until the end of August (0.17 ± 0.16 μg N g soil^{-1} day^{-1}; *t* test t = − 19.11, df = 45, $P < 0.0001$).

Soil %C, %N, potential respired C per g soil, potential respired C per g soil C, potential

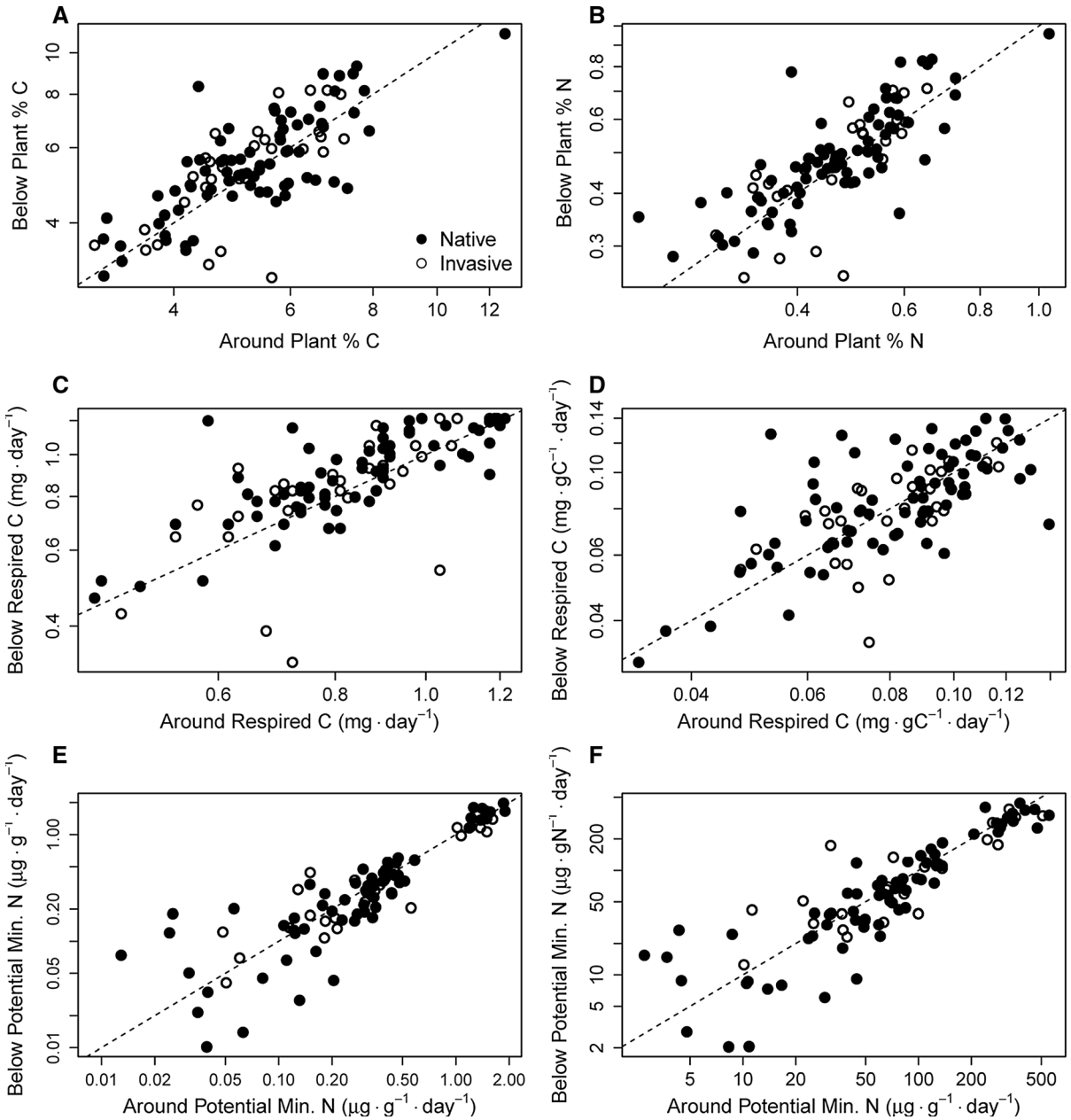

Fig. 2 Measurements from soil cores taken at the base and around individuals, including **a** %C, **b** %N, **c** potential respired C, **d** potential respired C per g soil C, **e** potential mineralized N, and **f** potential mineralized N per g soil N, along with 1:1 lines

mineralizable N per g soil, and potential mineralizable N per g N were also analyzed on a per root biomass basis (Table S2). Results were similar to those above: LMEs revealed no differences in natives versus invaders for any variable. Finally, there were no significant species differences for soil nutrient content and mineralization rates (Fig. S3), and no species differences for those variables per root biomass.

Considering all measured variables together, we found no systematic differences in soil attributes between invasive and native species (Fig. 3). PC 1 was

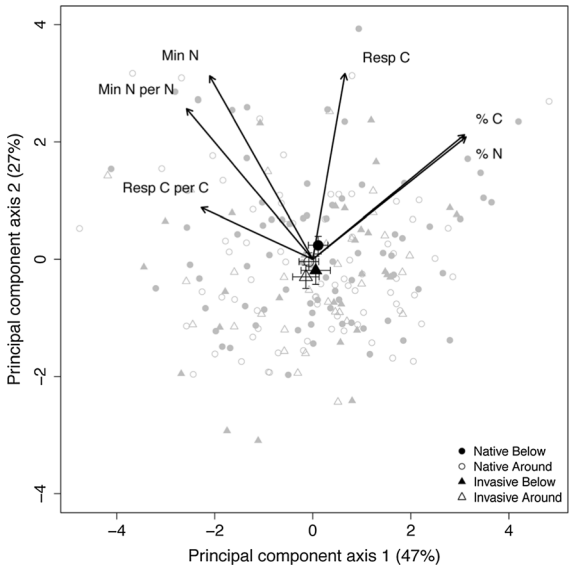

Fig. 3 Principal component analysis of six soil measurements. Black arrows are measurement vectors. Large circles and triangles represent centroids ± SE and small triangles and circles represent individual soil samples. Axes 1 and 2 represent 47% and 27% of the variation

most strongly related to %C and %N, and PC 2 was most closely related to respired C.

The average root biomass was 0.439 ± 0.292 g and ranged from 0.029 to 1.658 g. Root biomass did not differ between natives and invaders ($t = -0.55$, $df = 49$, $P = 0.59$). Potential respired C per g soil was positively related to root biomass (Fig. 4; adjusted $R^2 = 0.17$, $P < 0.001$), as was potential respired C per g soil C (adjusted $R^2 = 0.03$, $P < 0.01$). Potential mineralizable N per g soil and potential mineralizable N per g soil N were unrelated to root biomass. However, both relationships were significant when potential mineralizable N per g soil was modelled separately for samples taken before June 14th (adjusted $R^2 = 0.08$, $P < 0.05$) and samples taken after June 14th (adjusted $R^2 = 0.09$, $P < 0.001$). Root biomass was also positively related to %C (adjusted $R^2 = 0.03$, $P < 0.01$) and %N (adjusted $R^2 = 0.09$, $P < 0.01$).

Discussion

We targeted rhizospheric soil in this study because it would have been influenced by a combination of species-level effects on leaf and root litter quality, affecting soil C and N processes below plants, and root exudation, affecting fine-scale soil C and N transformations at the root-soil interface. Thus, measuring rhizospheric soil optimized detecting effects of invasive plants on soil processes and could provide a bellwether for ecosystem-level soil C and N impacts of invaders in this and similar forests experiencing early stages of plant invasions. However, in a deciduous temperate forest invaded by many species of shrubs

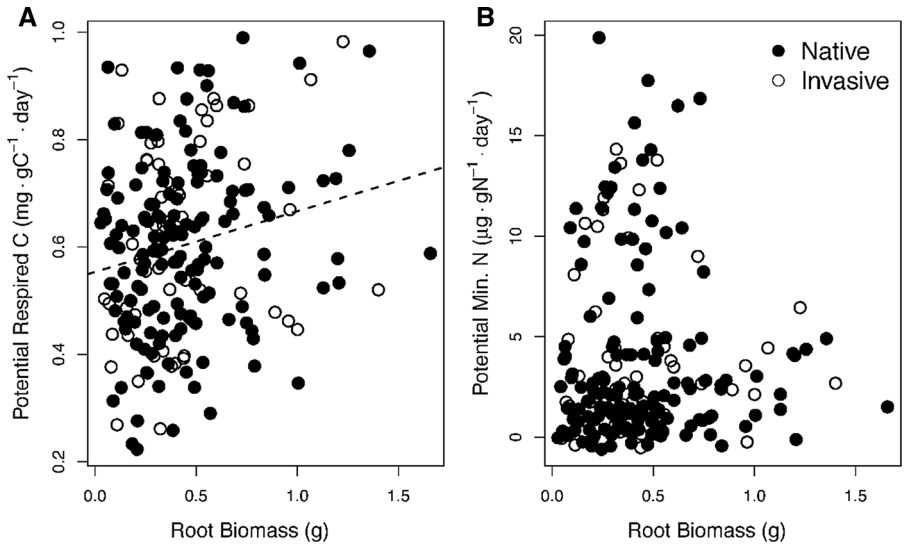

Fig. 4 Root biomass relationships with **a** potential respired C and **b** potential mineralized N per g soil. Regression line in panel A is from OLS regression

and small trees, we failed to find evidence that rooting zone soil processes, including potential rates of C and N mineralization, differed between native and invasive plant species. We also found native and invasive species to have similar amounts of inorganic N, %C, and %N in their rhizosphere, and have similar amounts of root mass in the top 5 cm of soil. These results do not support our hypothesis of greater microbial respiration and nutrient mineralization rates in the rooting zone of invasive species, nor are they consistent with studies showing increased nutrient availability in soils of invader populations (Ashton et al. 2005; Liao 2008; Schuster and Dukes 2014; Jo et al. 2017; Zhang et al. 2019). We propose two reasons for this lack of invader effect. First, some of the organic matter in the rhizosphere has its origin in leaf litter rather than roots or soil organisms, and unlike greenhouse or field studies where invaders form near single-species stands, ecosystems in our study were dominated by native canopy individuals that were similar across samples (mostly the native *Acer saccharum*). Thus, much of the organic matter substrate in our samples was derived from leaf litter of one native species, which likely diluted any potential invader effects on rhizosphere processes (Dreiss and Volin 2013; De Long et al. 2019). Second, even if leaf and root litter inputs were dominated by that of the invasive species in our study, litter traits may not have varied enough across our focal native and invasive woody species to drive differential decomposition processes (Freschet et al. 2012; Castro-Díez et al. 2014). For example, Jo et al. (2016) found no differences in leaf and root decomposability between native and invasive woody species using a field litter bag approach in this same forest stand.

Root biomass was a better predictor of rates of respired C and mineralized N than either nativity or species identity, and when soil C and N were considered on a root mass-specific basis there were no significant differences between natives and invaders. Because quantifying differences in root density or production across natives and invaders was not a focus of our study that targeted instead rhizosphere processes, our sampling density was likely insufficient to detect such differences in root production patterns, although invasive woody species have been found to produce more fine roots than natives in a common garden study (Jo et al. 2015). Thus, in situations where root productivity is higher for invasive understory species, it is likely that alteration of soil processes would follow, similar to the conclusion of Jo et al. (2016) that invader impacts on N availability are driven by greater litter inputs (i.e., quantity) rather than quality. Our root biomass measurements included the mass of both fine and coarse roots, and we did not examine root architecture, chemistry, and depth, which can also affect soil processes (Ehrenfeld 2003; Liao et al. 2008). However, in general, the strong positive relationships of soil C and N content (%) and mineralization with root biomass lend credence to the dominating effect that root processes, including root turnover and exudation, have on soil C and N dynamics (Isaac and Nair 2005; Krishna and Mohan 2017).

It is unclear why potential N mineralization was greater in soils collected before compared to after June 14th. One possible explanation is that rapid plant N uptake that usually occurs early in the summer (Bardgett et al. 2005) resulted in less available N to mineralize later. A second possibility is that high early growing season rates of rhizodeposition may have contributed to higher potential N mineralization in samples collected before mid-June. Studies have found that most of the C exuded from roots comes from C assimilated within 24 h (Johnson et al. 2002) and that rates of exudation are tied to recent rates of assimilation (Zagal 1994; Craine et al. 1999; Kuzyakov and Cheng 2001). Because the percentage of assimilated C allocated to exudation can be substantial (0.5–20%; Farrar et al. 2003) and the rates of assimilation by understory species at our study site are greatest early in the growing season before canopy closure (Martinez and Fridley 2018), which normally occurs by June 15th, the exudation of labile material and priming of N mineralization may have been greatest early in the growing season.

We note several caveats for interpreting results from this study. First, although soil inorganic N pools and potential C and N mineralization rates of rhizospheric soil would have responded to impacts of invasive species on plant residues (litter and exudation), other soil properties such as in situ N availability or soil microbial biomass may have been more sensitive measures of species effects on soil C and N processes. Second, we chose to study a forest that still had a high understory abundance of many native species. It could well be that forests with greater abundance of invasive species have reached a tipping

point where litter and root inputs of invaders dominate soil processes. Third, we chose invader/native contrasts of strong functional similarity; other invaders of more unique functional attributes (e.g., *Alliaria petiolata,* Wolfe et al. 2008; *Microstegium vimineum*, DeMeester and Richter 2010) may have generally stronger alterations of forest ecosystem functioning.

Conclusion

Our study of laboratory incubations of rhizospheric soils associated with native and invasive woody species suggests that invaders do not, on a per-root mass basis, alter forest soil C and N mineralization rates or total soil C and N content compared to native woody species. Although there is evidence that invaders increase C and N cycling in monoculture and greenhouse experimental settings, our study suggests understory woody plant invasions are unlikely to have large impacts on nutrient transformations and rhizosphere microbial communities unless they significantly increase forest root mass, alter rates of litter input, or impact the regeneration of canopy dominants. If woody invaders replace native understory communities without altering understory biomass or impacting canopy trees, their effects on rhizosphere processes may be minimal. However, rhizosphere impacts of other understory invaders in deciduous forests, including forbs and grasses, may be qualitatively different than what we show for woody species. Furthermore, levels of understory dominance by invasive species in our study area remain below the monocultural levels seen in other systems, where effects on canopy trees may accelerate further ecosystem change.

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