December 2019

The effect of invasive plants on soil microbial activity in a NY temperate forest

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Recommended Citation

Hull, Victoria Dawn, "The effect of invasive plants on soil microbial activity in a NY temperate forest" (2019). *Theses - ALL*. 370.
https://surface.syr.edu/thesis/370

ABSTRACT

Invasive woody plants are often strong competitors that can have large effects on ecosystem function. While there is evidence that Northeastern invasive species can increase nitrogen cycling in monocultures, little is known about how invasive plants alter biogeochemistry in the field. I hypothesized that the high-quality leaf and root litter of invaders would enhance the quality of soil organic matter, leading to greater belowground microbial activity and faster rates of nitrogen mineralization. In the summer of 2017, I conducted a field survey of invasive and native understory shrubs to see how invasive woody plants influence microbial activity in central New York temperate forests. I selected 105 shrubs and trees and took soil cores from directly below each plant and around each plant canopy; the latter used to account for site effects on soil properties. Inorganic N pools were measured by extracting fresh soil with KCl, and potential C and N mineralization rates were determined with 10-day laboratory incubations. Soil percent C and N, pH, and root biomass were also measured for each soil sample. I then used linear mixed models to determine the effect of nativity on each of these soil traits, with nativity, soil core location (below vs. around) and plant height as fixed effects. I used least squares regression models to determine their effects on potential rates of mineralized N and respired C. Contrary to my hypothesis, I found that invaders did not significantly alter any of the measured soil traits. Instead, root biomass and pH were better predictors of potential respired C and mineralized N. This suggests that plant quantity, not quality, controls available C and N pools, and plants that create more roots are able to better stimulate microbial activity regardless of nativity. Thus, understory invaders do not appear to alter soil biogeochemistry in the context of a native dominated overstory.

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B.A. Hamilton College, 2014

Thesis
Submitted in partial fulfillment of the requirements for the degree of Master of Science in Biology

Syracuse University
December 2019

ACKNOWLEDGEMENTS

I would first like to thank my thesis advisors, Dr. Douglas Frank and Dr. Jason Fridley, for their help and guidance with this project. I have learned so much over the past three years and I am incredibly grateful for the opportunity to join the Frank/Fridley labs. Without their endless advice and support, I never would have discovered my love for biostatistics, R, and teaching. I would also like to thank my committee member, Dr. Ruth Yanai, for her input and assistance with this project, and Dr. Susan Parks for agreeing to be part of my defense committee.

I owe a great deal to all the other members of the Frank/Fridley/Ritchie/Becklin labs, including Alexander Ebert, Neha Mohanbabu, Jacob Penner, Kelsey Martinez, Elise Hinman, and Luka Negoita. Their friendship was an invaluable part of this process and I know they will all be successful in whatever they choose to do. I always looked forward to our combined lab meetings, and I appreciated the many insights and teachings of Dr. Mark Ritchie and Dr. Katie Becklin during these meetings.

Finally, I owe a huge thanks to Justin Cestra for the many hours spent in lab sieving soil, preparing soil incubations, and helping me troubleshoot the CN machine, and to Barbara Hull for acting as my behind-the-scenes editor for all these years.

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CHAPTER 1

BACKGROUND

Invasive Species: From Species Management to Understanding Ecosystem Impacts

As human movement and global interactions have increased over the past few centuries, so too has the cross-continental exchange of species. Some of these exotic species have little ecological impact on native species, but others are accidentally introduced or escape their agricultural, horticultural, and other intended anthropogenic purposes and spread rapidly into novel environments. Ecologist Charles S. Elton was among the first to recognize the dangers of these “invasive species”, as he warned that movement of aggressive competitors to novel ecosystems can have dramatic effects on native biodiversity. Elton’s book, *The Ecology of Invasions by Animals and Plants* (1958), spawned decades of research into the ecology of invasive species and their effects on native ecosystems. There are an estimated 50,000 invasive species in the United States alone (Hellmann et al. 2008), and with the exponential growth of the human population and increase in anthropogenic movement and environmental fragmentation, it is expected that this number will increase.

In its nascent stages, invasion ecology was primarily concerned with the management of invasive species (Pyšek & Richardson 2010). Conservationists pushed for the eradication and prevention of introduced organisms, as researchers demonstrated that invaders could have severe environmental consequences. Some introduced species were found to contaminate soil and water sources, others damaged outdoor recreation and tourist attractions, and some species spread novel pathogens to humans, livestock, and agricultural species (Pyšek & Richardson 2010). To deal with these issues, management methods often included burning and physically removing species after they were already established. Awareness campaigns educated the public about the risk of spreading invaders, encouraging travelers to prevent the accidental transport of organisms like zebra mussels or garlic mustard. Biological controls (i.e. predators and diseases) were also introduced to reduce invasive populations (McEvoy & Coombs 1999).

While these restoration techniques are still in use today and have been successful in mitigating the impact of some invaders, it has been difficult for ecologists to address the complex effects that invasion can have on native ecosystems and to predict which species may invade next. Consequently, in the past twenty years research has evolved toward understanding why invaders are so successful compared to natives, resulting in a multitude of suggested mechanisms (Pyšek & Richardson 2010). One of the most commonly accepted mechanisms to come out of this research is the enemy-release hypothesis (Jeschke 2014). This hypothesis suggests that invaders flourish in new environments because they escape their natural predators, while their co-occurring native populations are still suppressed by predators and thus are at a disadvantage. Another popular hypothesis is that of invasional meltdown, in which a non-native species can facilitate the establishment of other non-natives, exacerbating the effects of invaders on native ecosystems (Simberloff & van Holle 1999, Jeschke 2014, Kuebbing et al. 2015). A third hypothesis is the propagule pressure hypothesis (Jeschke 2014), which posits that the high propagule pressure of non-natives allows them to invade novel ecosystems. This pressure may be due to the high number of individuals during a single introduction event, or multiple introduction events that increase the chance of an invasion.

Invasive Plant Traits

For non-native plants, much of the work addressing the mechanism of plant invasions has focused on their rapid growth and leaf functional traits. Studies have found that invasive plants are often fast-growing, highly productive species (Leishman et al. 2007, van Kleunen et al. 2010, Vilà et al. 2011), with high leaf nitrogen (N), high specific leaf area (SLA, dry mass per leaf surface area), and rapid carbon assimilation rates (Leishman et al. 2007, van Kleunen et al. 2010). Consequently, they cluster toward the resource-acquisitive end of the leaf economic spectrum (LES; Wright et al. 2004), with short-lived, "cheap" leaves that give high returns on investment in leaf mass and nutrients. Invaders have also been found to have later autumnal leaf phenology than natives (Fridley 2012), higher photosynthetic energy-use efficiency, and higher photosynthetic nitrogen-use efficiency (Heberling and Fridley 2013), which allows them to maintain high levels of productivity later into the season. Although there are exceptions to these general traits, quantifying invasive functional traits and growth structures has allowed ecologists to better understand why invaders impact ecosystem function and which habitats are most susceptible to rapid invasion (Ehrenfeld 2003, van Kleunen et al. 2010, Drenovsky et al. 2012).

Belowground interactions are an equally critical, yet comparatively understudied aspect of plant invasion ecology. This is partially due to the multifunctionality of roots and the complicated nature of fungal mutualisms, as these traits make it difficult to establish a root equivalent to the LES (McCormack et al. 2017). Recent studies and meta-analyses have suggested ways to identify the most ecologically significant root functional traits, resulting in multidimensional trait connections that include characteristics like root chemistry, morphology, architecture, and anatomy (Kong et al. 2014, Weemstra et al. 2016, McCormack et al. 2017, Ma et al. 2018). However, despite these efforts, there remains no widely-accepted root economic spectrum and further studies are needed to see how specific traits relate to a species' ability to acquire versus conserve nutrients belowground. Of those few studies that have looked at belowground root processes of invaders, invaders have had higher specific root length (SRL, root length per unit mass), finer root biomass, and more root N than their native counterparts (Jo et al.

2015). These traits are associated with fast rates of nutrient uptake, suggesting that invaders may fuel their rapid growth with more efficient roots. Plants can also compete indirectly through their effects on soil biogeochemistry, which involve mutualistic microbes like mycorrhizal fungi and rhizospheric bacteria. The relationship with these mutualists is highly dependent on species and site (Funk 2013, Stefanowicz et al. 2016, Bennett and Klironomos 2018), but if invaders are better able to stimulate these microbes, it may result in greater plant nitrogen uptake. Alternatively, if they can disrupt the mutualisms of neighboring species as is the case with allelopathic garlic mustard (Callaway et al. 2008), it eliminates more of their competition.

Rapid growth and high photosynthetic rates often allow invasive plants to take advantage of natural and anthropogenic disturbances, particularly in resource-rich environments. Habitats that are previously resistant to invasion may become susceptible after disturbance events, as high propagule pressure allows exotics to move in. Invaders can more quickly utilize soil resources and take advantage of high-light levels, consequently out-competing natives before they have the chance to re-establish. However, despite their high resource requirements, invaders have been found in areas with low resources (Funk 2013), including resource-limited soils in Hawaii (Funk & Vitousek 2007) and light-limited and nitrogen-limited forests in the northeast U.S. (Jo et al. 2015, Heberling & Fridley 2016). In these environments, the success of invaders is not only dependent on their ability to obtain resources, but to utilize them more efficiently than natives. In some low-resource habitats invaders also have traits similar to natives toward the lower end of the leaf economic spectrum and are able to invade due to their ability to fill vacant niches (Funk 2013). Understanding how invaders compete and influence soil and nutrient dynamics in these low-resource environments can give ecologists a more complete picture of invasive ecophysiology, allowing them to develop more general restoration policies (e.g. turf restoration to combat high invasibility, the addition of carbon substrates to immobilize nutrients and decrease rates of mineralization, and the removal of plant biomass to limit litter input; Kardol & Wardle 2010).

Plants and Soil Nitrogen Cycling

Invasive plants can have long-lasting impacts on ecosystems not just through direct competition with other plants, but also through their effects on soil biogeochemistry. Plants' influence on nitrogen cycling is of interest to plant ecologists, as nitrogen is an essential part of the enzymes that power photosynthesis and is used for the construction of cell walls, as well as defense, bioenergetics, nucleic acids, and other essential functions (Evert & Eichhorn 2013). As most of the N in the biosphere is atmospheric dinitrogen (N_2) that is inaccessible to plants, N is also one of the primary limiting factors of plant growth. Some of this nitrogen is made accessible to plants by nitrogen-fixing bacteria that convert N_2 to ammonia (NH_3), but this only accounts for approximately 15% of plant assimilated N (Schlesinger & Bernhard 2013). Other plants rely almost exclusively on the recycled nitrogen from dead organic material, as organic N is broken down by soil microbes. Although microbes often compete with plants for N, some microbes are mutualistic and release inorganic N in the form of ammonium (NH_4^+) and nitrate (NO_3^-), while others undergo such rapid turnover that the N in their structures is made available for plants. This process of turning organic N to inorganic N is known as mineralization, including organic N to NH_4^+ (ammonification) and NH_4^+ to NO_3^- (nitrification). Although it was once believed that these inorganic forms of N were the only forms available to plants, since the 1990s it has been widely recognized that N-containing monomers can also be taken up by plants (Schmiel & Bennett 2004).

Plants can influence nitrogen cycling through differences in leaf functional traits, root chemistry and morphology, and soil microbial interactions. Because leaf tissues account for 70% of litterfall in forests (Schlesinger & Bernhard 2013), it is unsurprising that the quality and quantity of leaf tissue has a large effect on the amount of N and carbon (C) in soil organic matter. Larger contributions of leaf N result in more soil N, and more leaf C can lead to greater soil C and a greater microbial N pool. Plant control of ecosystem processes is particularly apparent in the rhizosphere (i.e. the area of soil directly influenced by roots). In the rhizosphere, mutualistic fungi and carbon-limited bacteria cluster around the root tip to utilize the C released through exudation, the turnover and sloughing off of root cells, and the nutrient rich mucilage surrounding the root. These root influences on rhizospheric microbes can result in rhizosphere priming, i.e. the stimulation of decomposition of soil organic matter (SOM) and N mineralization by microbial communities. Priming effects are species dependent as stronger rhizosphere priming can increase the rate of SOM decomposition and thus N availability (Cheng 2009, Frank & Groffman 2009). Root biomass also increases plant uptake and thus the removal of N from soil (Bardgett & Wardle 2010).

Fast growing species can induce positive plant-soil feedbacks through both root and leaf pathways (Bennet and Klironomos 2018, Zhang 2019). The high SLA, high leaf N, and low leaf C:N of invaders’ leaves is often associated with higher quality leaf litter which return comparatively more nutrients to soil organic matter. Greater aboveground biomass also means that invaders can contribute more leaf litter than natives, so even when the quality of litter does not differ, the greater abundance of leaves associated with invaders can increase organic matter (Jo et al. 2017). Roots of invaders typically have higher root N and greater root production, which allows for higher root litter quality and greater N uptake belowground (Jo et al. 2014).

There is also evidence that root C exudation within the rhizosphere is linked to the rate of C assimilation of plants (Kuzyakov & Cheng 2001), and though no studies have tested this, it is possible that invaders may be able to increase the rate of exudation.

Objective of Study

In order to fully understand and mitigate the impacts of existing invasions on ecosystems, we need to study how invasive species influence soil biogeochemistry outside of experimental settings. It has been found that invaders can increase N cycling due to their rapid nutrient uptake rates, their high-quality root and leaf litter, and their lower leaf N resorption rates (Jo et al. 2017), but further work needs to be done to see how this applies to existing ecosystems. If invaders have dramatic effects on soil N and C, they can facilitate their own growth and potentially change the rate of nutrient fluxes for neighboring plants. Alternatively, if they do not change soil C and N, it indicates that there are other mechanisms through which they compete for soil N and it will be easier for ecosystems to recover after the removal of invaders. Thus, the objective of our study was to determine how invaders affect C and N cycling in the rhizosphere in a native-dominated northeastern U.S. forest.

CHAPTER 2

INTRODUCTION

Invasive species are strong competitors that can successfully establish outside of their native range and negatively affect native plant biodiversity and abundance (Soulé 1990, Grotkopp & Rejmánek 2007, Vilà et al. 2011). Such species are a worldwide ecological concern, as globalization increases opportunities for introduced species to find novel habitats (Hulme 2009), and the long-term consequences of invasion are not fully understood. To help prevent the spread of invasive species and to mitigate their impacts, it is important to study not only how they outcompete native species, but how they influence belowground processes (Ashton et al. 2005, Castro-Díez et al. 2009, Ehrenfeld 2010, Wardle & Peltzer 2017). If they have dramatic effects on nutrient cycling and soil biogeochemistry, it can facilitate further invasion and ecosystem change (Kuebbing et al. 2015, Bennett & Klironomos 2018).

Non-native species are typically resource-acquisitive plants that grow faster and are more productive than natives (Grotkopp & Rejmánek 2007, Leishman et al. 2007, van Kleunen et al. 2010, Vilà et al. 2011). Aboveground, they have leaf traits linked with 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. Jo et al. 2017). Invaders also have later leaf senescence (Fridley 2012) and higher photosynthetic energy-use efficiency than natives (Heberling & Fridley 2013), allowing them to maintain high levels of productivity later into the season. Despite their high resource demand, invaders can maintain their competitive advantage even in ecosystems with low resource supply (Funk 2007 & Vitousek, Funk 2013), including light- and nitrogen- limited deciduous temperate forests (Dreiss & Violin 2013, Heberling & Fridley 2016). Invaders must be able to outcompete natives for belowground resources, but comparatively little is known about the strategies that invasive species use to acquire soil nutrients to supply their growth and how those strategies may differ from those of native species. This is particularly true in northeastern forests of the USA where the canopy is still largely dominated by native species.

Nitrogen (N) is one of the primary limiting factors of plant growth, and it is important to understand how invaders influence the availability of soil N and compete with natives to obtain it. Plant-soil feedbacks can vary by species, as differences in chemical composition and the abundance of leaf and root litter can influence the quality and the amount of organic N returned to the soil (Chapman et al. 2006, Bennett & Klironomos 2018). This litter is decomposed by soil microbial communities, which convert organic N into inorganic forms that are readily available to plants. Plants can also influence the quality and composition of microbial communities within the rhizosphere (Li et al. 2006, Bardgett & Wardle 2010). Rhizosphere bacteria are heterotrophic and generally carbon-limited microbes that cluster around root tips, and they obtain carbon (C) through root turnover, the sloughing of root cells, the carbon-rich mucilage enveloping the root tip, and the exudation of organic acids, simple sugars, and acidic acids (Tan 2009, Bardgett & Wardle 2010). In return for C, these microbes can release N in the form of ammonium and nitrate. Plants that increase the abundance or quality of C to rhizospheric bacteria may increase their uptake of inorganic N, resulting in a positive feedback cycle through which plants can increase growth and thus return more C to the soil (Li et al. 2006, Bardgett & Wardle 2010, Bennett & Klironomos 2018).

Our objective was to determine how invaders in Eastern North America (ENA) influence soil C and N mineralization in the field, as plants that increase soil organic matter quality and foster high rates of microbial N mineralization are likely to increase their own N uptake. There is evidence that invaders alter N mineralization through both root and leaf pathways (Wedin &

Tilman 1990, Liao et al. 2008, Zhang et al. 2019), and microbes associated with invaders decompose litter faster than those associated with natives (Castro-Díez et al. 2009). This holds true for ENA shrub species, as monoculture studies show that invasive shrubs increase N cycling through more abundant leaf litter, higher SRL of fine roots, faster root turn over, and faster rates of N uptake (Jo et al. 2014, Jo et al. 2017). As plant-assimilated carbon can be rapidly transformed to exudates (Kuzyakov & Cheng 2001) and faster-growing species tend to have faster C assimilation rates (De Deyn et al. 2008), it is also possible that exudation rates are higher in invaders due to their high productivity. If invaders are capable of indirectly increasing N mineralization rates relative to nearby natives, it has important implications for how they may impact soil biogeochemistry.

We sampled soil from below and around non-native, invasive plants (hereafter referred to as “invaders”) and native, non-invasive plants (hereafter referred to as “natives”) in a deciduous forest in central New York, USA. We used short-term laboratory soil incubations to investigate how invasive species alter soil total C and total N, inorganic N pools, potential microbial respiration, and potential N mineralization rates in the field. We hypothesized that soil associated with invaders would have higher organic matter quality due to higher abundance and quality of root and leaf litter. We also hypothesized that this organic matter would lead to greater rates of potential C and N mineralization rates.

METHODS

Study Design and Species Selection

This study was conducted in Pompey, New York, USA (42°55’ N, 76°02’ W) in a closed canopy, secondary deciduous forest of *Acer saccharum* and *Fraxinus americana* canopy with frequent *Prunus serotina*, *Ostrya virginiana*, and *Carya cordiformis*. We measured the effect of plants on soil processes 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 selected three invasive and eight native woody species that were the most abundant in the forest understory (Table 1). We used spatial blocking to account for site effects with a total of 10 blocks. Block was conflated with time (Table 2), and 1-3 days were spent sampling each focal species within each block. 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 height 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. We sampled to 5 cm depth because roots from the target shrubs were primarily in the top 5 cm of soil. The five cores were pooled into a single combined sample so each individual shrub had a soil sample at the base of the shrub and around the shrub. 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 hours, and weighed. The soil pools of ammonium and nitrate were determined by extracting 10 g of soil with 50 ml 1M KCl following the methods of Robertson et al. (1999). Each sample was shaken for 10 minutes, 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 hours and stored until further analysis.

To measure lab 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, 100 mL of 1M 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 20mL scintillation vials, which were stored at -20 °C until further analysis. While the initial samples were being processed, the N_{final} jars were opened and vented for five minutes. A 20 mL scintillation vial with 2 mL of 2N 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 1N $BaCl_2$ and thymolphthalein was added as a pH indicator. NaOH samples were titrated with 0.5N HCl until the solution turned clear. Respired CO_2 was then calculated as ([B – T] x 0.5 x 6 mg C), where B was a blank titre of fresh NaOH, T was the sample titre, and 0.5 was the molarity of the HCl in moles/L.

Ammonium and nitrate were extracted from the incubated soils with 100 mL of 1M 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). Soil pH was determined using a 1:2 soil:water suspension and an Accumet AP71 pH meter (Waltham, MA).

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 the soil pools. Differences in soil measurements (i.e. soil C, soil N, potential mineralizable N, potential mineralizable N per soil N, and 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). Response variables were log transformed for both models to normalize residuals and we used the model:

$$y \sim \text{nativity} * \text{core sampling location} + \text{shrub height} + N(0, \sigma^2_{Block}) + N(0, \sigma^2_{Species})$$

where “nativity” is native or invasive and “core sampling location” is cores taken either below or around the plant. Differences between species were also assessed using LME with the following model:

$$y \sim \text{species} * \text{core sampling location} + \text{shrub height} + N(0, \sigma^2_{\text{Block}})$$

The relationship between potential respired C and potential mineralizable N vs. soil pH and root biomass were assessed using ordinary least squares regression. For the ordinary least squares regressions comparing pH and 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 (Supp. Fig. 1, t-test $t = -19.114$, $df = 45.004$, $p < 0.0001$). All statistical tests were performed in R 3.5 (R Core Team 2018).

RESULTS

Soil nutrient content and mineralization rates

There was no nativity effect on the soil inorganic N pool (Supp. Table 1, $t = -0.28$, $df = 41$, $p = 0.78$). There was also no difference in extractable organic N between cores taken below the shrubs vs. beyond the canopy of the shrubs ($t = 0.56$, $df = 47$, $p = 0.58$), and no significant interaction of nativity and core location ($t = 0.03$, $df = 47$, $p = 0.98$) (Fig. 1). There were no species-level differences in the inorganic N pool (Supp. Fig. 2).

There were no differences between natives and invasives for soil % C and % N (Supp. Table 1; $t = -0.58$, $df = 93$, $p = 0.57$ for % C; $t = -0.63$, $df = 93$, $p = 0.53$ for % N), and there was no interaction between core sampling location and nativity (Fig. 2a, 2b; $t = -0.02$, $df = 103$, $p = 0.98$ for core and % C interaction; $t = -0.64$, $df = 103$, $p = 0.52$ for core and % N interaction). There was also no significant difference in soil C:N between natives and invaders ($t = -0.26$, $df =$

93, p = 0.80) and no interaction effect between nativity and core sampling location on C:N (t = 2.14, df = 103, p = 0.06).

Nativity had no effect on potential respired C (Fig. 2C, Supp. Table 1, t = -0.95 df = 93, p = 0.34) and had no interaction with core sampling location (t = -1.15, df = 103, p = 0.25). Nativity also had no effect on potential mineralizable C per soil g C (Fig. 2D, Supp. Table 1, t = -0.30, df = 93, p = 0.77). Neither potential mineralized N per g soil (Fig. 2E) nor potential mineralized N per g soil N (Fig. 2F) differed between invaders and natives (t = -0.70, df = 93, p = 0.49 and t = -0.16, df = 93, p = 0.88, respectively). Potential mineralizable N differed by season (Supp. Fig. 1), and samples collected in the second week of June generally had more ammonium (1.28 ± 0.36 mg • $[\text{g dry soil} \cdot \text{day}]^{-1}$) than blocks sampled in the third week of June until the end of August (0.17 ± 0.16 mg • $[\text{g dry soil} \cdot \text{day}]^{-1}$).

Soil % C, % N, potential respired C, potential respired C per g soil C, potential mineralizable N per g soil, and potential mineralizable N per g N were also analyzed on a per root biomass basis (Supp. Table 2). Results were similar to those above; LMEs revealed no differences in natives vs. invaders for any variable.

There were no significant species differences for soil nutrient content and mineralization rates (Supp. Fig. 3). There were also no species differences for those variables per root biomass.

Relationships of Soil Processes with Root Biomass, and pH

The two significant predictors of potential mineralizable N and respired C were root biomass and pH (Fig. 3, Fig. 4). The average root biomass was 0.439 ± 0.292g (range of 0.029 to 1.658g) and our samples ranged from strongly acidic to moderately acidic (3.52 to 6.32, average of 4.94 ± 0.58). Neither pH nor root biomass differed between natives and invaders (t = 0.832, df = 57, p = 0.47 for pH, t = -0.55, df = 49, p = 0.59 for root biomass). Potential respired C was positively related to root biomass (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 respired C and potential respired C per g soil C were negatively related to soil pH (adjusted $R^2 = 0.26$, $p < 0.01$; adjusted $R^2 = 0.18$, $p < 0.0001$, respectively). pH was a significant negative predictor of potential mineralized N per g soil (adjusted $R^2 = 0.04$, $p < 0.01$) and potential min N per g soil N (adjusted $R^2 = 0.02$, $p < 0.05$). Potential mineralizable N and potential mineralizable N per g N increased with root biomass, but these relationships were not significant (adjusted $R^2 = 0.001$, $p = 0.58$ and adjusted $R^2 = 0.001$, $p = 0.42$, respectively). However, both relationships were significant when potential mineralizable N per g soil was modelled separately for samples taken before June 14th (adjusted $R^2 = 0.08$, $p < 0.05$ for root biomass(g); adjusted $R^2 = 0.24$, $p < 0.001$ for pH) and samples taken after June 14th (adjusted $R^2 = 0.09$, $p < 0.001$ for root biomass(g); adjusted $R^2 = 0.07$, $p < 0.001$ for pH). 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 found no significant differences between natives and invaders for potential rates of mineralizable N and respired C, and our hypothesis that rhizospheric soil associated with invaders would have higher potential rates of mineralizable N and respired C was not supported. There were also no significant differences in % C, % N, and inorganic N pools between natives and invaders, despite our prediction that invaders would increase both soil C and N availability through high quality leaf and root litter. Thus, while many studies have found that invaders increase soil C and N availability (Ashton et al. 2005, Liao 2008, Jo et al. 2017, Zhang et al.

2019), our results suggest that in a Northeastern native-dominated forest, understory invaders did not change soil C, soil N, and potential soil C and N fluxes.

Although unexpected, our lack of invader effect on biogeochemistry was not unprecedented. Canopy trees strongly influence C and N pools and potential mineralization rates throughout forest ecosystems (Dreiss & Volin 2013), as their high input of leaf litter can dominate understory litter contributions and their roots are often interwoven with the roots of understory individuals. Our canopy trees consisted of the same species across sites, so it is understandable that our soil traits were similar across focal understory species. Even if our target invasive shrubs did contribute more C and N than natives, we presumed this effect was hidden by the leaf litter and root influences of the native-dominated overstory species such as *Acer saccharum*. There is also evidence that the greater the differences in functional traits between invaders and natives, the stronger invaders' influence on soil nutrient cycling (Freschet et al. 2012, Lee et al. 2013, Castro-Díez 2014). As we did not examine leaf and root functional traits within this study, it is also possible that our particular focal species were not functionally different enough from natives to drastically change soil fluxes. Even if they were different, invaders have been found to have minimal effects on soil C and N when in mixed species communities compared to large invasive monocultures (De Long 2019). Alternatively, Castro-Díez et al. (2009) found that litter under invasive trees decomposed faster than litter under natives, but did not induce different rates of potential N mineralization. They posited that this was due to high rates of N uptake, and as we sampled after high periods of N uptake during the spring growing season, this may have been why our inorganic N pools, N cycling, and N availability were not greater under invaders. Furthermore, some of our mineralization values were negative, indicating that species may not influence the rate of potential N cycling due to high microbial immobilization of N (Laungani and Knops, 2012).

Root biomass was a better predictor of respired C and mineralized N than either nativity or species, and when soil C and N were considered on a root biomass basis there were no significant differences between natives and invaders (Supp. Table 2). Our focal species did not qualitatively differ in how they affected soil biogeochemistry, reinforcing Jo et al.'s (2016) findings that N availability under ENA invaders was driven by quantity rather than quality of leaf litter. It is important to note that while nativity was not a predictor of root biomass in our study, invaders have been found to produce more fine roots than natives (Jo et al. 2015). If there are highly productive invaders that create more leaves and roots, they may still change forest biogeochemistry. Our root biomass measurement also only included the mass of both fine and coarse roots; we did not examine root architecture, chemistry, and depth, which can also affect soil processes (Ehrenfeld 2003, Liao et al. 2008).

Soil pH was negatively correlated with C and N mineralization rates, but it is difficult to determine the mechanism behind this relationship. Respired CO_2 dissociates into carbonic acid in wet soil, so pH may simply be lower due to greater microbial respiration, including when bacteria mineralize N. On the other hand, microbial community composition is tightly linked to soil pH, especially when the community consists of soil bacteria (Rousk et al. 2010). If the microbes that prefer low pH respire/mineralize more rapidly, it may explain the higher potential respiration and mineralization rates we saw in more acidic soils. Plants also influence the pH of soil during nutrient uptake, and if any of our plants preferred NH_4^+ or NO_3^- it would make soil more acidic or basic, respectively (Tan 2009).

Some of the variation in our mineralization results was due to time of sampling, as samples obtained prior to June 14th had considerably higher rates of potential mineralization than samples obtained after June 14th. One possible explanation for this 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. Another potential cause is that this timing coincides with different stages of plant growth. As rhizosphere priming is correlated with plant phenology (Cheng 2009), differences in priming during the growing season may have affected microbial N mineralization vs. N immobilization.

In summary, our results suggest that invaders do not alter soil C and N mineralization nor total soil C and N content in a forest dominated by native canopy trees. While these invaders may drive increased C and N cycling in experimental settings, their influence on soil biogeochemistry has less impact in field conditions. Root biomass is a better predictor of potential C and N mineralization, and individuals that produced more roots have a greater ability to stimulate microbes and increase N availability regardless of identity. Future investigations of invaders should continue to study how woody invaders affect plant-soil processes under field conditions in forest ecosystems. Studies should also look at how root growth, morphology, and chemistry influence nutrient cycling and how those root traits differ between invaders and natives.

TABLES AND FIGURES

Table 1. Study species and species codes.

Species	**Nativity**	**Species Code**
Acer saccharum	Native	ACSA
Carya cordiformis	Native	CACO
Fraxinus americana	Native	FRAM
Lonicera* x *bella	Non-native	LOBE
Ostrya virginiana	Native	OSVI
Prunus serotina	Native	PRSE
Prunus virginiana	Native	PRVI
Rhamnus cathartica	Non-native	RHCA
Ribes cynosbati	Native	RICY
Rosa multiflora	Non-native	ROMU
Tilia americana	Native	TIAM

Table 2. The sampling date of each block.

Block	**Sampling Date**
1	June 12
2	June 13
3	June 20
4	June 21
5	June 28
6	June 30
7	July 19
8	July 25
9	August 2
10	August 12, 24, 25

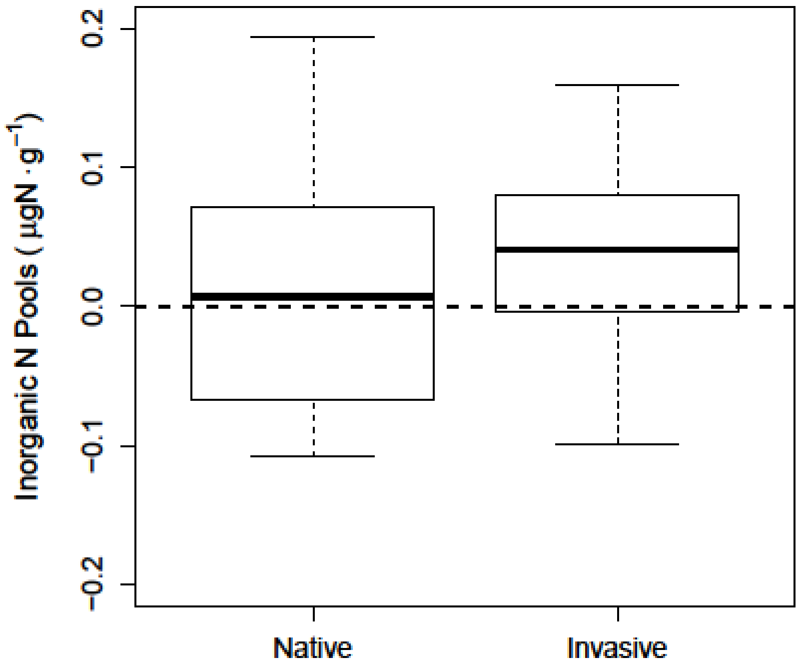


Figure 1. The natural log ratio of inorganic N pools for cores taken below and around the shrub. Log ratio was calculated as ln(Cores$_{Base}$/Cores$_{Around}$). Outlier is excluded for “Invasive” at y = -0.491.

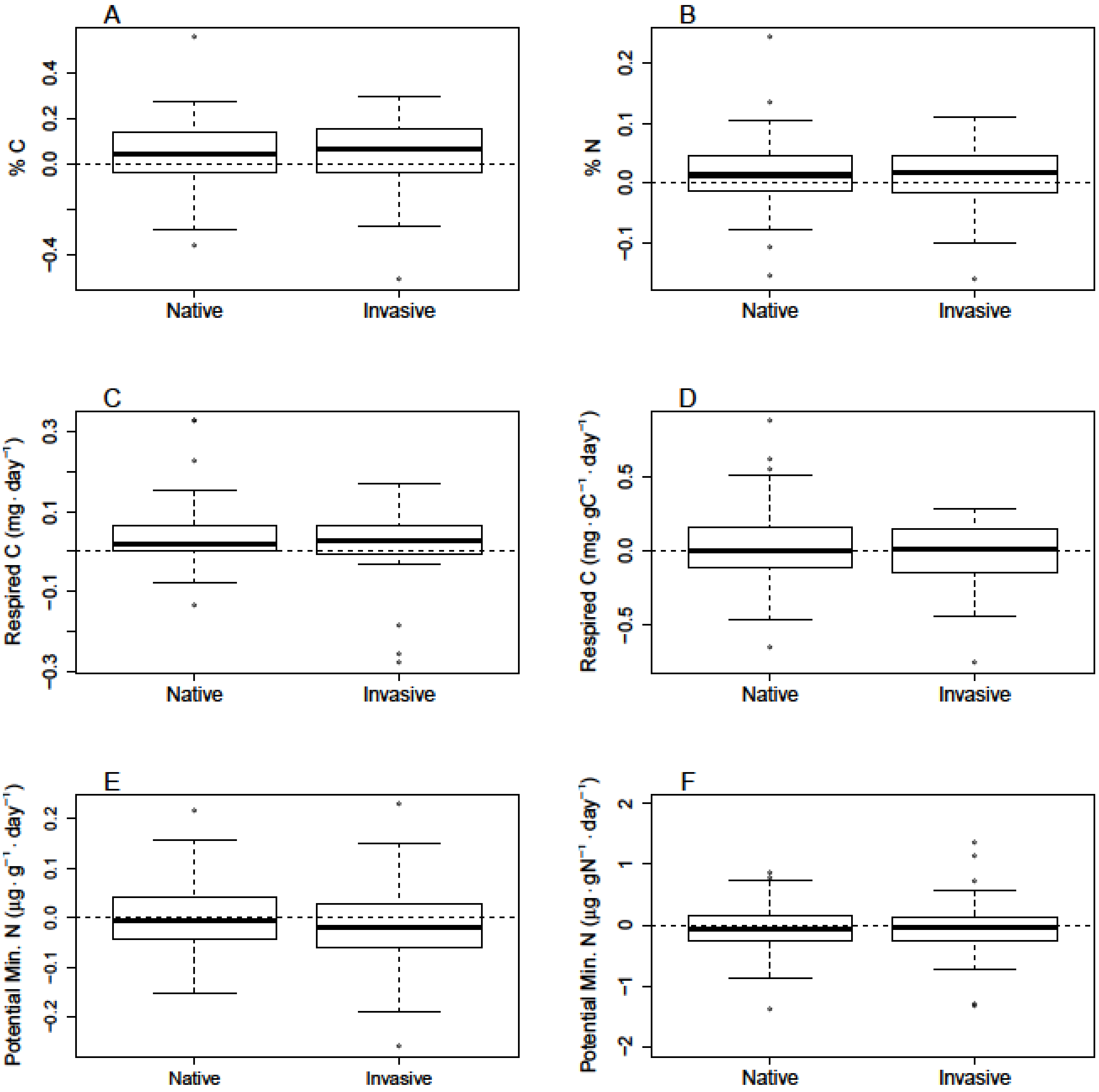


Figure 2. The log ratio of cores taken at the base and around the plants vs. nativity for A) % C, B) % N, C) Potential respired C, D) Potential respired C per g soil C, E) Potential mineralized N per g soil, F) Potential mineralized N per g soil N rate. Log ratio was calculated as $\ln(\text{Cores}_{\text{Base}}/\text{Cores}_{\text{Around}})$.

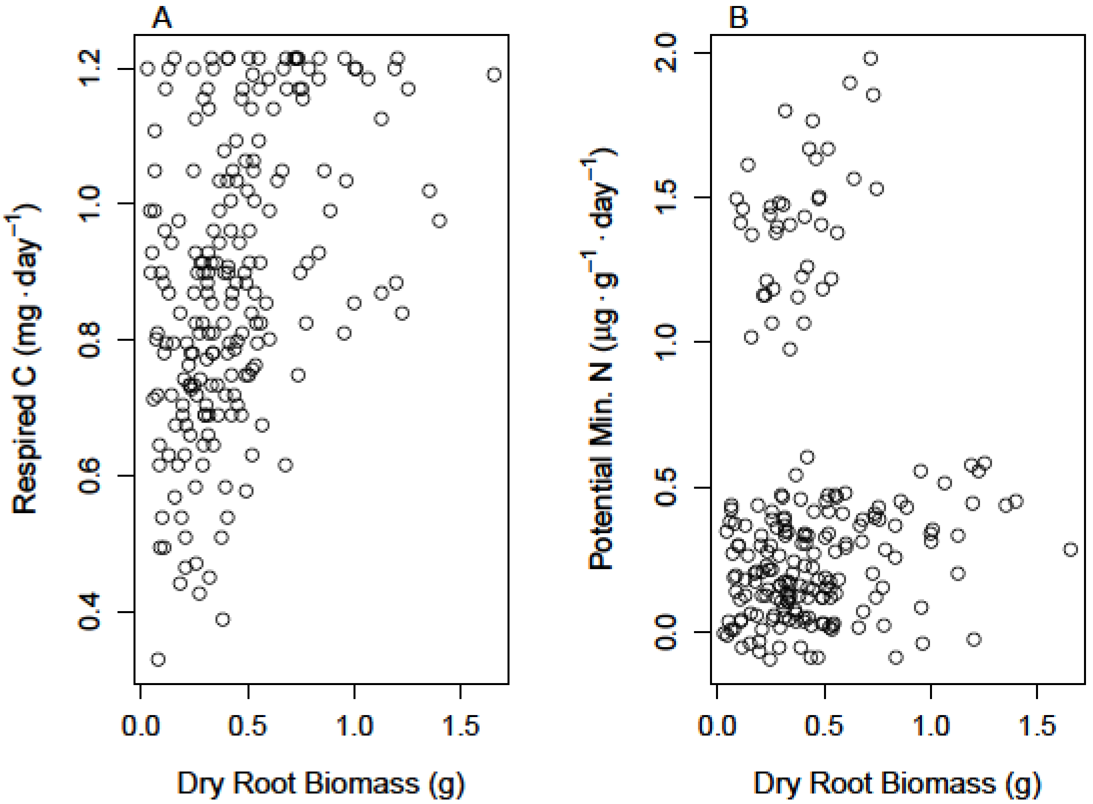


Figure 3. A) Potential respired C and B) Potential mineralized N per g soil vs. root biomass for all soil samples.

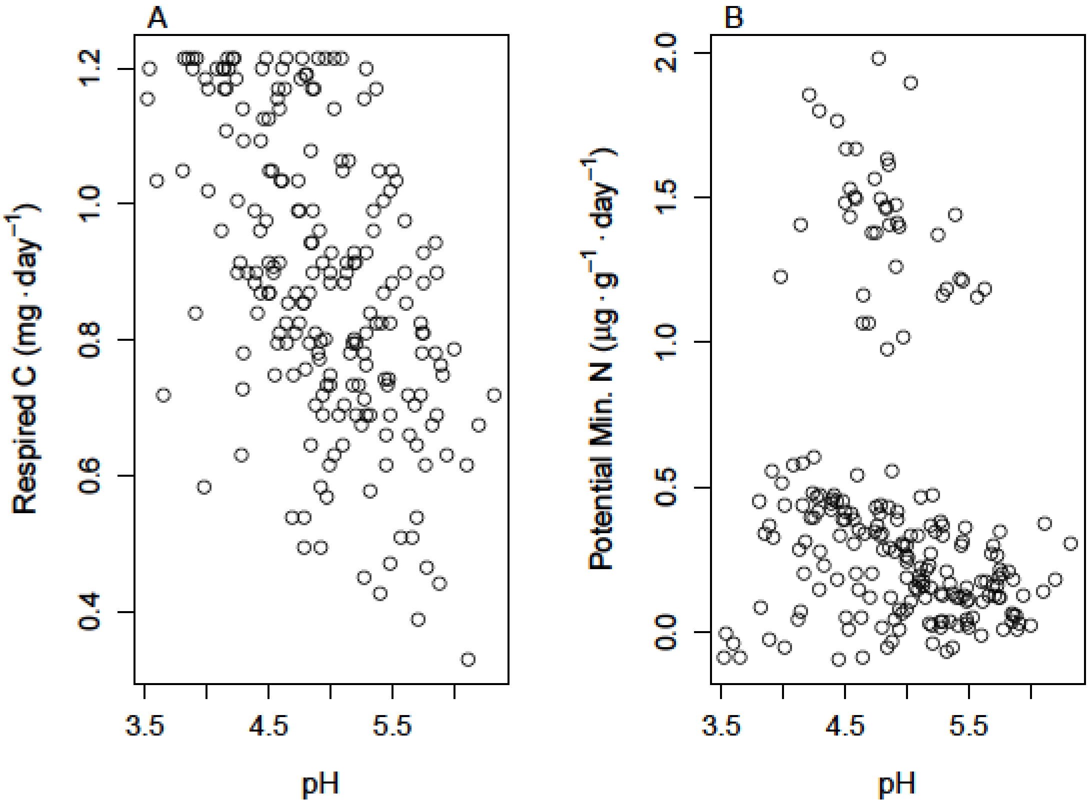
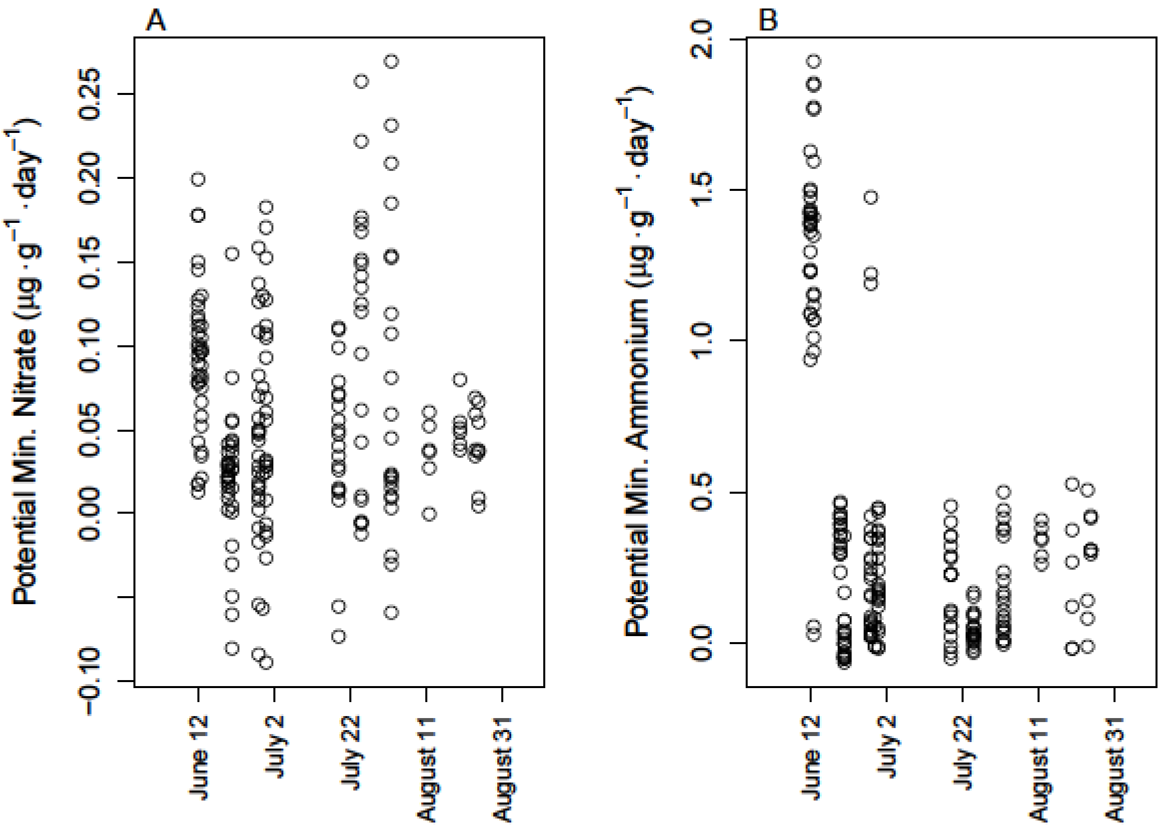
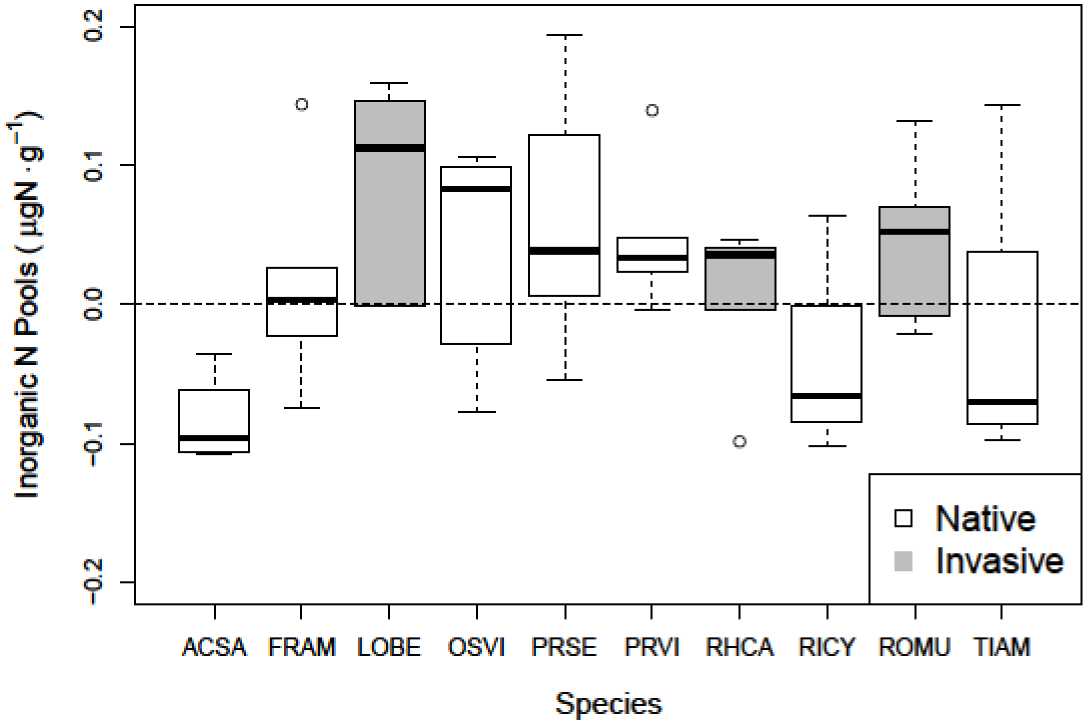


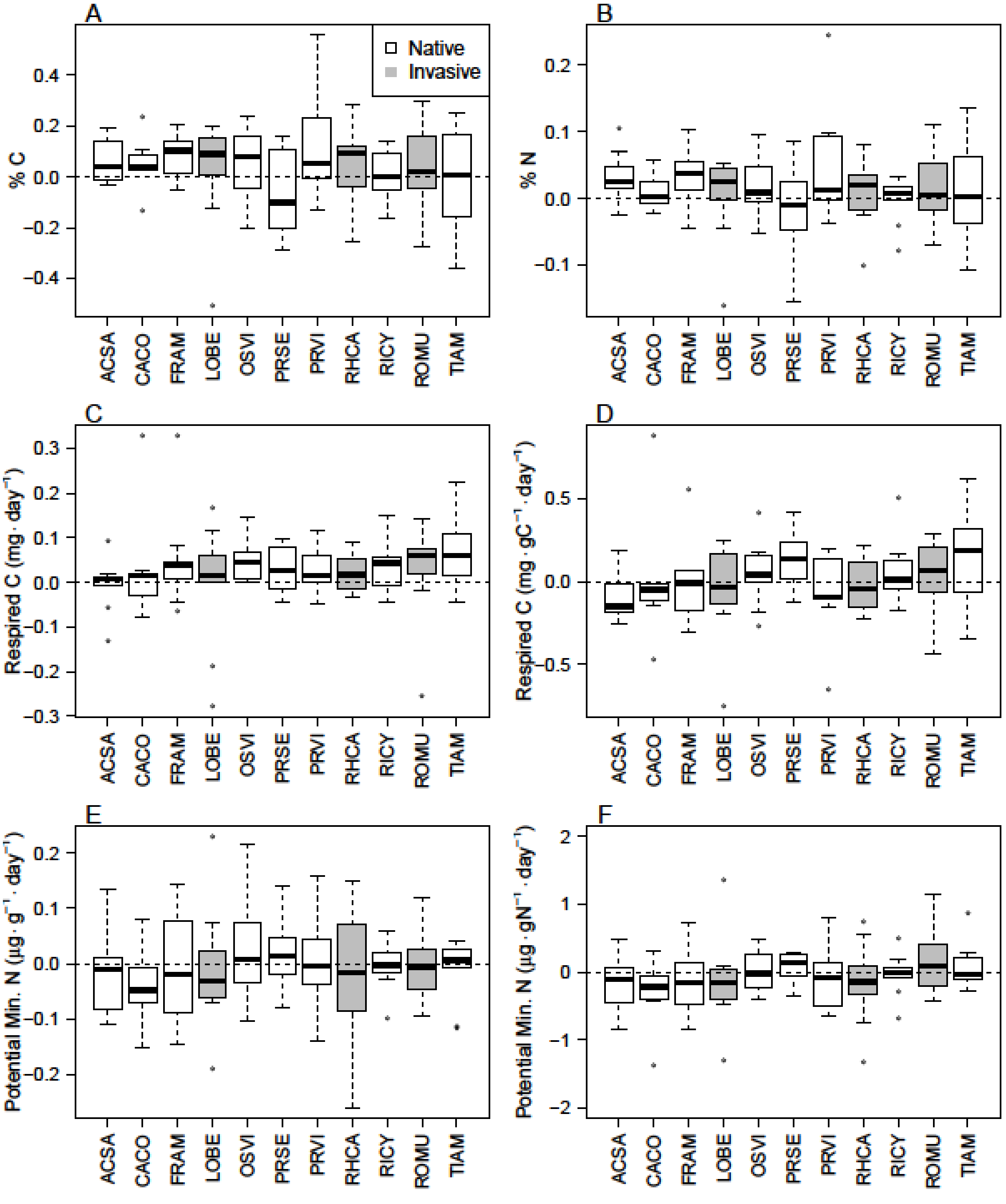
Figure 4. A) Potential respired C and B) Potential mineralized N per g soil vs. pH for all soil samples.



Supplementary Figure 1. Potential mineralized N per g soil across sampling dates for A) ammonium and A) bitrate.



Supplementary Figure 2. The natural log ratio of inorganic N pools for cores taken at the base and around the shrub. Log ratio was calculated as ln($\text{Core}_{\text{Below}}$ /$\text{Core}_{\text{Around}}$). White boxes are native species and grey boxes are invasive species. Outlier is excluded for LOBE at y = -0.491.



Supplementary Figure 3. The natural log ratio of cores taken below and around the plants vs. species for A) % C, B) % N, C) Potential respired C, D) Potential respired C per g soil C, E)

Potential mineralized N per g soil, F) Potential mineralized N per g soil N. Log ratio was calculated as $\ln(\text{Cores}_{\text{Base}}/\text{Cores}_{\text{Around}})$.

Supplementary Table 1. The mean ± SE for different measured soil traits.

	Native Below	Native Around	Invasive Below	Invasive Around
% C	5.677 ± 0.183	5.418 ± 0.169	5.505 ± 0.275	5.211 ± 0.207
% N	0.506 ± 0.017	0.479 ± 0.015	0.477 ± 0.024	0.462 ± 0.018
Potential respired C (mg • day^{-1})	0.935 ± 0.024	0.869 ± 0.044	0.862 ± 0.024	0.829 ± 0.035
Potential respired C per soil C (mg • [g soil C • day]$^{-1}$)	0.087 ± 0.003	0.084 ± 0.003	0.081 ± 0.004	0.081 ± 0.003
Potential mineralizable N (mg • [g soil • day]$^{-1}$)	0.469 ± 0.063	0.463 ± 0.060	0.402 ± 0.080	0.424 ± 0.088
Potential mineralizable N per soil N (mg • [g soil N • day]$^{-1}$)	101.747 ± 13.375	109.369 ± 14. 830	95.962 ± 19.985	103.4085 ± 23.260
Root biomass (g)	0.461 ± 0.036	0.425 ± 0.031	0.455 ± 0.054	0.399 ± 0.057
pH	4.907 ± 0.071	4.850 ± 0.063	5.082 ± 0.114	5.053 ± 0.097

Supplementary Table 2. The mean ± SE for different measured soil traits per root mass.

	Native Below	Native Around	Invasive Below	Invasive Around
% C	21.365 ± 3.300	21.164 ± 2.501	18.140 ± 3.156	24.638 ± 4.643
% N	1.895 ± 0.290	1.876 ± 0.221	1.571 ± 0.289	2.214 ± 0.429
Potential respired C (mg • day^{-1})	3.475 ± 0.584	3.367 ± 0.411	2.802 ± 0.549	3.927 ± 0.818
Potential respired C per soil C (mg • [g soil C • day]$^{-1}$)	0.318 ± 0.047	0.333 ± 0.041	0.281 ± 0.056	0.400 ± 0.084
Potential mineralizable N (mg • [g dry soil • day]$^{-1}$)	1.451 ± 0.254	1.601 ± 0.304	1.541 ± 0.352	1.876 ± 0.494
Potential mineralizable N per soil N (mg • [g soil N • day]$^{-1}$)	316.297 ± 52.585	382.322 ± 70.343	388.363 ± 91.723	443.591 ± 103.818

CHAPTER 3

LITERATURE CITED

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