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Effects of plant invasions on ecosystem processes: Linking above- and below-ground resource-use strategies of native and invasive species in Eastern U.S. forests

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ABSTRACT

Despite the increasing number of non-native invasive species worldwide and their potential impacts on ecosystems, the mechanisms that invaders alter ecosystem nutrient processes remain elusive. Invaders are often more productive than native species which suggests invaders may have different above- and below-ground resource-use strategies that can profoundly alter ecosystem processes. Here I investigated above- and below-ground plant traits and soil properties associated with resource-use strategies and soil nitrogen (N) dynamics for multiple native and non-native forest understory species in the Eastern U.S. to better understand invader impacts on ecosystem processes. In the first study, performed in a common garden, I examined the linkage between above- and below-ground resource-use strategies for native and invasive species that allow invaders to be more productive than co-occurring natives. Results showed that, despite invaders losing a significant amount of N from litter, they had greater root production and specific root length associated with a greater soil nutrient uptake capacity than natives. In the second study, I examined whether the different tissue traits are associated with litter decomposition rate and if invaders can increase nutrient cycling through faster litter decomposition than natives. Results revealed no differences in leaf and root decomposition rates between native and non-native forest understory woody species, suggesting that litter decomposition rate is not a process that invasive species affect with regard to soil nutrient processes in the Eastern U.S. forests. Finally, I investigated invader impacts on soil N processes in a monoculture experiment. After two growing seasons, invaders had greater above- and below-ground productivity. Invaders facilitated N cycling via greater litter N input into the soil that increased soil N availability, and had greater fine root production and SRL that increased plant N uptake. Although the greater aboveground production of invaders reduced soil

temperature and moisture, which can reduce soil microbial activity, the stimulatory effects of a greater flow of litter N to the soil appeared to overwhelm any negative effects that invaders had on the soil microclimate. Taken together, my results suggest that invaders have different above- and below-ground resource-use strategies and invaders' greater productivity is one of the major drivers that can significantly change ecosystem processes.

**EFFECTS OF PLANT INVASIONS ON ECOSYSTEM PROCESSES: LINKING ABOVE- AND
BELOW-GROUND RESOURCE-USE STRATEGIES OF NATIVE AND INVASIVE SPECIES
IN EASTERN U.S. FORESTS**

by

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Dissertation

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CHAPTER 1

Introduction

Over the past few centuries, species relocations globally have exploded through increased trade and transportation between countries (Mack et al. 2000; Guo et al. 2006; Hulme et al. 2008). Regardless of whether those species have been intentionally imported, some introduced species have spread beyond their native habitat and have become abundant elsewhere, causing substantial impacts on invaded ecosystems (Vitousek 1990; Gordon 1998; Mack et al. 2000, Ehrenfeld 2003; Liao et al. 2008, Vilà et al. 2011). Studies of invasive species attracted little attention until Charles Elton's 1958 book *The Ecology of Invasions by Animals and Plants* appeared. Since then, invasive species have attracted considerable attention and have been the topic of a steadily increasing number of investigations (Richardson and Pysek 2008). Furthermore, the 1980-90s SCOPE (Scientific Committee on Problems of the Environment) program on the Ecology of Biological Invasions and GISP (the Global Invasive Species Programme), with support from multiple international organizations (e.g. United Nations and the World Conservation Union), have boosted research on species invasions in many countries (Williamson 1999). However, how plant invasions alter ecosystem processes is still not well understood, except for a few well-studied invaders (Hulme et al. 2013).

Strategies of successful invaders

Invasion ecologists seek to understand the characteristics of species that make them successful invaders and characteristics of ecosystems that make them vulnerable to invasions (Richardson and Pysek 2006). Several hypotheses have been proposed to answer those questions,

such as those relating to enemy release, empty niches, disturbance, propagule pressure, novel weapons, pre-adaptation, and rapid evolution after introduction (Elton 1958; Keane and Crawley 2002; Wolfe 2002; Callaway and Ridenour 2004; Maron et al. 2004; Hierro et al. 2005; Schlaepfer et al. 2010). Testing those hypotheses using experimental approaches has been limited to relatively few species compared to the total number of invasive species in the world, making it difficult to generalize strategies of successful invaders. Nevertheless, recent meta-analyses have shown that invasive species often have greater rates of production and physiological activity than native species (Leishman et al. 2007; Liao et al. 2008; van Kleunen et al. 2010; Lamarque et al. 2011; Vilà et al. 2011). These results suggest invaders should have different carbon (C) and nitrogen (N)-use strategies to maintain their higher productivity and physiological activity compared to native species.

Resource-use strategies using a trait-based approach

A trait-based approach in ecology has been widely used to test resource-use strategies of plant species (Westoby et al. 2002). For example, fast-growing species usually have leaves with higher specific leaf area (SLA; leaf area per unit mass) and N concentrations, which are positively correlated to photosynthetic rates, in contrast to the slow-growing species with lower N and tough leaves. With respect to invasive plants, ecologists have reported some fast-growing invaders have higher leaf N and SLA than slow growing native species (Baruch and Goldstein 1999; Leishman et al. 2007). Despite the documented differences in aboveground resource-use traits associated with aboveground productivity between native and invasive species, it is still unclear how the greater invader aboveground C gain strategy is associated with belowground resource-use traits (e.g. root growth, SRL; specific root length) that necessarily must support

their greater leaf C uptake rates.

Importance of belowground traits

Roots are a substantial portion of a plant's biomass and play an important role in soil nutrient processes (Vogt et al. 1995; Jackson et al. 1997; Freschet et al. 2013). Roots take up water and nutrients and regulate soil nutrient availability in association with soil microbial activity (Chapin 1980; Hodge 2004). Because water and mineral nutrients limit plant production, the greater productivity of invasive species should be closely tied to belowground resource uptake ability and soil nutrient availability. However, compared to aboveground dynamics, there is a huge gap in the understanding of belowground processes due to difficulties in measuring root dynamics in situ (Nadelhoffer and Raich 1992; Wilson 2014). Without an understanding of belowground root traits that are associated with soil resource-use strategies, accurate estimates of the influence of invasive species on ecosystem processes, such as C and N cycling, will be unreliable.

Ecosystem effects of invaders

Despite a large number of studies addressing the difference in physiology or performance between native and invasive species, relatively few have focused on the consequences of species invasions on ecosystem processes (Strayer 2012; Hulme et al. 2013). Our knowledge of the impacts of invaders comes from several case studies of specific species, especially herbaceous species, and we still have limited data to generalize how invasives impact ecosystems (Hulme et al. 2013). Also, most ecosystem studies of invasions have been field studies without knowledge of preexisting site conditions, which has made it difficult to tease out

the changes in ecosystem properties by invaders (MacDougall and Turkington 2005; Stricker et al. 2015).

The two primary objectives of my dissertation research were to (1) compare above- and below-ground resource-use strategies between native and invasive species and (2) examine how invasive species influence ecosystem function. I performed a series of experiments to determine the effects of invasives on ecosystem processes.

Study System

Temperate deciduous forests are globally important ecosystems with respect to the quantity of C sequestered, water stored, and recreation provided (Pearce 2001; Bonan 2008). In the Eastern U.S., the expansion of non-native invasive species poses a major threat to forest ecosystem integrity (Howard et al. 2004; Fridley 2008). In this region, there are 449 invasive vascular plant species and woody invaders account for 39% of the total number of invasive species (Fridley 2008). However, there have been relatively few studies of those woody invaders, except a few noxious invaders such as a common buckthorn and exotic honeysuckles (Heneghan et al. 2006; Poulette et al. 2012). Fridley (2012) monitored the foliar phenology of focal native and invasive understory forest woody species in the Eastern U.S. and showed invaders increased annual C gain by keeping photosynthetically active leaves later in the season. I expanded his study to include belowground resource-use traits to better understand mechanisms of successful invasion and how above- and below-ground resource use strategies of invaders impact soil processes. The species I used for this dissertation are forest understory woody species in the Eastern U.S. I addressed the following general questions: Do invaders have different above- and below-ground resource-use strategies to support their greater productivity compared to the native

species? What are the effects of their invasion on ecosystem nutrient dynamics?

Research overview

My dissertation examined a suite of above- and below-ground resource-use traits for a range of temperate forest understory woody species in the Eastern U.S. to determine how those different resource-use strategies can affect ecosystem processes, especially soil N dynamics.

Chapter 2: Linking above- and below-ground resource-use strategies for native and invasive species of temperate deciduous forests

In this chapter I examined whether invaders have different resource use strategies. I compared aboveground and belowground plant traits between native and invasive liana and shrub species in the Eastern U.S. Non-native invasive species are often more productive than co-occurring natives (Liao et al. 2008; van Kleunen et al. 2010; Vilà et al. 2011). Because productivity is closely tied to plant N use, high invader productivity should be closely associated with N use strategy. However, little is known about the linked above- and below-ground C and N use strategies of native and invasive plants.

I measured shoot and root attributes and soil properties associated with 10 native and 14 non-native, invasive forest shrubs and lianas of the Eastern U.S. in a common garden in Syracuse, New York (USA), including leaf growth and chemistry (C, N), root growth, specific root length (SRL), root tissue density, and soil C and N concentration, each determined at two-month intervals (July-November). Non-native species had greater leaf and root production, leaf N content, and SRL, but lower leaf N resorption rates and root N content than natives. Soil N content associated with non-natives was significantly lower than that of native species.

The results suggest that the greater aboveground productivity of invasive forest species

is linked to greater production of fine roots that may increase the capacity of invasives to take up soil resources. In addition the findings suggest that invasives facilitate plant-soil N feedbacks compared to the strategy of slow growing native species that is biased toward recycled plant N. Such differences in N use strategy between native and non-native species could significantly impact forest soil nutrient cycling.

Chapter 3: More of the same? In situ leaf and root decomposition rates do not vary between 80 native and non-native deciduous forest species

Recent studies have demonstrated that invasive species exhibit greater productivity and produce more labile litter (e.g. high leaf N, low tissue density) than natives (Leishman et al. 2007; van Kleunen et al. 2010; Osunkoya et al. 2010). The increased quantity and quality of litter of the invaders should have a significant impact on rates of litter decomposition and nutrient cycling in ecosystems. Previous studies have compared litter decomposition rates between native and invasive species and reported invaders had faster litter decomposition rates than natives (Heneghan et al. 2002; Ashton et al. 2005; Trammell et al. 2012). However, most studies have only included leaf decomposition of a small number of species, which precludes the ability to draw generalizations about leaf and root litter decomposition patterns of invaders.

In the third chapter I examined decomposition rates of leaves of 42 native and 36 non-native species and fine roots of 23 native and 25 non-native temperate forest understory woody species in the Eastern U.S. I tested whether non-native species had different litter-associated traits than natives and how different traits of invaders may have influenced decomposition rates of the two groups. Among the leaf and root traits that differed between native and invasive species, only leaf nitrogen was significantly associated with decomposition rate. However, native and non-native species did not differ systematically in leaf and root decomposition rates. The

results indicate that litter decomposition is not a major driver by which invasive species affect North American temperate forest soil C and nutrient processes.

Chapter 4: Impacts of invasive plants on soil N dynamics: a monoculture comparison of Eastern U.S. forest species

In the fourth chapter I examined how invasive species affect soil N processes using a monoculture experiment. In the previous chapters, I determined the differences in plant traits and litter decomposition rates (leaves and fine roots), and suggested different resource-use strategies of invasive species and their possible impacts on nutrients dynamics in ecosystems. In this chapter, I describe results of a monoculture experiment on 10 species (five native and five invasive) to test how the different plant traits of native and invasive species mediated soil N cycling.

I found that invaders influenced soil N processes by having greater productivity than natives. Invaders accelerated plant-soil N cycling via (1) greater litter production and N concentration that led to increasing soil N availability, and (2) greater fine root production and SRL that increased plant N uptake. The greater aboveground production of invaders reduced soil temperature and moisture, which can reduce soil microbial activity. However, the stimulatory effects of a greater flow of plant litter (substrate) to the soil appeared to overwhelm any negative effects that invaders had on soil microclimate.

Overall, the results of this dissertation highlight the importance of linking above- and below-ground processes to better understand invasion strategies and demonstrate that invaders have significant impacts on ecosystem nutrient processes.

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CHAPTER 2

Linking above- and below-ground resource use strategies for native and invasive species of temperate deciduous forests

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Abstract

Non-native invasive species are often more productive aboveground than co-occurring natives. Because aboveground productivity is closely tied to plant nitrogen (N) uptake and use, high invader leaf productivity should be associated with root growth and plant N use strategies. However, little is known about the above- and below-ground carbon (C) and N use strategies of native and invasive plants. We measured shoot and root attributes and soil properties associated with 10 native and 14 non-native, invasive forest shrubs and lianas of the Eastern U.S. in a common garden in Syracuse, New York (USA), including leaf growth and chemistry (C, N), root growth, specific root length (SRL), root tissue density, and associated soil C and N concentration, each determined at two-month intervals (July-November). Non-native species had greater leaf and root production, leaf N concentration, and SRL, but lower leaf N resorption rates and root N concentration than natives. Soil N concentration associated with non-natives was significantly lower than that of native species. Our results suggest that greater aboveground productivity of invasive forest species is linked to greater production of fine roots that may increase the capacity of invaders to take up soil resources. In addition, our findings suggest that invaders have a looser, more open plant-soil N cycle compared to the strategy of slow growing native species that emphasizes recycled plant N. Such differences in N use strategy between native and non-native species would significantly impact forest soil nutrient cycling.

Key-words: Invasion ecology, nitrogen resorption, root traits, specific root length, nitrogen cycling, Eastern USA

Introduction

Invasive plant species are often found to grow faster aboveground than co-occurring natives across a wide variety of ecosystems (Liao et al. 2008; van Kleunen et al. 2010; Vilà et al. 2011), including temperate forests (Herron et al. 2007; Fridley 2012). Explanations for this successful invasion strategy have been sought in terms of aboveground traits associated with leaf economics (e.g., higher photosynthetic rate, specific leaf area [SLA], leaf nitrogen [N] concentration) (Baruch and Goldstein 1999; Funk and Vitousek 2007; Leishman et al. 2007; Leishman et al. 2010; Osunkoya et al. 2010; Ordonez and Olff 2013). Few if any studies, however, have examined the belowground traits presumably required to support a high rate of aboveground physiological activity. In particular, it remains unclear whether faster rates of aboveground productivity by invaders are associated with qualitatively different strategies of root production, allocation, and nutrient uptake compared to native species in the invaded habitat.

Because plant productivity is often limited by available N in terrestrial ecosystems, the way in which invasive plants harvest and use N is likely to be an important component of their success and an important component of their impacts on nutrient cycling (Laungani and Knops 2009). However, linkages between how carbon (C) and N are acquired and used by invaders are poorly understood because rooting behaviors of invasive plants have been rarely investigated. In a comparison of over 70 native and invasive shrubs and lianas in Eastern U.S. forests, Fridley (2012) found that non-native species had substantially (4-wk) delayed autumnal leaf senescence, which would seemingly limit the capacity of invaders to recycle N from senescing leaves given the time typically required for nutrient resorption in deciduous species (Weih 2009). Additional analyses by Heberling and Fridley (2013) of the leaf characteristics of a subset of these species corroborated that invaders had both more productive and longer-lived leaves with greater

photosynthetic capacity and leaf N concentration, such that, on average, more C was produced per unit N over the lifetime of the leaf. If invaders are investing more C and nutrients in leaves, what are the implications for whole plant function, and particularly belowground resource allocation?

Root foraging behavior and nutrient uptake capacity in general have received scant attention in native-invader comparisons but could be a primary mechanism of invader advantage in N-limited ecosystems (Laungani and Knops 2009). In theory, C gains by more productive invaders could be invested belowground in the form of greater allocation to fine roots, higher specific root length (SRL), greater nutrient uptake kinetics, or morphological changes to roots that favor nutrient exchanges with soil microbes (Chapin 1980; Hodge 2004; Craine 2011). In temperate deciduous forests, for example, the C subsidy that invaders get from exhibiting a longer growing season (Fridley 2012) could be invested into greater soil nutrient foraging and uptake. However, there has as yet been no systematic comparison of the rooting behavior of native and invasive plants in temperate forests.

Here we report a comparative analysis of above- and below-ground traits and resource foraging behaviors of 10 native and 14 non-native, invasive shrub and lianas of Eastern U.S. deciduous forests, focusing on a subset of those reported in Fridley's (2012) study of leaf phenology and Heberling and Fridley's (2013) study of leaf-level metabolism. Our objective was to test the hypothesis that the higher aboveground productivity of invaders is supported by greater investment in root structures associated with high rates of N uptake (fine root production and SRL). Secondly, we aimed to integrate leaf-level traits (photosynthetic capacity, N concentration, SLA, and N resorption rate) and seasonal root growth and morphology to address whether native and invasive species in this ecosystem have different coupled C - N use strategies

that could drive large changes in forest nutrient dynamics as a result of increasing invader dominance.

Materials and methods

Study design and species

Our study was conducted in 2011 at an experimental garden in Syracuse, New York, USA (43°03' N, 76°09' W), on plants established in 2006-2007 (Fridley 2012). Plants were covered by shade cloth (80% light reduction) from May 20 to October 24 annually to simulate forest understory conditions. From the garden collection of over 70 species of native and non-native species present in deciduous forests of the Eastern U.S., we selected 10 native and 14 non-native, invasive shrub and liana species on the basis of their ecological importance and taxonomic breadth, including native and non-native species of 10 genera and nine families (Table 1). Each species was represented by individuals present in three replicate blocks (N=3), except for *Lonicera morrowii* (N=2).

Leaf and root sampling

Three to five healthy leaves were collected at random from each plant every two months, July to November, to determine leaf N and C concentration. Ten leaves were sampled from *Berberis thunbergii* due to their small size. Leaves were pooled for each individual and sample date for analysis. To determine leaf N resorption, abscised leaves were collected after branches of each plant were gently shaken. Leaves were sampled every other day from October to November. Because of a marked increase in the rate of leaf abscission after the first frost date (October 27), leaves that abscised before and after this date were analyzed separately.

Root production was determined using point-in-space ingrowth cores, which allow for

sequential root sampling from the same locations, to predict root production during the measurement period (Milchunas et al. 2005). Ingrowth cores (4 cm diameter x 10 cm height) were constructed with plastic netting (1 x 1 cm mesh). Two ingrowth cores were installed on opposite sides and 15 cm from the main stem of each plant in May 2011. After installation, cores were filled with root-free soil collected from within the garden. To prevent root intrusion from neighboring plants, a 45 cm wide x 15 cm deep aluminum shield was installed 20 cm on the outside, relative to the target individual, of each ingrowth core to a 12 cm depth. Soil cores were sampled every two months, July to November, using a stainless core sampler (4 cm diameter). There was no significant soil disturbance around any of the ingrowth cores during the experiment. After sampling, ingrowth cores were refilled with root-free soil collected during the previous sample date. Soil cores were kept frozen until processed.

Leaf traits

The total leaf area of each individual was measured in July, September, and November 2011. We selected five branches randomly and counted the number of leaves attached to each branch. Leaf area was measured using a portable leaf area meter (LI-3000C, LI-COR Biosciences, Lincoln, Nebraska, USA) on three leaves evenly distributed between the tip and base of each branch. Total branch length was measured for each individual plant. Total leaf area for each of the five branches was calculated by multiplying average leaf area of the three selected leaves and the total leaf number of each branch. Leaf area per unit branch length for each branch was calculated by dividing total leaf area by branch length. Total leaf area for each individual ($\text{m}^2 \text{ plant}^{-1}$) was calculated by multiplying total branch length and average leaf area per unit branch length. For small plants, leaf area was measured for six leaves randomly selected from the plant and total leaf number was determined for the entire plant.

Leaves sampled for C and N concentration were dried at 60 °C for > 2 days and ground with a hand mill to a fine powder. Total C and N concentration were determined using an elemental CN analyzer (NC 2100, Thermo Quest CE Instruments, Milan, Italy). Leaf N resorption rate was determined by the following equation (Vergutz et al. 2012):

$$\text{Leaf N resorption rate} = \frac{N_{\max} - N_{\text{abscised}} \times \text{MLCF}}{N_{\max}} \times 100$$

Where N_{\max} = maximum leaf N concentration of leaves collected in July and September, N_{abscised} = leaf N concentration of abscised leaves, and MLCF = mass loss correction factor for each species calculated from changes in leaf mass per unit area between fresh leaves sampled in August and abscised leaves collected at the end of the growing season in 2013. Leaf N resorption rates before and after the first frost were determined separately. To obtain an estimate of the maximum leaf N resorption potential of each species, we used the maximum resorption value of calculations using abscised leaves before and after the first frost date.

Root traits

We pooled roots present in paired ingrowth cores for each individual and sample date. Roots were picked with forceps from the soil collected from the cores and washed gently with distilled water. Plants that had no roots in their ingrowth cores for all three sampling periods were excluded from the analyses. After removing roots and organic debris, soils were sieved (2 mm), dried, and stored at room temperature until used to refill cores in the field. A subset of each soil sample was used to determine C and N concentration. Live roots were separated based on root morphology and color, scanned with a transparency scanner (Umax Power Look II, Umax Technologies, Inc., Taiwan) and analyzed for length and volume using DELTA-T SCAN software (Kirchhof and Pendar 1993). We measured traits on roots $\leq 1\text{mm}$ in diameter

(representing 98.7% of roots collected from ingrowth cores) that were younger than 2 months and assumed to be involved in resource foraging rather than storage. Separated roots were dried at 60 °C for > 2 days to measure biomass and total C and N concentration was determined using same method for leaf tissue analysis. Root growth (length and biomass) for each ingrowth period, SRL (m g^{-1}), and root tissue density (RTD; g cm^{-3}) were calculated based on root biomass and image analyses.

Statistical Analyses

Plant and soil traits were compared across native and non-native species using linear mixed effects (LME) models. Nativity was treated as a fixed effect and block, genus, and individual plants were treated as random effects. Genus was included as a random effect to account for correlated trait variation contributed by shared phylogeny. *Frangula* and *Rhamnus* are sister genera in the Rhamnaceae (Richardson et al. 2000) and were treated as one group in LMEs. We tested for fixed effects by comparing full models to a null model with only the random effects based on maximum likelihood with the 'lme4' package for R (Bates 2010). Total leaf area, root production (total root length), and SRL data were normalized with log transformation. Post-hoc tests were conducted to evaluate pair-wise differences in measured traits between sampling times (Table 2) using the *glht* function in the R 'multicomp' package (Hothorn et al. 2012). We performed a principal component analysis (PCA) to determine multivariate trait patterns of native and non-native species using all measured variables plus SLA, leaf dry matter content (LDMC), and maximum C assimilation rate (A_{max}) measured on the same individuals in a previous study (Fridley 2012). Total N and C concentrations of plant tissue and soil in July were used for the PCA analysis because majority of plants showed a peak above- and below-ground growth during that period and excluding September and November data did

not change ordination patterns. A bivariate relationship of SRL and leaf N resorption rate was analyzed via standardized major axis (SMA) regression. We tested for differences in elevation and slope between fitting lines for each group and a shift between groups along their common axis using the 'smatr' package for R (Warton and Warton 2007; Warton et al. 2012). All statistical tests were performed in R version 2.14.1 (R Development Core Team 2011).

Results

Leaf traits

Non-native species produced greater total leaf area (m²) than natives and had higher leaf N concentration and a lower leaf C:N ratio (Table 2). Leaf N decreased and the C:N ratio increased from July to November for both native and non-native species (Table 2). Natives had significantly greater leaf N resorption rates ($P=0.018$, Fig. 1). Rates of resorption ranged more widely among invasive species compared to native species; invasive honeysuckles including *L. fragrantissima*, *L. japonica*, and *L. morrowii* had particularly low leaf N resorption rates (< 50%), while *Celastrus* spp., *Viburnum* spp., *Frangula caroliniana*, *L. canadensis*, and the common native shrubs *Hamamelis virginiana* and *Lindera benzoin* had high resorption rates (> 65%) (Fig. 1).

Root traits and associated soil properties

We found significant differences between native and non-native species in all root traits measured (Table 2). Non-native species had greater fine root production, SRL, RTD, and root C:N ratio, and lower root N concentration. Several traits varied seasonally, such as root production; however, SRL, RTD, root N, and root C:N ratio did not (Table 2). Soil N concentration was significantly higher under native shrubs and lianas and lower in July

compared to September and November. Soil N concentrations among roots of non-native species were on average 11% lower than those associated with natives during the growing season (July and September), but recovered to the similar level as those of native species in November (Table 2). Soil C:N ratio was highest in July and decreased in September and November (Table 2).

Multivariate trait analysis

A principal components analysis that included all the plant and soil characteristics showed significant separation between native and non-native species along PC1 ($P=0.022$) and 2 ($P<0.001$) axes, but not axis 3 ($P=0.54$) (Fig. 2). The PC1 axis, which accounted for 25.2% of trait variation, separated species according to traits associated with tissue chemistry and leaf morphology (leaf N and CN ratio, root N and CN ratio, SLA, and LDMC; Fig. 2 and Table S1). The PC2 axis, which accounted for 13.9% of trait variation, discriminated species based on their belowground N foraging ability (fine root production and SRL), tissue chemistry (root N and CN ratio, leaf C), and RTD (Fig. 2 and Table S1). The PC3 axis accounted for 11.0% of trait variation and was most closely associated with soil chemistry (soil C, N, and CN ratio) (Table S1). On the PC1 and PC2 plane, invaders were clustered toward a suite of traits linked to higher above- and below-ground growth rates (leaf N, SLA, total leaf area, photosynthetic rate, fine root production, and SRL) as opposed to natives, which exhibited traits related to a more conservative growth strategy (higher LDMC, leaf N resorption rate, leaf C, and CN ratio) (Fig. 2).

Leaf N resorption and root foraging ability

SRL declined with increased leaf N resorption rate, and SMA analysis revealed a significant shift ($P<0.001$) along a common slope for native and non-native species ($r^2 = 0.21$, $P<0.001$, Fig. 1). Invasive honeysuckles (*L. fragrantissima*, *L. japonica*, and *L. morrowii*) had low leaf N resorption rates, but high SRL, in contrast to native shrubs (e.g., *H. virginiana*, *L.*

benzoin, *F. caroliniana*, and native *Viburnum* spp.) that had relatively high resorption rates and low SRL (Fig. 1). We did not find any other significant bivariate correlations between above- and below-ground traits.

Discussion

Across a wide variety of ecosystems, non-native invasive species typically exhibit higher rates of productivity than co-occurring natives (Liao et al. 2008; van Kleunen et al. 2010; Vilà et al. 2011). This is generally true for invaders in Eastern U.S. forests. Results of our work on this group of deciduous forest species (Fridley 2012; Heberling and Fridley 2013; this study) show that, compared to both widespread and closely related native species, invaders on average have higher maximum photosynthetic capacity, higher leaf N concentration, faster rates of leaf production and shoot elongation, and a greater total amount of root production. Greater whole-plant productivity of invaders begs the question as to how such rates of production are maintained under the same resource conditions as natives. One possibility is that where plant growth is limited by soil N supply, invaders exhibit greater photosynthetic N use efficiency at the leaf level (Funk and Vitousek 2007; Leishman et al. 2010; Ordonez et al. 2010; Ordonez and Olff 2013). This is true in our study system only as a consequence of the greater leaf longevity of invaders (Heberling and Fridley 2013), and comes with the apparent cost of lower leaf N resorption. If invaders are investing more photosynthate in leaves to promote longevity but are losing more leaf N as a result of delayed senescence, how are they able to maintain such high leaf N over the growing season?

In this study we focus on the hypothesis that greater invader productivity is part of an integrated strategy of shoot and root foraging behavior, where greater light harvesting ability is

driven by differences in N uptake and use throughout the growing season. Very few studies have addressed differences in root traits and foraging behavior between native and invasive species or have attempted to integrate above- and below-ground resource foraging strategies for invaders of high productivity (Craine and Lee 2003). Our measurements on 10 native and 14 non-native invasive woody species common to Eastern U.S. forests revealed greater rates of fine root proliferation, higher SRL, and lower root N in invaders. The higher root N concentrations of native species may be indicative of more effective mycorrhizal symbioses. However, as most of our study species, including non-natives, have mycorrhizal roots (Brundrett et al. 1990; Wang and Qiu 2006; Akhmetzhanova et al. 2012), whether non-native species associate with more effective N foraging mycorrhizal symbionts remains to be tested. Allocation to fine roots with high SRL is associated with nutrient foraging ability (Eissenstat 1991; Reich et al. 1998; Comas and Eissenstat 2004; Hodge 2004), suggesting invaders are more effective foragers for soil nutrients including N (Liao et al. 2008; van Kleunen et al. 2010; Vilà et al. 2011). To our knowledge, these are the first results suggesting a distinct belowground growth strategy for invaders across a taxonomically diverse sample of native and non-native species.

The negative relationship between SRL and leaf N resorption may indicate an overall tradeoff between the production of fine, physiologically active roots for efficient root N foraging (Reich et al. 1998) and plant N retention. Dispersion around the linear function in Fig. 1 may in part be due to a relatively large phylogenetic effect on SRL (high between-genus effect in Table S2). Invaders in our study exhibited significantly lower leaf N resorption rates during leaf senescence than natives. These results are consistent with recent meta-analyses of leaf nutrient resorption rates showing that species of lower leaf N have higher N resorption rates (Kobe et al. 2005; Vergutz et al. 2012).

Why should invaders exhibit higher rates of N uptake, along with corresponding lower N resorption rates, than native species in Eastern U.S. forests? We suggest that the explanation may hinge on the time required for nutrient resorption (Weih 2009), which necessitates relatively early initiation of autumnal leaf senescence and results in reduced C gain at the end of the growing season. Fridley (2012) showed that, with only a few exceptions, invaders in our study exhibited later leaf senescence and greater autumnal C gain than native species. With reduced time for senescence before damaging frosts, invaders lose a greater amount of leaf N than natives but in return get a C subsidy that can be up to a fourth of annual C gain (Fridley 2012). In turn, this added energetic resource could fuel greater N foraging ability of invaders, allowing more effective recapture of lost N before the next growing season. We expect this strategy to be more associated with species adapted to habitats of high N supply rates, where re-uptake of lost N would be less costly (Chapin 1980; Craine 2011). If true, it remains a mystery why invaders would adopt this strategy in contrast to the N conservation strategy adopted by natives, although enhanced supply rates of N across Eastern North America in the 20th Century from industrial and agricultural pollution (Aber et al. 1989) or nitrification-stimulating earthworm invasions (Nuzzo et al. 2009) may be contributing factors. Future studies of native-invader performance across a N gradient would help resolve this issue.

Replacement of more nutrient-conserving native species with non-native species that have both more nutrient-rich leaf litter and greater capacity for nutrient uptake is likely to shift rates of nutrient cycling in invaded deciduous forests (Liao et al. 2008). In this study, invaders reduced the soil N concentration 7% more than natives during the growing season. We note that our study soils were not subject to the same rate and type of leaf litter input found under canopy trees and likely did not support the same microbial communities as natural forest stands.

Nevertheless, we predict that rates of forest nutrient cycling have increased and the competition for mineralized N has strengthened significantly as a result of increasing dominance of non-native shrubs and lianas, potentially changing ecosystem C and nutrient fluxes and shifting the composition of microbial communities (Kourtev et al. 2002; Ashton et al. 2005; Liao et al. 2008; Lee et al. 2012). Experiments designed to isolate long-term plant-soil feedbacks in stands dominated by native and invasive understory species would go a long way toward improving our understanding of changes in ecosystem functioning in temperate forests as a result of species invasions.

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Table 1. Study species. Species in bold are non-native invaders (for nativity and invasive derivations see Fridley 2008).

Family	Species	Species symbol
Berberidaceae	<i>Berberis thunbergii</i>	BETH
Celastraceae	<i>Celastrus orbiculatus</i>	CEOR
	<i>Celastrus scandens</i>	CESC
Elaeagnaceae	<i>Elaeagnus commutata</i> *	ELCO
	<i>Elaeagnus multiflora</i> *	ELMU
	<i>Elaeagnus umbellata</i> *	ELUM
Rhamnaceae	<i>Frangula alnus</i>	FRAL
	<i>Frangula caroliniana</i>	FRCA
	<i>Rhamnus cathartica</i>	RHCA
	<i>Rhamnus davurica</i>	RHDA
Caprifoliaceae	<i>Lonicera canadensis</i>	LOCA
	<i>Lonicera fragrantissima</i>	LOFR
	<i>Lonicera japonica</i>	LOJA
	<i>Lonicera maackii</i>	LOMA
	<i>Lonicera morrowii</i>	LOMO
	<i>Lonicera sempervirens</i>	LOSE
	<i>Lonicera tatarica</i>	LOTA
Adoxaceae	<i>Lonicera villosa</i>	LOVIV
	<i>Viburnum dilatatum</i>	VIDI
	<i>Viburnum lantana</i>	VILA
	<i>Viburnum prunifolium</i>	VIPR
	<i>Sambucus racemosa</i>	SARA
Hamamelidaceae	<i>Hamamelis virginiana</i>	HAVI
Lauraceae	<i>Lindera benzoin</i>	LIBE

* N-fixing species.

Table 2. Plant and soil attributes associated with nativity (Native vs. Non-native) and sampling date (Time) for three sampling periods (July, September, and November).

Traits	Units	Mean (n) ± SE						ML test* (P value)		
		Native			Non-native			Nativity × Time	Nativity	Time
		July	September	November	July	September	November			
Total leaf area (TLA) [†]	m ²	2.96 ^a (30) ± 1.19	3.42 ^{ac} (30) ± 1.33	0.61 ^d (30) ± 0.21	4.03 ^{bc} (41) ± 0.46	4.72 ^b (40) ± 0.50	1.99 ^a (41) ± 0.45	0.7436	< 0.001	< 0.001
Leaf N concentration (LN)	% mass	2.79 ^{ab} (30) ± 0.14	2.61 ^b (30) ± 0.10	1.69 ^c (25) ± 0.10	3.19 ^c (40) ± 0.14	3.10 ^{ac} (41) ± 0.13	2.17 ^d (37) ± 0.13	0.3681	< 0.001	< 0.001
Leaf C:N ratio (LCN)		18.0 ^a (30) ± 0.91	18.5 ^a (30) ± 0.71	28.9 ^c (25) ± 1.56	15.7 ^a (40) ± 0.65	15.9 ^a (41) ± 0.59	24.3 ^b (37) ± 1.62	0.1455	0.0015	< 0.001
Fine root production (TFRL) [†]	m 100cm ⁻³ soil	0.38 ^{ab} (23) ± 0.09	0.50 ^{ab} (23) ± 0.16	0.10 ^c (23) ± 0.04	0.58 ^b (38) ± 0.08	0.81 ^b (38) ± 0.16	0.19 ^{ac} (38) ± 0.06	0.5037	0.0498	< 0.001
Specific root length (SRL) [†]	m g ⁻¹	67.8 ^a (22) ± 6.3	70.7 ^{ab} (19) ± 8.3	69.8 ^a (16) ± 8.1	86.3 ^{ab} (37) ± 6.6	113.2 ^{ab} (35) ± 10.5	98.5 ^b (25) ± 10.5	0.7358	0.0019	0.6097
Root tissue density (RTD)	g cm ⁻³	0.14 ^a (22) ± 0.01	0.16 ^{ab} (19) ± 0.01	0.14 ^a (16) ± 0.02	0.18 ^{ab} (37) ± 0.01	0.18 ^{ab} (35) ± 0.01	0.20 ^b (25) ± 0.01	0.1163	0.0036	0.3446
Root N concentration (RN)	% mass	3.35 ^{ab} (22) ± 0.12	3.27 ^{bc} (16) ± 0.16	3.53 ^b (13) ± 0.13	3.00 ^{ac} (35) ± 0.13	2.90 ^c (31) ± 0.13	2.66 ^c (19) ± 0.07	0.4139	0.0042	0.6509
Root C:N ratio (RCN)		13.9 ^{ab} (22) ± 0.75	15.2 ^{bc} (16) ± 0.98	13.4 ^b (13) ± 0.61	15.0 ^{bc} (35) ± 0.61	16.4 ^c (31) ± 0.71	17.0 ^{ac} (19) ± 0.40	0.1717	0.0161	0.3317
Soil N concentration (SN)	% mass	0.23 ^{ab} (23) ± 0.003	0.27 ^d (23) ± 0.005	0.25 ^{cd} (23) ± 0.003	0.21 ^a (38) ± 0.005	0.24 ^{bc} (38) ± 0.009	0.25 ^{cd} (38) ± 0.004	0.2430	0.0204	< 0.001
Soil C:N ratio (SCN)		13.0 ^a (23) ± 0.28	12.0 ^b (23) ± 0.23	11.9 ^b (23) ± 0.10	13.3 ^a (38) ± 0.25	12.0 ^b (38) ± 0.24	11.9 ^b (38) ± 0.09	0.3673	0.6673	< 0.001

* Maximum likelihood ratio tests were used to assess significant trait differences between native and non-native species and over the growing season.

† Tested after log transformation.

Figure Legends

Fig. 1 Relationships between specific root length (SRL) and leaf N resorption rate. The dark gray arrow indicates the shifted distribution of non-natives and the light gray arrow indicates the shifted distribution of native species along a common slope (solid line). Point symbols indicate species identity as listed in Table 1. Error bars are \pm SE. In box plots, white boxes represent natives and gray boxes represent non-natives. Asterisks on the box plots represent significance level of mean differences between native and non-native species (* $P < 0.05$, ** $P < 0.01$, and *** $P < 0.001$).

Fig. 2 Principal Components Analysis of leaf and root traits of native and non-native shrubs and lianas from a common garden experiment. (a) Species scores along two major principal components (PC1 and PC2) and (b) vectors representing the coefficients of the traits on the principal components. See Table 2 and Table S1 for descriptions of the trait abbreviations (“LNrsp” denotes leaf N resorption rate). The symbol beside each point indicates species identity (see Table 1). Error bars are \pm SE. Box plots indicate a separation of species scores for each principal component by nativity. White boxes represent natives and gray boxes represent non-natives. Asterisks on the box plots represent significance level of mean differences between native and non-native species (* $P < 0.05$, ** $P < 0.01$, and *** $P < 0.001$).

Fig. 1

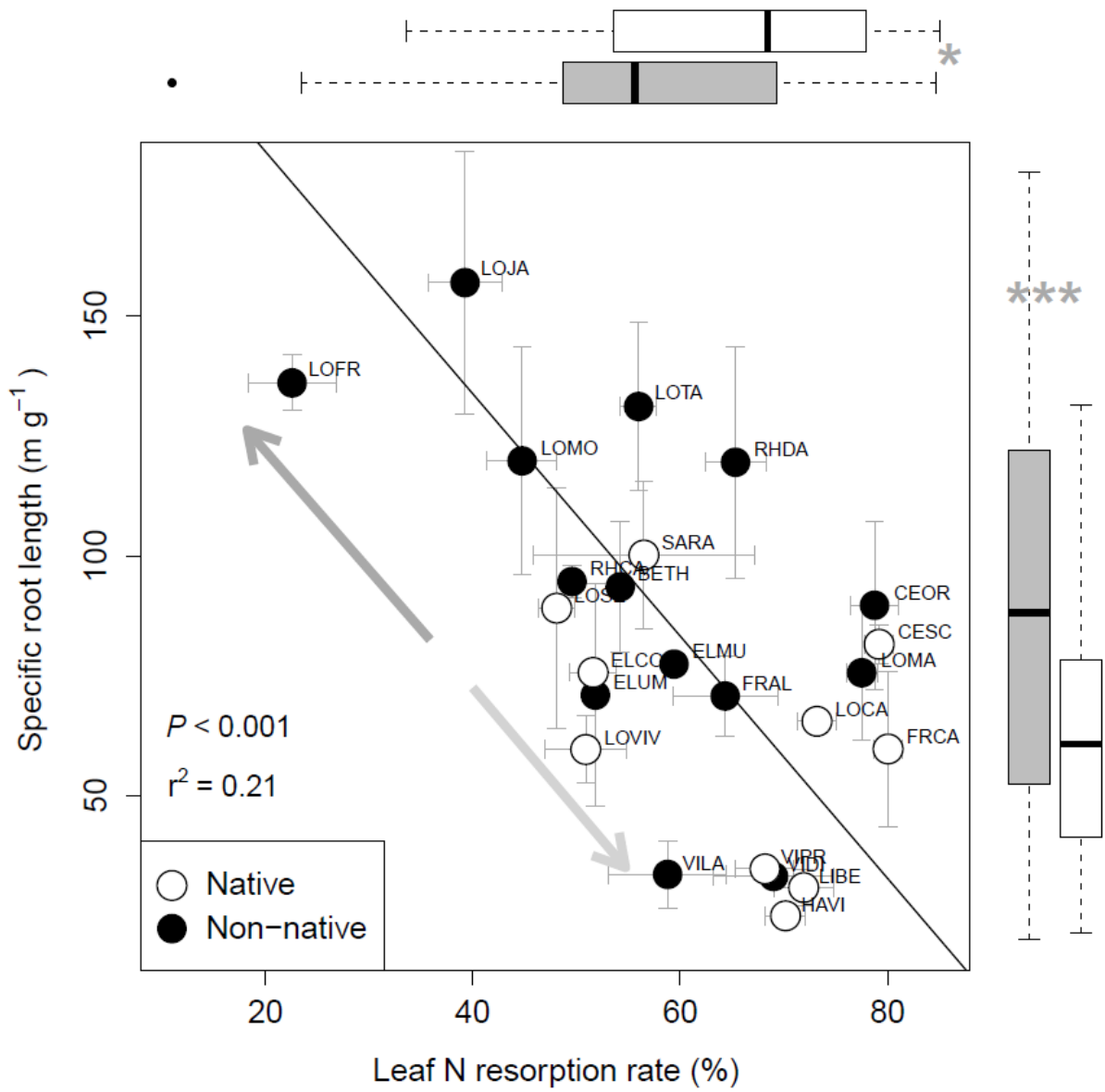
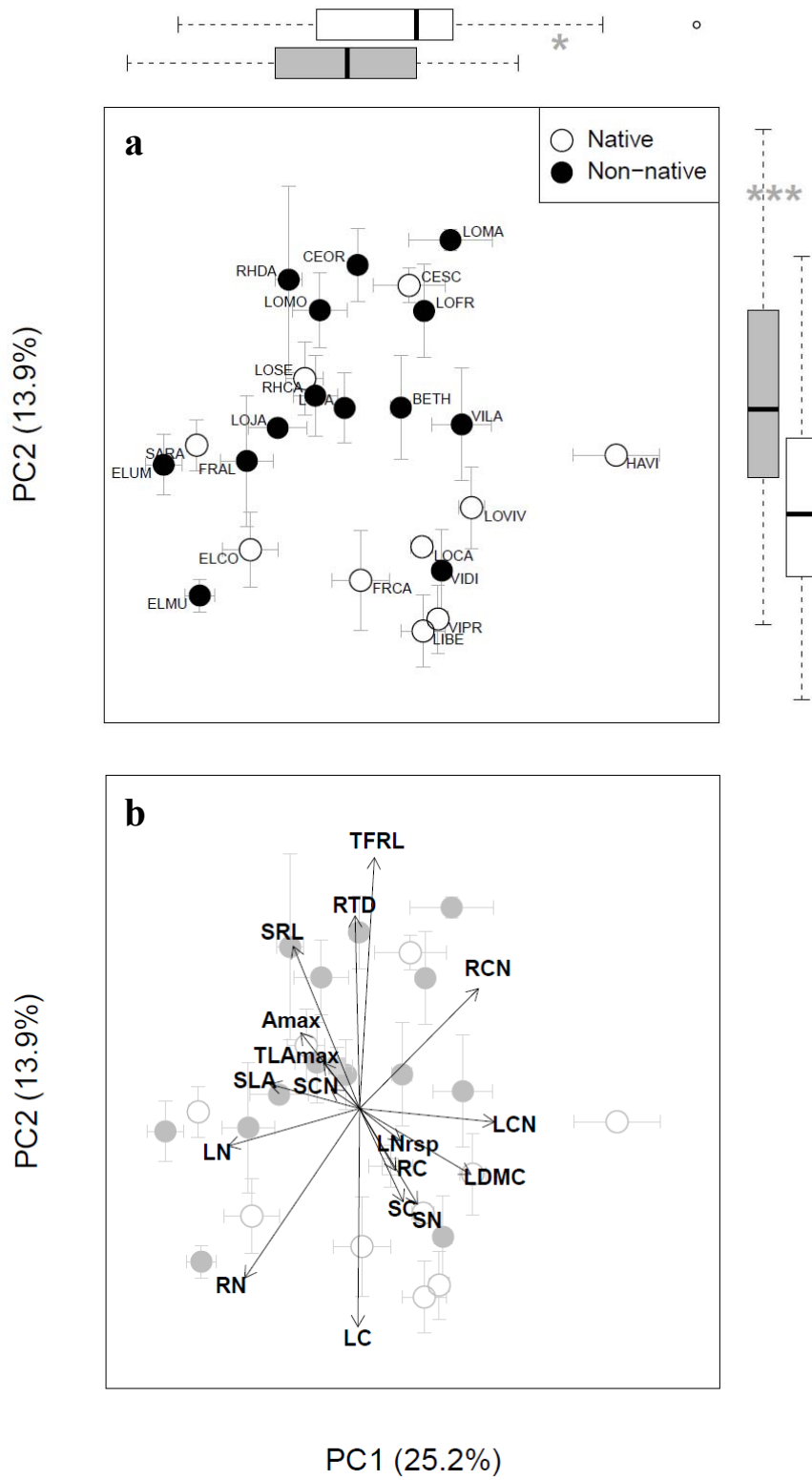


Fig. 2



Supplementary Material

Table S1. Eigenvector scores of species traits and associated soil properties in three main PCA axes. Values in parentheses indicate proportion of variance accounted for by each axis.

Abbrev.	Traits	PC1 (25.2 %)	PC2 (13.9 %)	PC3 (11.0 %)
LCN*	Leaf C:N ratio	0.423	-0.027	0.011
LN*	Leaf N concentration	-0.412	-0.074	-0.127
RCN*	Root C:N ratio	0.373	0.238	-0.158
RN*	Root N concentration	-0.360	-0.336	0.152
LDMC	Leaf dry matter content	0.349	-0.131	-0.140
SLA	Specific leaf area	-0.282	0.048	-0.017
SRL	Specific root length	-0.208	0.322	0.289
A_{max}	Maximum C assimilation rate	-0.185	0.150	0.261
SN*	Soil N concentration	0.181	-0.189	0.561
SC*	Soil C concentration	0.137	-0.185	0.450
LN_{rsp}	Leaf N resorption rate	0.129	-0.064	-0.193
TLA_{max}[†]	Maximum total leaf area	-0.113	0.090	-0.153
RC*	Root C concentration	0.113	-0.123	0.211
SCN*	Soil C:N ratio	-0.090	0.038	-0.259
TFRL	Fine root production	0.047	0.497	0.109
RTD*	Root tissue density	-0.014	0.382	-0.017
LC*	Leaf C concentration	-0.005	-0.433	-0.250

* Values measured in July were used for this analysis.

[†] Maximum value of total leaf area measured in July and September.

Table S2. Proportion of variance components for plant and soil attributes.

Traits	Proportion of total variance			Coefficient of variation (%)
	Between genus	Between species	Within species	
Maximum total leaf area (TLA _{max}) ^{†‡}	0.00	0.24	0.76	141.5
Leaf N resorption rate (LN _{rsp})	0.15	0.68	0.17	24.7
Leaf N concentration (LN) [*]	0.70	0.14	0.17	28.9
Leaf C concentration (LC) [*]	0.49	0.31	0.20	3.6
Leaf C:N ratio (LCN) [*]	0.67	0.07	0.26	27.7
Specific leaf area (SLA)	0.50	0.33	0.17	31.7
Maximum C assimilation rate (A _{max})	0.09	0.30	0.61	25.0
Leaf dry matter content (LDMC)	0.11	0.68	0.20	18.0
Fine root production (TFRL) [‡]	0.26	0.28	0.45	76.7
Specific root length (SRL) [‡]	0.59	0.17	0.24	12.3
Root tissue density (RTD) [*]	0.00	0.24	0.76	31.2
Root N concentration (RN) [*]	0.59	0.16	0.25	24.1
Root C concentration (RC) [*]	0.43	0.11	0.45	7.1
Root C:N ratio (RCN) [*]	0.77	0.11	0.12	27.1
Soil N concentration (SN) [*]	0.06	0.00	0.94	12.0
Soil C concentration (SC) [*]	0.05	0.03	0.92	12.7
Soil C:N ratio (SCN) [*]	0.00	0.00	1.00	11.0

[†] Maximum value of total leaf area during the growing season (July to September); [‡] log transformed before calculation; ^{*} Values measured in July were used for this analysis since most plants exhibited the greatest growth during the period.

CHAPTER 3

More of the same? In situ leaf and root decomposition rates do not vary between 80 native and non-native deciduous forest species

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Abstract

Invaders often have greater rates of production and produce more labile litter than natives. The increased litter quantity and quality of invaders should increase nutrient cycling through faster litter decomposition. However, the limited number of invasive species that have been included in decomposition studies has hindered the ability to generalize their impacts on decomposition rates. Further, previous decomposition studies have neglected roots. We measured litter traits and decomposition rates of leaves for 42 native and 36 non-native woody species, and those of fine roots for 23 native and 25 non-native species that occur in temperate deciduous forests throughout the Eastern United States. Among the leaf and root traits that differed between native and invasive species, only leaf nitrogen was significantly associated with decomposition rate. However, native and non-native species did not differ systematically in leaf and root decomposition rates. We found that among the parameters measured, litter decomposer activity was driven by litter chemical quality rather than tissue density and structure. Our results indicate that litter decomposition rate *per se* is not a pathway by which forest woody invasive species affect North American temperate forest soil carbon and nutrient processes.

Key words: plant invasions, leaf and root decomposition, nutrient cycling, understory woody species, temperate deciduous forests, Eastern United States

Introduction

Although non-native woody species are increasingly recognized as dominant invaders in many temperate ecosystems, such as deciduous forests (Howard *et al.*, 2004; Fridley, 2008), their impact on biogeochemical processes is poorly understood. It is clear that a few well studied species can influence ecosystem carbon (C), nutrient, and soil microbial processes (Ehrenfeld *et al.*, 2001; Kourtev *et al.*, 2002; Ashton *et al.*, 2005). For example, the invasive shrubs *Rhamnus cathartica* and *Lonicera maackii* in North America exhibit greater productivity and faster litter decomposition than co-occurring native species, which has been shown to alter soil nutrient cycling (Harrington *et al.*, 1989; Heneghan *et al.*, 2006; Arthur *et al.*, 2012). However, these are but two of over 100 woody invaders spreading across North America (Fridley, 2008), and it remains unclear if faster litter decomposition, a major component of terrestrial biogeochemistry, is a general phenomenon of plant invasions.

Nutrient cycling in temperate forest ecosystems is mainly driven by decomposition of plant tissue, particularly leaves and roots (Vogt, 1991). Plant tissue quality, a combination of tissue chemistry (e.g. nitrogen [N], C/N ratio, lignin) and structure (e.g. specific leaf area [SLA], specific root length [SRL], tissue density), is a key driver of decomposition rate, because tissue quality regulates activities of soil organic matter decomposers, including microbes and soil fauna (Silver & Miya, 2001; Cornwell *et al.*, 2008; Chapin *et al.*, 2011; Aulen *et al.*, 2012; García-Palacios *et al.*, 2013). Impacts of non-native, invasive species on litter decomposition rates should therefore be driven by systematic differences in tissue chemistry and structure compared to natives, if such differences exist; although soil microbial community composition can also play an important role in litter decomposition (Strickland *et al.*, 2009).

Non-native, invasive plants are often more productive than natives (Liao *et al.*, 2008;

Grotkopp *et al.*, 2010; van Kleunen *et al.*, 2010; Fridley & Craddock, 2015). Thus invaders likely possess leaf and root traits associated with greater C gain (e.g. high N and SLA) and nutrient uptake (e.g. high SRL) (Leishman *et al.*, 2007; Osunkoya *et al.*, 2010; Brym *et al.*, 2011; Ordonez & Olff, 2013; Jo *et al.*, 2015). For example, woody forest invaders in the Eastern U.S. differ in C and nutrient acquisition strategies compared to co-occurring native species, which is reflected in differences in leaf and root structure and chemistry, including greater leaf litter N concentration and SRL (Heberling & Fridley, 2013; Jo *et al.*, 2015). We hypothesize that such differences in tissue structure and chemistry lead to systematic differences in litter decomposition rate between native and non-native species, which has never before been examined across a large taxonomic array of species. Moreover, very little information exists for root decomposition rates of native and invasive species, precluding examination of how root decomposition may be linked to the different resource use patterns of the two groups. Given that roots constitute a substantial portion of annual plant productivity and litter input (Jackson *et al.*, 1997; Freschet *et al.*, 2013), invaders could have significant impacts on nutrient cycling due to root inputs alone, independent of their effects on leaf litter processes.

In this study, we tested for differences in litter decomposition rates across a large sample of native and non-native woody species present in temperate deciduous forests of the Eastern U.S. Leaf and root decomposition rates were measured in the field for 78 and 48 species, respectively. Our primary objective was to compare leaf and root decomposition rates of non-native species with those of native species. Secondly, we tested whether non-native species had different litter-associated traits than natives and how different traits of invaders may have influenced decomposition rates of the two groups, controlling for phylogenetic relatedness across species and co-varying environmental factors.

Materials and Methods

Litter collection and preparation

We included leaves of 42 native and 36 naturalized, non-native species of Eastern U.S. (Fridley, 2008), and fine roots for a subset of 23 native and 25 non-native species in the decomposition experiment. Two species of root samples were not used in leaf samples, leaving a total representation of 80 species in the study (Table S1). These species represented 26 genera in 17 families, with both native and non-native species included in most taxonomic units. Senesced leaves were collected immediately after abscission in autumn 2012 from 5-6 yr old plants established in an experimental garden in Syracuse, New York, USA (43°03' N, 76°09' W). Roots were collected in December 2012 from plants propagated by cuttings from a subset of the garden plants or saplings (*Acer*) in 2011 and grown in pots at least for one growing season in the experimental garden with soil from the garden. For most species, we used first- to third-order roots, but first- to second-order roots were used for *Elaeagnus angustifolia*, *E. commutata*, *Lindera benzoin*, *L. oblongifolia*, and *Shepherdia argentea*, in order to exclude secondary structural roots (Hishi, 2007; Guo *et al.*, 2008). Roots were washed with distilled water to remove all soil particles. Leaves and roots were dried at 60 °C for > 2 days.

For each species, ca. three grams of dried leaves was inserted into each of twelve 20 × 20 cm or 10 × 20 cm bags (fiberglass screening, mesh size 1 mm), depending on leaf size. Similarly, 200 mg of dried roots of each species was placed in each of twelve 5 × 10 cm N-free polyester bags (mesh size 50 µm, Ankom Technology, Macedon, New York, USA). The filled bags were sealed with a heat sealer. Nine hundred eighteen and 546 litterbags were used in the leaf and root decomposition experiments, respectively. Each species was represented by 12 litterbags unless limited by total leaf or root material. These included three species of six bags

each (*Acer platanoides* for leaf and root; *Dirca palustris* and *E. angustifolia* for root), and seven species of nine bags (*L. canadensis*, *L. villosa*, and *Hydrangea paniculata* for leaf; *A. saccharum*, *Berberis vulgaris*, *Sambucus racemosa*, and *S. argentea* for root).

Site selection and litterbag incubation

In May 2013, three adjacent 10 × 10 m blocks were laid out in a typical deciduous forest for the area located in Pompey, New York, USA (42°54'N 76°02'W). The overstory was a mature and moderately shaded secondary forest dominated by sugar maple (*A. saccharum*). In each block, four leaf litterbags for each species were placed on the soil surface, and four root litterbags for each species were buried in a vertical orientation at a depth of 5 to 15 cm. One leaf and one root litterbag per species per block (N=3 per species) was collected after 1, 3, 6, and 18 months to determine mass loss. Two samples were collected after 1, 3, and 18 months for those species with 6 litterbags and three (in month 1) and two (in months 2, 6, and 18) samples were collected for species with nine litterbags. Mean annual temperature and precipitation during the two years of the experiment (2013 & 2014) were 9.3°C and 1119 mm, respectively, at SUNY ESF station located 17 km north from the study site (National Oceanic and Atmospheric Administration [NOAA] National Climatic Data Center, USA).

Trait analyses and sample processing

Properties of leaves and roots for each species were analyzed using subsamples of the initial materials. Tissue N and C concentrations (%_{mass}; [N], [C]) were determined with an elemental CN analyzer (NC 2100, Thermo Quest CE Instruments, Milan, Italy). Klason lignin concentration (%_{mass}) was determined using wet chemistry after removing water and ethanol extractives from the tissue (TAPPI, 2002; Sluiter *et al.*, 2005). Because Klason lignin contains both true lignin and other acid-insoluble compounds (Prescott 2010), we used the term ‘acid-

insoluble residue (AIR)' instead of 'lignin.' We included the proportion of mass removed from the tissue during the extraction process ($\%_{\text{mass}}$; [WEE]) as a predictive trait for decomposition rate (McClaugherty *et al.*, 1985). WEE consists of non-structural components of the biomass, including sugars, nitrogenous materials, protein, ash, chlorophyll, waxes, and other minor components (Sluiter *et al.*, 2005). We also measured specific leaf area (a ratio of area to dry weight [$\text{cm}^2 \text{g}^{-1}$]; SLA) for leaves, specific root length (a ratio of length to dry weight [m g^{-1}]; SRL), root dry matter content (a ratio of dry to water saturated weight [mg g^{-1}]; RDMC), and root tissue density (a ratio of dry weight to volume [g cm^{-3}]; RTD) to determine how functional and structural traits influence litter decomposition rates. Leaf area, root length, and volume were measured on scanned images using Delta-T SCAN software (Delta-T Devices Ltd., Cambridge, UK).

Litter was collected from harvested litterbags, dried at 60 °C for > 2 days, and weighed to determine mass loss during decomposition. Root litter mass remaining was corrected for soil contamination using the ash weight of the collected samples inside the litterbags, initial roots, and soils at the site following Harmon *et al.* (1999). Decomposition rate (k) of leaves and roots for each species was calculated by fitting a single exponential model ($y = e^{-kt}$) to the proportion of litter dry mass remaining (y) over the decomposition period (t , year) of 12 samples for each species (except for those with six or nine samples) using a nonlinear regression function (*nls*) in R (Olson, 1963). Mean r^2 of the regressions for leaf and root mass remaining were 0.90 and 0.50, respectively.

Phylogenetic tree construction

To account for the taxonomic dependence of our species-level comparison, we created a phylogeny (Fig. S1) for our studied species using Phylomatic (ver. 3; Webb & Donoghue, 2005),

with branch lengths estimated via the BLADJ algorithm in Phylocom (ver. 4.2) based on the node ages from the file ‘agescl3’ (Gastauer & Meira-Neto, 2013). Generic polytomies were resolved using the most up-to-date literature phylogenies for *Lonicera* (Rehder, 1903; Theis *et al.*, 2008; Howarth *et al.*, 2011), *Viburnum* (Clement & Donoghue, 2012), *Berberis* (Kim *et al.*, 2004), *Hydrangea* (Samain *et al.*, 2010), *Cornus* (Xiang *et al.*, 2006), *Euonymus* (Blakelock, 1951; Simmons *et al.*, 2012), and *Acer* (Li *et al.*, 2006).

Statistical analyses

We fit a hierarchical predictive model of tissue decomposition by jointly modeling the independent effects of traits on decomposition rate, and, simultaneously, whether those traits differed across native or non-native species groups, for both leaf and root decomposition (Fig. 1a & Fig. 2a). In this way, we could distinguish between effects of traits themselves on decomposition rate and whether such traits varied significantly by nativity. To do this, we used a Bayesian approach that accounted for phylogenetic autocorrelation across species, following the model of de Villemereuil *et al.* (2012) using JAGS in R 3.12 (Plummer, 2003; R Development Core Team, 2014). Decomposition rates were log-transformed to meet normality assumptions. As covariates we included two categorical variables, species’ nativity (non-native=1, native=0) and whether plants associated with N-fixing bacteria (N-fixer=1, non-N-fixer=0). All other covariates of continuous variables were standardized by subtracting their mean and dividing by two standard deviations to enable effect size comparisons with categorical predictors (Gelman & Hill, 2006). We included six covariates for leaf decomposition (Fig. 1a) and eight for root decomposition (Fig. 2a). The models allowed us to estimate posterior coefficients (β s) to determine the relative effects of parameters on dependent variables. Non-informative priors for the coefficients (β s) were sampled from a normal distribution of mean 0 and variance 1000. The

de Villemereuil *et al.* (2012) model includes estimation of phylogenetic signal (Pagel's λ) in the initial litter traits and decomposition rates, from zero (no phylogenetic signal) to 1 (strong phylogenetic signal). We ran three parallel MCMC chains in JAGS for 20,000 iterations after a 5000-iteration burn-in. We assessed model convergence using the Gelman-Rubin convergence diagnostic (\hat{R}), where $\hat{R}=1$ at convergence (Gelman *et al.*, 2014). All parameters in the models had $\hat{R}<1.1$. The regression models included the hierarchical model are available in Table S2.

Results

Traits driving leaf and root decomposition rates across species

Among leaf litter traits, only chemical traits significantly affected leaf decomposition rates (Fig. 1a,c). $[N]_{\text{leaf}}$ and $[WEE]_{\text{leaf}}$ increased, and $[C]_{\text{leaf}}$ decreased, leaf decomposition rates ($\beta_{7, 8, 10}$; Fig. 1a,c). $[AIR]_{\text{leaf}}$ and SLA had no significant impact on decomposition rate ($\beta_{9, 11}$; Fig. 1a,c). The mean effect size of standardized values for $[N]_{\text{leaf}}$, $[C]_{\text{leaf}}$, and $[WEE]_{\text{leaf}}$ were similar to each other, suggesting that those traits had equivalent effects on leaf decomposition rate ($\beta_{7, 8, 10}$; Fig. 1a,c). Including phylogeny did not influence the effect of leaf litter traits on leaf decomposition rate (Fig. 1a,c). Root decomposition rate was negatively affected by $[C]_{\text{root}}$, $[AIR]_{\text{root}}$, and SRL ($\beta_{10, 11, 13}$; Fig. 2a,c), and positively correlated with $[WEE]_{\text{root}}$ (β_{12} ; Fig. 2a,c). $[AIR]_{\text{root}}$ had the largest effect size among root traits (β_{11} ; Fig. 2a,c). After including phylogenetic autocorrelation, $[WEE]_{\text{root}}$ and SRL effects on root decomposition rate increased in magnitude ($\beta_{12, 13}$; Fig. 2a,c). We detected relatively strong phylogenetic signals for both leaf and root tissue chemistry (e.g. $[AIR]$ and $[WEE]$) and weak signals for SLA, RTD, and RDMC (Table 1), suggesting that structural traits were less conserved across the phylogeny than tissue chemistry.

Non-native effects on leaf and root traits

For leaves, $[N]_{\text{leaf}}$ was greater and SLA was lower for non-native compared to native species ($\beta_{2,6}$; Fig. 1a,b; Table 1; Fig. S2), but nativity was not significantly associated with $[C]_{\text{leaf}}$, $[AIR]_{\text{leaf}}$, or $[WEE]_{\text{leaf}}$ (β_{3-5} ; Fig. 1a,b; Table 1; Fig. S2). The significant non-native effect on $[N]_{\text{leaf}}$ appeared after applying phylogenetic autocorrelation (β_2 ; Fig. 1a,b). Nativity had no effect on root chemical traits (β_{2-6} ; Fig. 2a,b; Table 1; Fig. S2), but non-natives had lower RTD and RDMC, two structural traits, than natives when including the phylogenetic autocorrelation ($\beta_{7,8}$; Fig. 2a,b; Table 1).

Effects of trait differences between native and non-native species on decomposition rates

Among the leaf and root traits that differed by nativity, only $[N]_{\text{leaf}}$ was significantly associated with decomposition rate (Fig. 1). However, overall, leaf and root decomposition rates were unaffected by nativity (Wilcoxon's rank-sum test, k_{leaf} : $P = 0.92$, k_{root} : $P = 0.53$; Fig. 3). Neither leaf nor root decomposition rates exhibited a strong phylogenetic signal (Table 1).

N-fixer effects on leaf and root decomposition

The N-fixer effect (species in the Elaeagnaceae; see Table S1 for the species list) on leaf decomposition rate was not significant (Wilcoxon's rank-sum test: $P = 0.73$; Fig. 3). However, N-fixers had significantly lower root decomposition rates than non-N-fixers (Wilcoxon's rank-sum test: $P < 0.01$; Fig. 3). N-fixers had significantly higher $[N]$ for both leaves and roots (β_1 , Fig. 1a,b; β_1 , Fig. 2a,b). Also, N-fixers had significantly higher $[AIR]_{\text{root}}$ (30 ± 5.7 [SD] % vs. 20 ± 5.3 [SD] %; Wilcoxon's rank-sum test: $P < 0.001$) and a lower $[WEE]_{\text{root}}$ ($38 \pm 9.8\%$ vs. $45 \pm 5.9\%$; $P = 0.057$).

Discussion

In situ measurements of leaf and root decomposition rates for 78 and 48 species,

respectively, revealed no significant differences between native and non-native species.

However, a few invaders exhibited markedly higher leaf decomposition rates than others. In general, tissue chemistry rather than structural traits controlled leaf and root decomposition rates. However, those traits that influenced decomposition rates were generally not those that varied between native and non-native species, whether or not phylogenetic autocorrelation was included in the analyses.

Traits that control decomposition rates of leaves and roots

We found that chemical properties of leaves (N, C, and WEE) and roots (C, WEE, and AIR) were correlated with leaf and root decomposition rates. It was surprising that AIR, primarily composed of lignin, had no effect on leaf decomposition rates as it is often associated with slower leaf and root k values (Melillo *et al.*, 1982; Cornwell *et al.*, 2008; Aulen *et al.*, 2012; Freschet *et al.*, 2012), which was also the case for root decomposition in this study. However, leaf decomposition rate may sometimes be more closely aligned with litter C and N concentrations than lignin (Taylor *et al.*, 1989). Furthermore, in our study, the variance of leaf AIR concentration was 27% less than that of root AIR concentration across species (Table 1), suggesting leaf AIR was relatively invariable across this particular species sample. We also note that, to our knowledge, no previous study has compared root decomposition between woody N-fixers and non-N-fixers. A higher root AIR concentration and a lower WEE for N-fixers compared to non-N-fixers may have reduced root decomposition rates for the N-fixers, which is consistent with the overall results that AIR and WEE were negatively and positively, respectively, associated with root decomposition among all species (Fig. 2). Overall, our findings support the prevailing idea that substrate chemistry is a major factor controlling leaf and root decomposition rates (Melillo & Aber, 1982; Taylor *et al.*, 1989; Silver & Miya 2001; Cornwell *et*

al., 2008; Aulen *et al.*, 2012; Freschet *et al.*, 2012).

In global scale analyses that include diverse plant functional groups, SLA is positively linked to leaf decomposition rate (Cornwell *et al.*, 2008; Pietsch *et al.*, 2014). SLA was not associated with leaf decomposition in the present study, suggesting that the relationship may not occur among species within a single group of plants (e.g. herbaceous, woody). For roots, SRL was negatively related to decomposition rate, although the effect size was relatively small compared to other chemical traits. Given that most of our study species are associated with arbuscular mycorrhizae (Brundrett *et al.*, 1990; Wang & Qiu, 2006; Akhmetzhanova *et al.*, 2012) and that thicker roots tend to have a greater association with arbuscular mycorrhizae (Kong *et al.*, 2014; Eissenstat *et al.*, 2015), lower SRL roots may contain more recalcitrant, mycorrhizal associated compounds (e.g. low concentration of soluble carbohydrates, high acid insoluble residue concentration) (Langley & Hungate, 2003; Sun *et al.*, 2013). The negative association between decomposition rate and SRL in our study suggests that factors other than mycorrhizal abundance drive root decomposition rates.

Leaf and root decomposition rates of native and non-native species

One of the most striking results of this study was that leaf and root decomposition rates did not differ between native and non-native species, which contrasts with the facilitating effects of invading species on forest litter decomposition that have been reported in other studies (Liao *et al.*, 2008; Castro-Díez *et al.*, 2014). For example, the litter decomposition rate of invasive species was 134% higher than co-occurring native species in forest ecosystems in a global meta-analysis (Liao *et al.*, 2008). The perception that invaders have high litter decomposition rates may stem from a bias to include invaders in decomposition studies that have noticeable impacts on ecosystems (Hulme *et al.*, 2013). In comparison, our study included most of the widespread

woody invaders of Eastern U.S forests (Fridley, 2008), but without bias as to their presumed ecosystem effects, and only examined differences on a mass basis, excluding potential differences in litter quantity or environmental differences between sites dominated by native or non-native species. We also included root tissue in our comparison.

It was counterintuitive that nativity did not influence leaf litter decomposition, when non-natives had higher leaf N, which was positively linked to decomposition among the study species (Fig. 1). We suggest that the positive leaf N impact of invaders on the leaf decomposition rate was diluted by the combined effect of other litter traits that influenced decomposition rate (Fig. 1). Nevertheless, three non-native species (*L. xylosteum*, *L. periclymenum*, and *R. cathartica*) had markedly higher leaf decomposition rates (Fig. 1). Two of those species, *L. xylosteum* and *R. cathartica*, are considered noxious weeds, which spread aggressively and have proven difficult to control in Eastern U.S. (USDA, 2015). This result suggests that the qualitative effects of decomposing litter of invasive species on nutrient cycling in Eastern U.S. forests are species-specific (Fig. 3).

Litter quality is one of several drivers of nutrient cycling in forests, and non-native species may influence this process in other ways. For example, non-native invaders may alter soil nutrient dynamics by changing soil microbial community composition and activity (Kourtev *et al.*, 2002; Hawkes *et al.*, 2005; Holly *et al.*, 2009). Further, considering the greater productivity rates of many invaders (Liao *et al.*, 2008; Castro-Díez *et al.*, 2013; Fridley & Craddock, 2015), non-natives are likely to impact ecosystem processes by increasing litter production. All else equal, similar litter quality but greater quantity may shift the balance toward greater rates of nutrient cycling in ecosystems dominated by fast growing invaders (Reich *et al.*, 1997).

Results from examining litter decomposition of 80 woody species contrast the growing perception that non-native species, in general, increase terrestrial processes by producing rapidly decomposing litter. We found that leaf decomposition rates were exceptionally high for three invasive shrub species. However, overall, there was no evidence that leaf or root litter decomposition rates differed between native and non-native woody species found in deciduous forests of Eastern North America. Consequently, the impact of woody invasives on litter decomposition in Eastern U.S. forests is species specific, and not generalizable.

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Table 1 Mean of initial litter traits and decomposition rates by nativity and Pagel's lambda (λ) with 95% credible interval (CI) as an estimator of phylogenetic signal in the litter traits and decomposition rates. A λ close to zero indicates a low phylogenetic signal in the trait, while a λ close to 1 implies a strong phylogenetic signal.

Traits		Units	Native		Non-native		λ (95% CI)
			Mean (SD)	N	Mean (SD)	N	
Leaf	N leaf	% _{mass}	0.902 (0.326)	42	1.10 (0.507)	36	0.418 (0.042, 0.813)
	C leaf	% _{mass}	47.0 (2.76)	42	46.3 (2.19)	36	0.344 (0.031, 0.734)
	AIR leaf	% _{mass}	15.0 (5.10)	42	15.3 (5.45)	36	0.454 (0.067, 0.818)
	WEE leaf	% _{mass}	49.9 (7.91)	42	50.8 (8.39)	36	0.386 (0.031, 0.766)
	SLA	cm ² g ⁻¹	138 (30.4)	42	118 (24.5)	36	0.156 (0.004, 0.459)
	k leaf	year ⁻¹	4.47 (2.92)	42	6.67 (9.21)	36	0.394 (0.034, 0.772)
Root	N root	% _{mass}	1.59 (0.604)	23	1.60 (0.803)	25	0.303 (0.012, 0.775)
	C root	% _{mass}	44.1 (1.42)	23	43.9 (2.08)	25	0.228 (0.007, 0.650)
	AIR root	% _{mass}	21.6 (6.31)	23	21.2 (6.04)	25	0.813 (0.494, 0.982)
	WEE root	% _{mass}	45.0 (7.21)	23	43.8 (6.31)	25	0.743 (0.336, 0.974)
	SRL	m g ⁻¹	32.8 (15.3)	23	40.5 (14.8)	25	0.240 (0.008, 0.662)
	RTD	g cm ⁻³	0.349 (0.101)	23	0.298 (0.081)	25	0.215 (0.009, 0.620)
	RDMC	mg g ⁻¹	265 (56.0)	23	239 (34.4)	25	0.174 (0.006, 0.525)
	k root	year ⁻¹	4.91 (2.32)	23	4.53 (1.37)	25	0.374 (0.020, 0.842)

N_{leaf}, mass-based leaf nitrogen concentration; C_{leaf}, mass-based leaf carbon concentration; AIR_{leaf}, mass-based leaf acid-insoluble residue concentration; WEE_{leaf}, mass-based leaf WEE (water and ethanol extractive) concentration; SLA, specific leaf area; k_{leaf}, leaf decomposition rate; N_{root}, mass-based root nitrogen concentration; C_{root}, mass-based root carbon concentration; AIR_{root}, mass-based root acid-insoluble residue concentration; WEE_{root}, mass-based root WEE (water and ethanol extractive) concentration; SRL, specific root length; RTD, root tissue density; RDMC, root dry matter content; k_{root}, root decomposition rate

Figure legends

Figure 1 Hypothesized relationships between nativity and leaf decomposition rate modeled by leaf litter traits (a) and estimated mean posterior parameter values without (gray) and with (black) phylogenetic autocorrelation for the relationships (β_1 - β_{11}) with 95% credible intervals of the parameters (b, c). See Table 1 for the phylogenetic signal (Pagel's λ) of each dependent variable for the relationships. N_{leaf} , mass-based leaf nitrogen concentration; C_{leaf} , mass-based leaf carbon concentration; AIR_{leaf} , mass-based leaf acid-insoluble residue concentration; WEE_{leaf} , mass-based leaf WEE (water and ethanol extractive) concentration; SLA, specific leaf area

Figure 2 Hypothesized relationships between nativity and root decomposition rate modeled by root traits (a) and estimated mean posterior parameter values without (gray) and with (black) phylogenetic autocorrelation for the relationships (β_1 - β_{15}) with 95% credible intervals of the parameters (b, c). See Table 1 for the phylogenetic signal (Pagel's λ) of each dependent variable for the relationships. N_{root} , mass-based root nitrogen concentration; C_{root} , mass-based root carbon concentration; AIR_{root} , mass-based root acid-insoluble residue concentration; WEE_{root} , mass-based root WEE (water and ethanol extractive) concentration; SRL, specific root length; RTD, root tissue density; RDMC, root dry matter content

Figure 3 Litter decomposition rates for leaf (a) and root (c) for native and non-native species. Natives are labeled blue and non-natives red. Non-native invasives are denoted with asterisks (*). Histograms show distributions of leaf and root decomposition rates for native and non-native species (b, d). Statistical significance for overall native vs. non-native comparisons were tested

with Wilcoxon's rank-sum test (b, d). NS, not significant.

Figure 1

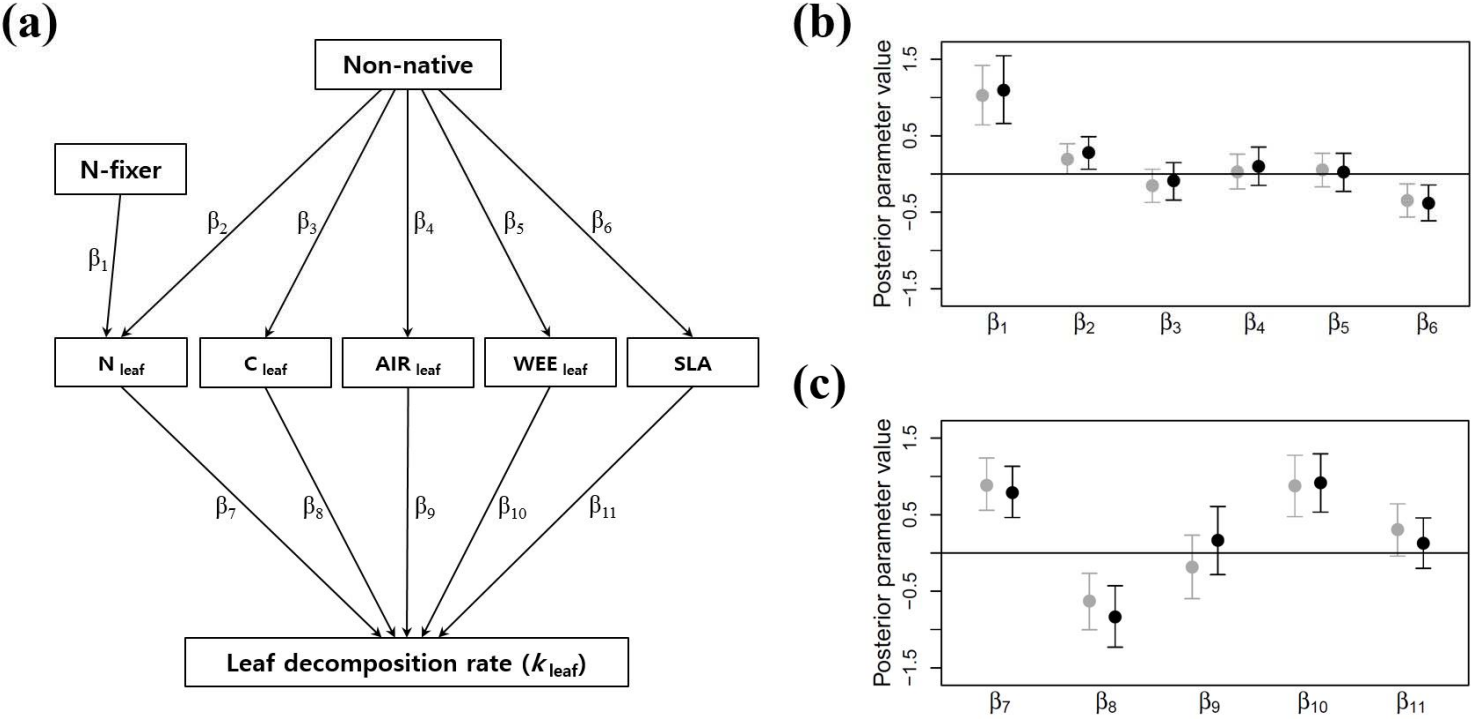
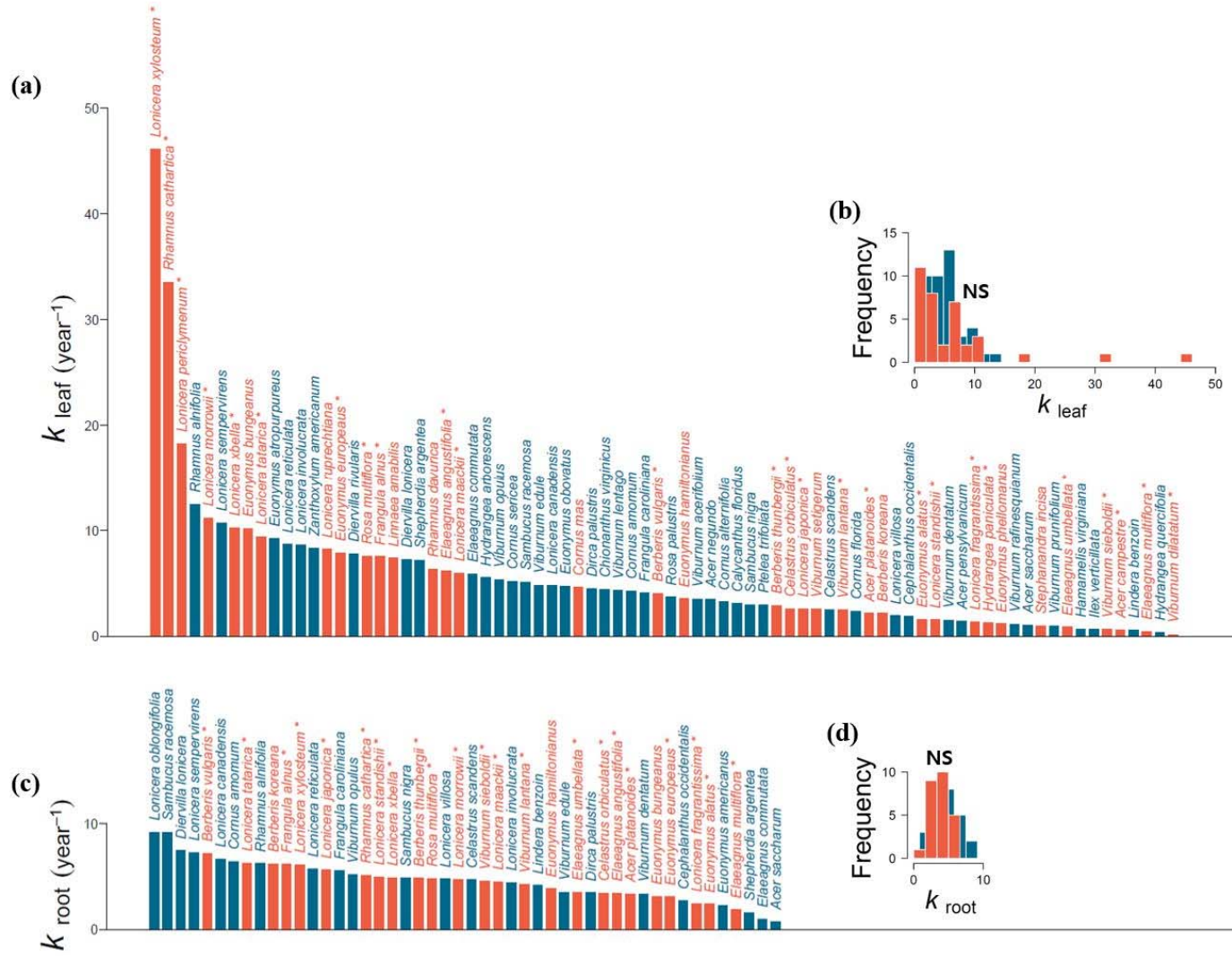
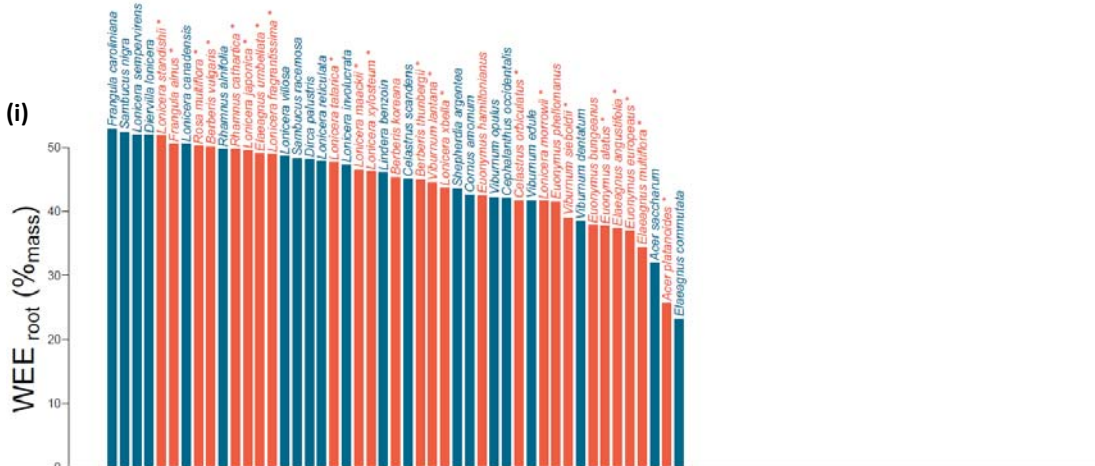
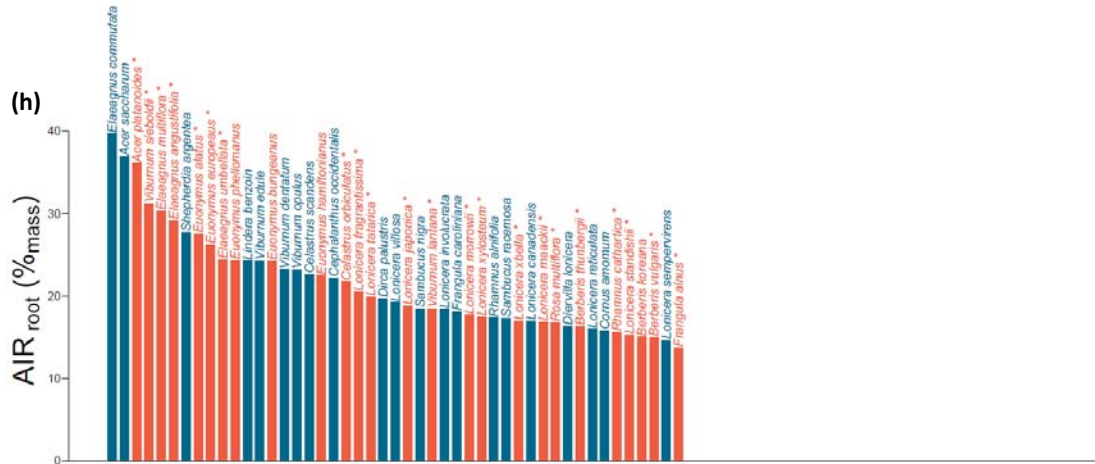
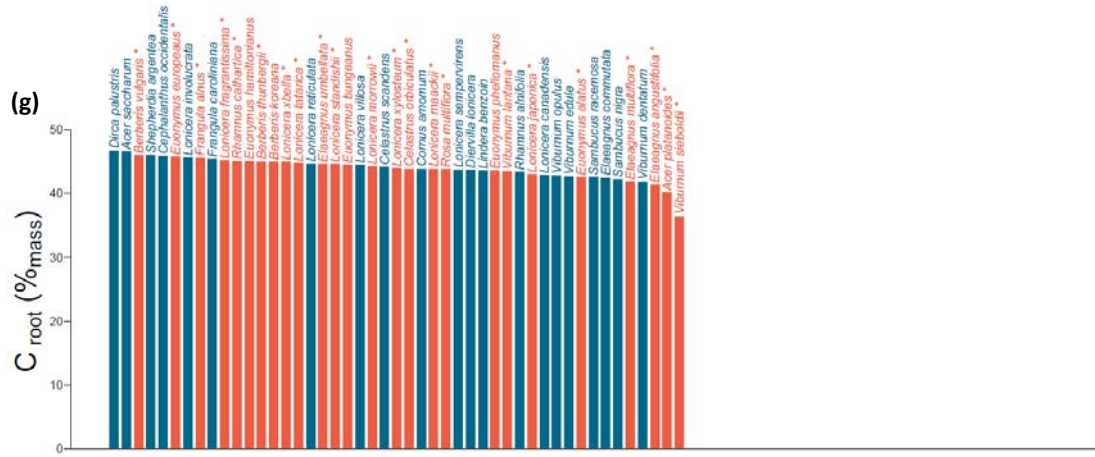


Figure 3





Species

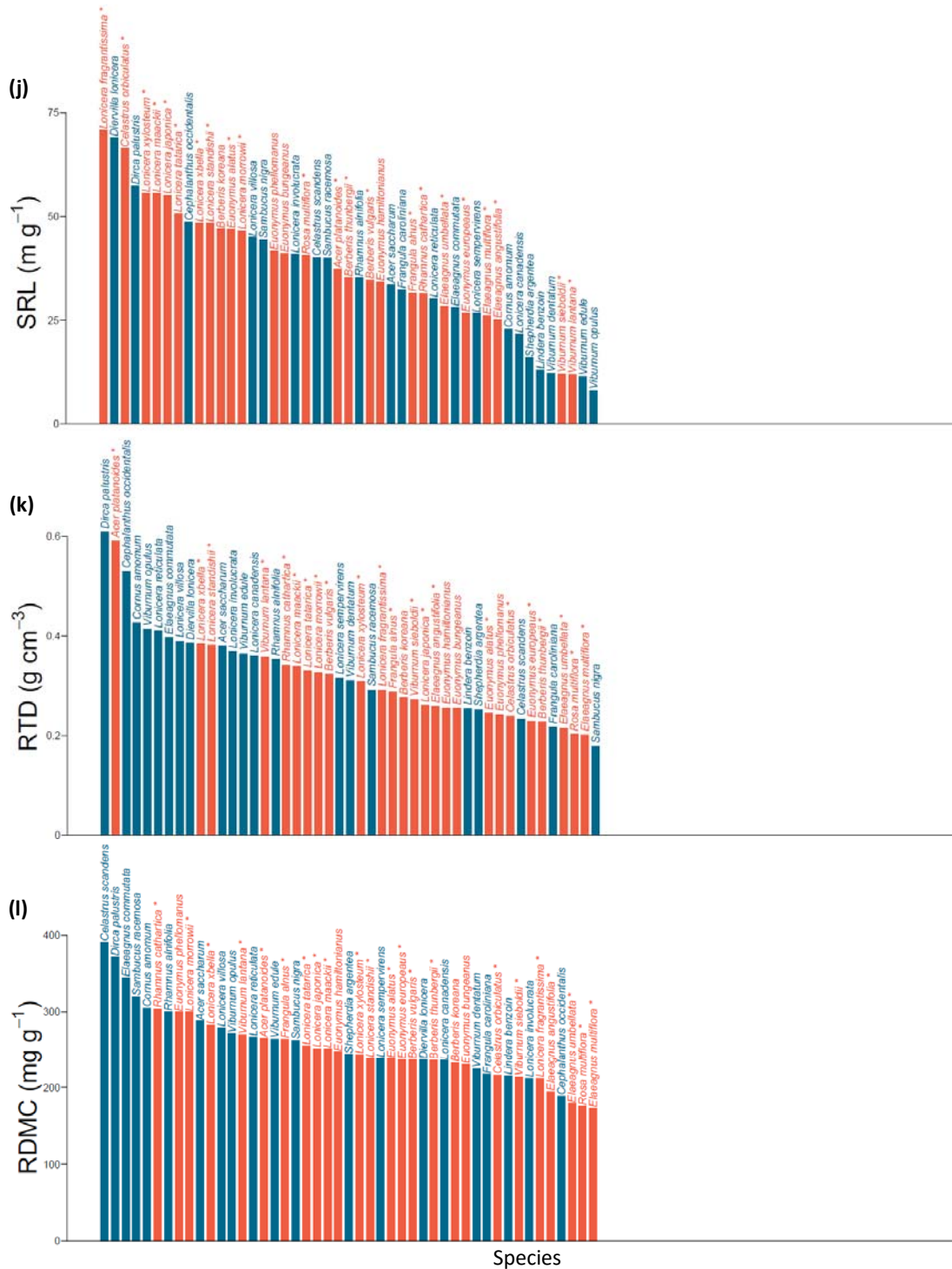


Fig. S2 Leaf and root traits for native and non-native species. Natives are labeled blue and non-natives red. Non-native invasives are denoted with asterisks (*). (a) N_{leaf}, (b) C_{leaf}, (c) AIR_{leaf}, (d) WEE_{leaf}, (e) SLA, (f) N_{root}, (g) C_{root}, (h) AIR_{root}, (i) WEE_{root}, (j) SRL, (k) RTD, and (l) RDMC.

Table S1 Summary of leaf and root trait data for each species.

General				Leaf Traits						Root Traits							
Family	Species	Growth Form	Eastern U.S. Nativity/Invasive Status	N_{leaf}	C_{leaf}	AIR_{leaf}	WEE_{leaf}	SLA	k_{leaf}	N_{root}	C_{root}	AIR_{root}	WEE_{root}	SRL	RTD	RDMC	k_{root}
Aquifoliaceae	<i>Ilex verticillata</i>	shrub/tree	Native	0.79	52.0	23.7	49.9	91	0.77								
Berberidaceae	<i>Berberis koreana</i>	shrub	Non-native	0.62	46.3	11.8	60.1	105	2.27	1.76	45.1	15.1	45.4	47.2	0.28	233	6.28
	<i>Berberis thunbergii</i>	shrub	Non-native invasive	0.50	46.0	8.6	63.8	109	3.03	2.15	45.1	16.4	45.1	35.5	0.23	237	4.96
	<i>Berberis vulgaris</i>	shrub	Non-native invasive	0.68	45.9	11.6	62.0	114	4.17	2.11	46.0	15.1	50.2	34.9	0.32	237	7.27
Caprifoliaceae	<i>Diervilla lonicera</i>	shrub	Native	0.56	46.9	13.5	51.7	163	7.35	1.42	43.8	16.4	52.0	69.2	0.39	237	7.55
	<i>Diervilla rivularis</i>	shrub	Native	0.61	48.7	17.2	55.9	121	7.89								
	<i>Linnaea amabilis</i>	shrub	Non-native	1.22	47.3	19.8	45.9	91	7.47								
	<i>Lonicera x bella</i>	shrub	Non-native invasive	1.31	47.9	16.2	56.9	121	10.32	1.15	45.0	17.1	43.8	48.6	0.39	283	4.98
	<i>Lonicera canadensis</i>	shrub	Native	1.21	46.4	16.7	46.3	160	4.88	1.18	43.0	17.1	50.6	21.9	0.36	236	6.76
	<i>Lonicera fragrantissima</i>	shrub	Non-native invasive	1.01	48.8	20.2	46.7	94	1.47	1.08	45.2	20.6	49.0	71.0	0.29	213	2.54
	<i>Lonicera involucrata</i> var. <i>involucrata</i>	shrub	Native	1.15	44.2	15.3	50.3	119	8.75	1.17	45.7	18.5	47.4	41.2	0.37	213	4.51
	<i>Lonicera japonica</i>	liana	Non-native invasive	1.01	45.3	23.3	45.1	133	2.70	0.89	43.0	18.9	49.6	55.3	0.26	253	5.73
	<i>Lonicera maackii</i>	shrub	Non-native invasive	0.99	46.0	15.9	50.6	135	6.06	1.01	43.9	16.9	46.5	55.8	0.34	252	4.61
	<i>Lonicera morrowii</i>	shrub	Non-native invasive	1.31	46.2	13.4	58.7	117	11.27	1.24	44.3	17.8	41.7	46.8	0.33	300	4.85
	<i>Lonicera oblongifolia</i>	shrub	Native							1.74	43.8	18.2	50.9	34.5	0.34	246	9.29
	<i>Lonicera periclymenum</i>	liana	Non-native invasive	1.07	45.6	11.1	56.9	160	18.35								
	<i>Lonicera reticulata</i>	shrub/liana	Native	0.69	44.1	10.0	54.4	125	8.77	1.12	44.7	16.1	47.9	30.5	0.41	267	5.85
	<i>Lonicera ruprechtiana</i>	shrub	Non-native	0.86	44.9	13.3	59.2	138	8.32								
	<i>Lonicera sempervirens</i>	liana	Native	0.86	45.1	9.7	53.0	150	10.78	0.86	43.8	14.8	52.1	26.8	0.32	239	7.37
	<i>Lonicera standishii</i>	shrub	Non-native invasive	0.96	47.8	12.8	44.0	101	1.66	1.08	44.7	15.3	51.9	48.6	0.38	240	5.07
	<i>Lonicera tatarica</i>	shrub	Non-native invasive	1.74	45.4	19.2	55.6	103	9.52	1.71	44.8	20.0	47.7	50.9	0.33	256	6.38
	<i>Lonicera villosa</i> var. <i>villosa</i>	shrub	Native	0.65	48.2	21.2	36.7	135	2.04	1.54	44.5	19.3	48.7	45.2	0.39	280	4.88
	<i>Lonicera xylosteum</i>	shrub	Non-native invasive	2.05	45.9	18.7	51.6	128	46.20	1.16	44.0	17.6	46.3	55.8	0.31	244	6.20
	<i>Sambucus nigra</i> spp. <i>canadensis</i>	shrub/tree	Native	1.45	47.1	21.3	49.3	138	3.10	1.70	42.3	18.5	52.5	44.6	0.18	263	4.96
<i>Sambucus racemosa</i>	shrub/tree	Native	1.03	47.9	18.1	45.6	152	5.21	2.02	42.6	17.4	48.4	40.2	0.29	321	9.27	
<i>Viburnum acerifolium</i>	subshrub/shrub	Native	0.84	50.2	18.5	53.7	138	3.64									
<i>Viburnum dentatum</i>	shrub/tree	Native	0.66	54.6	22.0	53.1	140	1.63	1.12	41.9	23.3	38.5	12.4	0.31	226	3.45	
<i>Viburnum dilatatum</i>	shrub	Non-native invasive	0.54	48.5	25.5	43.3	106	0.26									

Table S1 Continued.

Caprifoliaceae	<i>Viburnum edule</i>	shrub	Native	1.13	49.2	13.2	55.9	124	4.93	1.38	42.7	24.4	41.7	11.6	0.37	265	3.64
	<i>Viburnum lentana</i>	shrub/tree	Non-native invasive	1.04	48.3	14.2	55.4	70	2.60	0.89	43.5	18.5	44.5	12.1	0.36	270	4.33
	<i>Viburnum lentago</i>	shrub/tree	Native	0.84	48.2	11.3	52.7	107	4.41								
	<i>Viburnum opulus var. americana</i>	shrub/tree	Native	0.88	47.0	10.2	59.0	137	5.43	1.11	42.9	23.2	42.3	8.3	0.41	272	5.26
	<i>Viburnum prunifolium</i>	shrub/tree	Native	0.52	52.2	16.6	53.0	79	1.09								
	<i>Viburnum rafinesquianum</i>	shrub	Native	0.74	50.2	17.9	49.2	107	1.26								
	<i>Viburnum setigerum</i>	shrub	Non-native	0.79	51.5	18.9	52.2	95	2.68								
	<i>Viburnum sieboldii</i>	shrub/tree	Non-native invasive	1.31	47.3	23.1	46.3	71	0.76	1.30	36.5	31.3	39.1	12.2	0.27	215	4.65
Calycanthaceae	<i>Calycanthus floridus</i>	shrub	Native	0.65	46.6	15.2	50.6	151	3.19								
Celastraceae	<i>Celastrus orbiculatus</i>	liana	Non-native invasive	0.57	41.9	8.0	57.9	133	2.71	1.27	43.9	21.9	41.7	66.7	0.24	217	3.54
	<i>Celastrus scandens</i>	liana	Native	0.67	41.3	7.1	56.0	143	2.62	1.53	44.2	22.7	45.2	40.4	0.23	392	4.80
	<i>Euonymus alatus</i>	shrub	Non-native invasive	0.50	46.6	22.3	43.4	98	1.72	1.91	42.6	27.6	37.8	47.0	0.25	238	2.53
	<i>Euonymus americanus</i>	subshrub	Native							1.82	44.4	23.4	36.8	39.6	0.21	162	2.40
	<i>Euonymus atropurpureus</i>	shrub/tree	Native	0.94	45.9	12.2	50.5	135	9.33								
	<i>Euonymus bungeanus</i>	shrub/tree	Non-native	0.75	40.3	9.2	67.5	130	10.24	1.58	44.6	24.3	37.9	41.3	0.26	231	3.22
	<i>Euonymus europeus</i>	shrub/tree	Non-native invasive	0.75	44.5	11.3	58.2	117	7.95	1.54	45.8	26.3	37.0	26.9	0.23	238	3.21
	<i>Euonymus hamiltonianus sieboldianus</i>	shrub/tree	Non-native	0.71	44.5	6.8	41.5	106	3.67	1.58	45.2	22.6	42.6	34.5	0.26	248	3.96
	<i>Euonymus obovatus</i>	subshrub/shrub	Native	0.74	45.6	13.9	58.4	163	4.83								
	<i>Euonymus phellomanus</i>	shrub	Non-native	0.51	46.5	16.2	52.2	92	1.28								
	Cornaceae	<i>Cornus alternifolia</i>	tree/shrub	Native	0.48	47.7	8.3	67.9	107	3.36							
<i>Cornus amomum</i>		shrub	Native	1.47	50.8	16.5	55.6	98	4.39	1.22	43.9	15.9	42.7	23.1	0.43	305	6.52
<i>Cornus florida</i>		shrub/tree	Native	0.56	47.8	7.4	61.6	136	2.48								
<i>Cornus mas</i>		shrub/tree	Non-native	0.90	45.5	5.7	64.3	120	4.74								
<i>Cornus sericea</i>		shrub/tree	Native	0.84	46.4	8.9	59.9	149	5.31								
Elaeagnaceae	<i>Elaeagnus angustifolia</i>	shrub/tree	Non-native invasive	1.86	46.3	14.0	40.1	138	6.30	2.36	41.5	29.3	37.4	25.4	0.26	196	3.53
	<i>Elaeagnus commutata</i>	shrub	Native	1.36	44.9	12.1	45.9	144	5.96	2.95	42.6	39.8	23.3	28.3	0.40	345	1.10
	<i>Elaeagnus multiflora</i>	shrub	Non-native invasive	2.23	50.9	23.4	36.3	121	0.55	3.84	41.9	30.4	34.5	26.4	0.20	174	1.96
	<i>Elaeagnus umbellata</i>	shrub	Non-native invasive	2.03	48.1	8.9	38.8	115	1.00	3.94	44.7	24.5	49.2	28.7	0.22	180	3.64
	<i>Shepherdia argentea</i>	shrub	Native	1.72	46.6	14.8	45.1	122	7.26	3.38	46.0	27.8	43.6	16.2	0.25	245	1.72
Hamamelidaceae	<i>Hamamelis virginiana</i>	shrub/tree	Native	0.58	47.0	14.6	50.0	125	0.78								
Hydrangeaceae	<i>Hydrangea arborescens</i>	shrub	Native	1.30	44.9	12.1	54.3	138	5.65								
	<i>Hydrangea paniculata</i>	shrub	Non-native invasive	0.64	47.3	18.5	46.1	164	1.36								
	<i>Hydrangea quercifolia</i>	shrub	Native	0.46	46.2	22.5	39.3	129	0.48								
Lauraceae	<i>Lindera benzoin</i>	shrub/tree	Native	0.85	50.7	19.1	44.1	176	0.70	2.22	43.6	24.4	46.2	13.2	0.26	216	4.26

Table S1 Continued.

Oleaceae	<i>Chionanthus virginicus</i>	shrub/tree	Native	0.59	46.6	12.5	52.3	181	4.53								
Rhamnaceae	<i>Frangula alnus</i>	shrub/tree	Non-native invasive	0.98	46.1	6.0	47.4	171	7.63	0.99	45.6	13.9	50.7	31.8	0.29	265	6.24
	<i>Frangula caroliniana</i>	shrub/tree	Native	0.80	46.6	16.5	45.7	132	4.20	1.76	45.5	18.2	53.0	32.5	0.22	218	5.63
	<i>Rhamnus alnifolia</i>	shrub	Native	1.41	43.2	12.5	47.9	133	12.57	1.49	43.4	17.4	49.9	35.4	0.36	301	6.33
	<i>Rhamnus cathartica</i>	shrub/tree	Non-native invasive	2.14	43.6	19.3	53.8	113	33.62	0.99	45.2	15.7	49.8	31.6	0.34	305	5.22
	<i>Rhamnus davurica</i>	shrub/tree	Non-native	1.11	42.4	11.4	59.1	104	6.43								
Rosaceae	<i>Rosa multiflora</i>	subshrub/liana	Non-native invasive	1.91	45.2	18.8	41.6	92	7.67	1.04	43.9	16.8	50.3	40.8	0.20	177	4.91
	<i>Rosa palustris</i>	subshrub	Native	0.68	46.7	9.2	48.4	100	3.81								
	<i>Stephanandra incisa</i>	shrub	Non-native	0.86	47.3	22.7	39.9	158	1.10								
Rubiaceae	<i>Cephalanthus occidentalis</i>	shrub/tree	Native	1.03	47.8	23.9	39.0	260	1.96	1.20	45.9	22.3	42.1	48.9	0.53	189	2.83
Rutaceae	<i>Ptelea trifoliata</i>	shrub/tree	Native	0.89	44.8	8.2	57.8	134	3.09								
	<i>Zanthoxylum americanum</i>	shrub/tree	Native	1.30	44.7	15.9	55.4	122	8.43								
Sapindaceae	<i>Acer campestre</i>	shrub/tree	Non-native invasive	0.86	47.2	14.8	46.5	146	0.71								
	<i>Acer negundo</i>	shrub/tree	Native	1.47	43.7	19.2	32.7	191	3.63								
	<i>Acer pensylvanicum</i>	shrub/tree	Native	0.59	47.6	25.1	31.8	143	1.54								
	<i>Acer platanoides</i>	shrub/tree	Non-native invasive	1.21	46.3	14.6	39.8	145	2.27	1.52	40.2	36.2	25.7	37.4	0.59	266	3.48
	<i>Acer saccharum</i>	shrub/tree	Native	1.23	47.6	20.7	44.5	157	1.20	1.59	46.6	37.0	32.1	33.8	0.38	289	0.88
Thymelaeaceae	<i>Dirca palustris</i>	shrub	Native	0.68	40.8	5.3	31.8	164	4.60	1.00	46.8	19.8	48.3	57.6	0.61	372	3.58

Growth Form from USDA PLANTS; Eastern U.S. Nativity/Invasive Status from Fridley (2008); N_{leaf} , mass-based leaf nitrogen concentration (%); C_{leaf} , mass-based leaf carbon concentration (%); AIR_{leaf} , mass-based leaf acid-insoluble residue concentration (%); WEE_{leaf} , mass-based leaf WEE (water and ethanol extractive) concentration (%); SLA, specific leaf area ($\text{cm}^2 \text{g}^{-1}$); k_{leaf} , leaf decomposition rate derived from a single exponential model (year^{-1}); N_{root} , mass-based root nitrogen concentration (%); C_{root} , mass-based root carbon concentration (%); AIR_{root} , mass-based root acid-insoluble residue concentration (%); WEE_{root} , mass-based root WEE (water and ethanol extractive) concentration (%); SRL, specific root length (m g^{-1}); RTD, root tissue density (g cm^{-3}); RDMC, root dry matter content (mg g^{-1}); k_{root} , root decomposition rate derived from a single exponential model (year^{-1})

Table S2 Regression models used in the hierarchical model.

Leaf decomposition model (Fig. 1)	
Dependent variables	Regression components
$N_{leaf\ i} \sim N(\mu_{N\ leaf\ i}, \sigma^2_{N\ leaf}, \Sigma)$	$\mu_{N\ leaf\ i} = \alpha_1 + \beta_1 \times N\text{-fixer}_i + \beta_2 \times non\text{-native}_i$
$C_{leaf\ i} \sim N(\mu_{C\ leaf\ i}, \sigma^2_{C\ leaf}, \Sigma)$	$\mu_{C\ leaf\ i} = \alpha_2 + \beta_3 \times non\text{-native}_i$
$AIR_{leaf\ i} \sim N(\mu_{AIR\ leaf\ i}, \sigma^2_{AIR\ leaf}, \Sigma)$	$\mu_{AIR\ leaf\ i} = \alpha_3 + \beta_4 \times non\text{-native}_i$
$WEE_{leaf\ i} \sim N(\mu_{WEE\ leaf\ i}, \sigma^2_{WEE\ leaf}, \Sigma)$	$\mu_{WEE\ leaf\ i} = \alpha_4 + \beta_5 \times non\text{-native}_i$
$SLA_{leaf\ i} \sim N(\mu_{SLA\ leaf\ i}, \sigma^2_{SLA\ leaf}, \Sigma)$	$\mu_{SLA\ leaf\ i} = \alpha_5 + \beta_6 \times non\text{-native}_i$
$k_{leaf\ i} \sim N(\mu_{k\ leaf\ i}, \sigma^2_{k\ leaf}, \Sigma)$	$\mu_{k\ leaf\ i} = \alpha_6 + \beta_7 \times N_{leaf\ i} + \beta_8 \times C_{leaf\ i} + \beta_9 \times AIR_{leaf\ i} + \beta_{10} \times WEE_{leaf\ i} + \beta_{11} \times SLA_{leaf\ i}$
Root decomposition model (Fig. 2)	
Dependent variables	Regression components
$N_{root\ i} \sim N(\mu_{N\ root\ i}, \sigma^2_{N\ root}, \Sigma)$	$\mu_{N\ root\ i} = \alpha_1 + \beta_1 \times N\text{-fixer}_i + \beta_2 \times non\text{-native}_i$
$C_{root\ i} \sim N(\mu_{C\ root\ i}, \sigma^2_{C\ root}, \Sigma)$	$\mu_{C\ root\ i} = \alpha_2 + \beta_3 \times non\text{-native}_i$
$AIR_{root\ i} \sim N(\mu_{AIR\ root\ i}, \sigma^2_{AIR\ root}, \Sigma)$	$\mu_{AIR\ root\ i} = \alpha_3 + \beta_4 \times non\text{-native}_i$
$WEE_{root\ i} \sim N(\mu_{WEE\ root\ i}, \sigma^2_{WEE\ root}, \Sigma)$	$\mu_{WEE\ root\ i} = \alpha_4 + \beta_5 \times non\text{-native}_i$
$SRL_{root\ i} \sim N(\mu_{SRL\ root\ i}, \sigma^2_{SRL\ root}, \Sigma)$	$\mu_{SRL\ root\ i} = \alpha_5 + \beta_6 \times non\text{-native}_i$
$RTD_{root\ i} \sim N(\mu_{RTD\ root\ i}, \sigma^2_{RTD\ root}, \Sigma)$	$\mu_{RTD\ root\ i} = \alpha_6 + \beta_7 \times non\text{-native}_i$
$RDMC_{root\ i} \sim N(\mu_{RDMC\ root\ i}, \sigma^2_{RDMC\ root}, \Sigma)$	$\mu_{RDMC\ root\ i} = \alpha_7 + \beta_8 \times non\text{-native}_i$
$k_{root\ i} \sim N(\mu_{k\ root\ i}, \sigma^2_{k\ root}, \Sigma)$	$\mu_{k\ root\ i} = \alpha_8 + \beta_9 \times N_{root\ i} + \beta_{10} \times C_{root\ i} + \beta_{11} \times AIR_{root\ i} + \beta_{12} \times WEE_{root\ i} + \beta_{13} \times SRL_{root\ i} + \beta_{14} \times RTD_{root\ i} + \beta_{15} \times RDMC_{root\ i}$

N , normal distribution; μ , mean; σ^2 , variance; and Σ , correlation structure based on shared branch lengths in the phylogeny (de

Villemereuil *et al.*, 2012); α , intercept; β , slope

CHAPTER 4

Impacts of invasive plants on soil N dynamics: a monoculture comparison of Eastern U.S. forest species

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Abstract

Although it is widely believed that non-native invasive species pose a major threat to the integrity of forest ecosystems, their impact on ecosystem processes like N cycling is not well understood, particularly for woody invaders. To examine how different plant traits of native and invasive species mediate soil N cycling, we established monocultures of five native and five invasive understory woody species common to Eastern U.S. forests. We found that invaders promoted soil N processes by having greater above- and belowground productivity than natives. Invaders facilitated N cycling through greater litter N input into the soil that increased soil N availability, and exhibited greater fine root production and SRL that increased plant N uptake. The greater aboveground production of invaders reduced soil temperature and moisture, which can reduce soil microbial activity. However, the stimulatory effects of a greater flow of plant litter to the soil appeared to overwhelm any negative effects that invaders had on soil microclimate. Although N cycling is likely more complex in natural forest ecosystems than in our experimental monocultures, the rapid changes in soil N processes observed in our system within relatively short period of time suggest that invaders may be one of the major drivers of forest ecosystem functioning.

Key words: plant invasions, plant-soil feedback, inorganic nitrogen pool, monoculture experiment, nitrogen cycling, understory woody species, Eastern United States

Introduction

Plant-driven changes in soil nitrogen (N) cycling influence plant performance, species composition, and ecosystem function (Vitousek et al. 1987; Wedin and Tilman 1990; Craine et al. 2002). Plants alter soil N cycling in several ways. They add N to the soil primarily as leaf and root litter and take it up after microbes transform N into forms that can be absorbed (Binkley and Hart 1989; Chapin et al. 2011). Patterns of this plant-soil feedback vary among species (Wedin and Tilman 1990; Bezemer et al. 2006). For example, fast-growing species with a resource acquisitive strategy (e.g. high leaf N and low leaf toughness) promote nutrient cycling, while slow-growing species with a retentive strategy (e.g., low leaf N, high leaf toughness) reduce nutrient cycling (Chapin 1980; Orwin et al. 2010; Reich 2014). Such findings indicate that plant traits can drive ecosystem functioning.

The expansion of non-native, invading species poses a major threat to the integrity of North American ecosystems (Howard *et al.*, 2004; Fridley, 2008), but their impact on specific ecosystem processes like N cycling is not well understood. Invaders tend to be relatively fast growing species with associated traits (e.g. rapid growth, high leaf N) that are expected to accelerate plant-soil N cycling (Liao et al. 2008; van Kleunen et al. 2010; Vilà et al. 2011). However, it remains unclear whether invasives affect soil N processes and how traits of invasives may be mechanistically linked to soil N dynamics.

A major impediment to understanding the impact of invaders on soil nutrient dynamics is that no study has unambiguously examined the impact of invading species on soil processes. Previous investigations conducted under field conditions have been confounded by varying initial soil conditions and the influence of coexisting species on soil processes (MacDougall and Turkington 2005; Stricker et al. 2015). In this study, we conducted a monoculture experiment in

a common garden, which isolated the effects of species on the soil system (Wedin and Tilman 1990; Craine et al. 2002; Eviner 2004) to examine how understory woody invaders influence plant-soil N dynamics in the Eastern U.S. forests.

Invading shrub species of Eastern U.S. forests have higher leaf production, leaf N concentration, and produce more roots that on average are finer (i.e., greater specific root length, SRL) than native shrubs (Heberling and Fridley 2013; Fridley and Craddock 2015; Jo et al. 2015a). Greater production of litter that is potentially of greater quality coupled with greater growth of fine roots should facilitate both the mineralization rate and root uptake of soil N. However, the concomitant effects of greater leaf area on soil temperature (via greater shading) and moisture (via increased evapotranspiration) may also impact soil N cycling. Presently it remains unclear how shifts in plant traits and soil microclimate from invader dominance may interact to influence soil N dynamics.

Here, we conducted a two-year monoculture experiment in an experimental garden that included five native and five congener invasive understory woody species of temperate deciduous forests in the Eastern U.S. to develop a mechanistic understanding of how plants in general and invasive shrubs and lianas, in particular, influence plant-soil N cycling. We hypothesized that invaders facilitate N cycling by increasing the rate of N mineralization and plant N uptake. We tested the hypothesis using a Bayesian hierarchical regression model that incorporated various components that affect soil N availability and plant N uptake, measured during the monoculture experiment, and several plant traits available from previous studies.

Methods

Study species and experimental design

Species effects on soil processes for native and invasive non-native species were studied in monoculture plots in Syracuse, New York, USA (43°03'N, 76°09'W). The experiment included five native species (*Celastrus scandens*, *Frangula caroliniana*, *Lonicera canadensis*, *L. sempervirens*, and *L. villosa*) and five congener invasive species (*C. orbiculatus*, *F. alnus*, *L. fragrantissima*, *L. japonica*, and *L. morrowii*). Pairs of native and invasive congeneric species helped control for phylogenetic effects. In 2011, plants were propagated in a greenhouse using cuttings of individuals that were established in 2006–2007 in an adjacent experimental garden (Fridley 2012), with the exception that whole individuals of *L. canadensis* were transplanted from a nearby field location. The size of the sampled *L. canadensis* plants was comparable to that of the propagated plants.

In spring 2012, we established three blocks with 11 monoculture plots (2.5 x 2.5 m²) in each block, including three bare (control) plots. A 50 cm deep trench was dug around each plot and lined with a plastic sheet to prevent roots invading from outside the plot. In each plot, 3 conspecific individuals were planted. The surface of each plot was covered with a shade cloth and watered daily during the first growing season in 2012 to prevent summer moisture stress and prevent weed growth. The shade cloth was removed in spring 2013 to allow for above-ground plant-soil feedbacks to occur. Weeds in the plots were removed weekly during the growing season.

Plant production and N pool

In April 2015, before bud break, we harvested aboveground biomass in each plot. Total fresh biomass was measured. Total dry biomass was derived using the fresh : dry biomass ratio determined on stem and branch subsamples for each species. To estimate leaf litter production, the number of leaves produced and average mass per leaf were determined for each plot. We

counted number of leaf scars on the subsampled branches for each species and determined leaf number per unit branch biomass. Average leaf mass for each species was measured from the leaves (> 100 leaves) collected from the parent plants of the cuttings at the adjacent experimental garden in October 2013. Total leaf production (kg plot^{-1}) was determined by multiplying the average leaf mass, the leaf number per unit branch biomass, and the total branch biomass.

In September 2013, nine soil cores (4 cm diameter \times 10 cm height) were collected at random locations in each plot to determine standing root biomass. Roots were picked right after collecting each core and were kept in an icebox until moved to the laboratory. All other organic debris was removed from the soil before it was used to fill the ingrowth core. We sampled 3 additional cores at random locations in 4 plots where no roots were found in the 9 cores. At each of the nine (or 12) locations where a soil core was removed, we installed a point-in-space ingrowth core (Milchunas et al. 2005), which allowed for sequential root sampling from the same locations. Ingrowth cores (4 cm diameter \times 10 cm height) were constructed with plastic (1 \times 1 cm) mesh. Each ingrowth core was filled with root-free soil collected from the extracted soil core. Ingrowth cores were sampled every 2 months, May to November, 2014. Roots were picked in the site immediately after each ingrowth core was pulled from the soil, and the ingrowth cores were refilled with the soil after all roots were picked. The picked roots were pooled by plot and kept frozen until processed. In the laboratory, the picked roots were cleaned using deionized water and separated into fine (1 to 3 order) and coarse roots with secondary growth. Roots were dried at 65 °C for > 2 days before being weighed. Plot 0-10 cm root production during a sampling period was determined by multiplying mean root production among cores in a plot and the plot to core area ratio and 12-month root production was derived by summing root production from September 2013 to September 2014. Total root biomass in 0-10 cm soil per plot

was estimated by summing standing root biomass in September 2013 and root production across all sampling periods for ingrowth cores.

We determined the plant N pool to estimate plant N uptake during the experiment by multiplying tissue N concentrations for leaf litter, branch, stem, coarse root, and fine root with corresponding tissue biomass measured. N concentrations of branch and stem for each species was measured from the subsamples taken from the final harvest. Roots for N analysis were sampled using soil cores (4 cm diameter and 10 cm deep) in November 2014. We collected 3 cores 15 cm from the main stem of each plant, total 9 cores per each plot. We separated fine and coarse roots as described above. All of the dried plant tissue samples were ground and N concentrations on a mass basis (%) for each species were measured using a CN elemental analyzer (NC2100 Soil, CE Instruments).

Soil inorganic N pool and microclimate

Soil inorganic N pool size during the growing season for each plot was measured using Plant Root Simulator (PRS) probes (Western Ag Innovations) in 2014. PRS probes adsorb mineralized N (NO_3^- -N and NH_4^+ -N) onto their surface membrane and provide a time-integrated measure of soil solution inorganic N concentration during the sampling interval (PRS probe N). Consequently, PRS probe N is a function of the difference between inorganic N production by microbial activity and inorganic N uptake by plant roots. PRS probe N was measured during two intervals, May to June and July to August, 2014. Four pairs of anion and cation exchange resin membrane ($1 \times 10 \text{ cm}^2$) probes were inserted 10 cm deep in the soil in each plot. After each incubation, probes were collected, rinsed with deionized water, and shipped to Western Ag Innovations (Saskatchewan, Canada) for analysis. The average values of the two measurements were used as an estimate of soil inorganic N pool during the growing season. To determine how

plants affect soil microclimate, soil moisture content (%) and temperature (°C) in 0-10 cm soil were measured in each plot, using time domain reflectometry (HydroSense Soil Water Measurement System, Campbell Scientific) and a soil thermometer (Rapitest Digital Soil Thermometer, Luster Leaf Products), five times three days after five major rainfall events June to November 2014 We took four measurements in each plot. Analyses were performed on plot-averaged values.

Statistical analyses

We tested a model (Fig. 1) of the effects of invaders on plant-soil N processes using a hierarchical Bayesian approach. Our model included 13 sub-models to examine the independent effects of plant traits and soil microclimate on soil inorganic N pool, and, simultaneously, whether those factors are influenced by invader-induced changes in plant functional traits. Fourteen variables were incorporated in the model, including one categorical variable, species invasiveness (non-native invasive=1, native=0). Plant functional traits included in the model (Fig. 1, traits in shaded boxes) were collected from previous studies performed by our research group. We used leaf and litter N concentration ($[N]_{\text{leaf}}$ and $[N]_{\text{litter}}$) and leaf N resorption rate (%) from Jo et al. (2015a), and leaf and root decomposition rates (k_{root} and k_{leaf}) and specific root length (m g^{-1} , SRL) from Jo et al. (2015b). A block intercept was included in the sub-model for soil inorganic N pool, and a genus intercept was added in invasiveness predictor sub-models, as random effects to account for correlated variation in measurements contributed by block design and shared phylogeny. Except for the categorical variable, all other continuous variables were standardized by subtracting their mean and dividing by two standard deviations to enable effect size comparisons (Gelman and Hill 2006). The posterior values for the regression coefficients (β s) were estimated to determine the relative effects of parameters on the dependent variable in a

Bayesian framework fit by Markov chain Monte Carlo (MCMC) optimization using JAGS in R 3.12 (Plummer 2003; R Development Core Team 2014). We used non-informative priors for all β regression coefficients (mean=0, variance=1000) in the model (Fig. 1). To ensure convergence, we ran three parallel MCMC chains in JAGS for 100,000 iterations after a 5000-iteration burn-in. Simple invader-native differences were addressed via the Wilcoxon rank sum test.

Results

The soil inorganic N pool was marginally greater (Fig. 2c, $P = 0.07$) in plots of native compared to invasive species. Invaders had greater $[N]_{\text{litter}}$ and leaf production rates that were positively associated with the litter N pool (Fig. 1&3, β_{3-5} & 8-11). Litter N pool, in turn, was positively correlated with the soil inorganic N pool (Fig. 1&3, β_{18}). Invaders had greater $[N]_{\text{leaf}}$ (Fig. 3, $P(\beta_3 > 0) = 0.89$) and a lower leaf N resorption rate (Fig. 1&3, β_4) than native species, which led to a greater $[N]_{\text{litter}}$ (Fig. 1&3, β_{8-9}). Invaders had greater leaf and fine root production (Fig. 1&3, β_5 , $P(\beta_6 > 0) = 0.94$; Fig. 2a). Together, $[N]_{\text{litter}}$ and leaf production increased the litter N pool significantly (Fig. 1&3, $P(\beta_{10} > 0) = 0.88$, β_{11}). The effect size of $[N]_{\text{litter}}$ on soil N pool was relatively small compared to that of leaf production (Fig. 1&3, β_{10-11}). Leaf decomposition rates did not differ between invaders and natives (Fig. 1&3, β_1), but invaders had lower root decomposition rates than natives (Fig. 1&3, $P(\beta_2 < 0) = 0.90$). Both leaf and root decomposition rates did not affect the soil inorganic N pool (Fig. 1&3, β_{16-17}).

Invader-driven changes in leaf and fine root production and SRL affected the soil inorganic N pool negatively (Fig. 1&3, β_{19-21}) by way of reducing soil temperature and moisture content and increasing plant N uptake (Fig. 1&3, β_{12-15} ; Fig. 2b). Leaf production was negatively associated with soil temperature (Fig. 1&3, β_{12}) and soil moisture content (Fig. 1&3, $P(\beta_{13} < 0) =$

0.87). Both fine root production and SRL were positively associated with plant N uptake (Fig. 1&3, β_{14} , $P(\beta_{15}>0) = ,0.84$). The soil inorganic N pool was positively correlated with soil temperature (Fig. 1&3, β_{19}) and soil moisture content (Fig. 1&3, β_{20}), and negatively affected by plant N uptake (Fig. 1&3, β_{21}). The mean effect size of N uptake on the soil inorganic N pool was greater than that of soil temperature and moisture content (Fig. 1&3, β_{19-21}).

Discussion

Results of our 2-year monoculture experiment using five native and five invasive forest understory woody species in the Eastern U.S. support our hypothesis that invaders facilitate N cycling by increasing soil N availability and plant N uptake. We found that invaders' increased aboveground production resulted in greater litter biomass and N input to the soil as a substrate for soil microbes. Greater belowground production of fine roots with high SRL increased the capacity for invaders to take up soil N that was mineralized at accelerated rates compared to those rates in soil with natives. Litter decomposition rate on a mass basis had no effect on soil N availability and the inhibitory influence of aboveground production on soil microclimate was overwhelmed by the facilitating effects of greater invasive litter production on soil N availability.

Invaders often produce greater quality and quantity of litter compared to co-occurring natives, and are hypothesized to facilitate a positive plant-soil feedback (Liao et al. 2008; Castro-Díez et al. 2014). We found previously that greater leaf N concentration and a lower leaf N resorption rate led to a greater litter N concentration in Eastern U.S. forests invaders (Jo et. al. 2015a). Together with a greater leaf production of invaders that we found in this study, we showed that invaders enhance N flux into the soil where it is taken up by the plants, increasing plant-soil feedbacks. It is not surprising that leaf and root decomposition rates had no impact on

soil N availability, given that decomposition values from a previous large study found that leaf and root decomposition rates did not differ between invasive and native understory woody species (Jo et al. 2015b). There has been considerable interest in comparing litter decomposition rates between native and invasive species because of, presumably, a close link between the decomposition rate and soil N availability (Scott and Binkley 1997; Allison and Vitousek 2004; Ashton et al. 2005). But results of this and the previous study suggest that the quantity of litter (substrate) may be the major driver of soil N mineralization. These effects were measured during the two year period after plants were established in the monoculture plots. Considering a greater productivity of invaders compared to the natives, we expect that invader effects will strengthen with time.

The soil inorganic N pool size we measured is a function of mineral N production and plant N uptake. The soil N pool was weakly smaller for plots with invasives, the group that stimulated N mineralization the most through a greater litter N input to the soil, because of the simultaneous greater capacity to take up the available N with a greater production of finer roots than natives. Although no comparative studies exist on woody invaders, Windham and Ehrenfeld (2003) found that greater N mineralization and uptake of a common reed (*Phragmites australis*) counterbalanced its impacts on soil N pool, which suggests rapid N cycling after *P. australis* invasions. Increased N mobility through rapid N cycling may cause increasing N loss from leaching. However, given no difference found in rhizosphere soil N concentration between native and invasive plots after two growing seasons (data not shown), greater plant-induced N mineralization rates may not necessarily result in increased leaching under invasive shrubs and lianas in our study.

We note that invaders could alter soil microclimate that can affect soil N processes in our study system, despite the relatively short study period. Soil moisture and temperature are important components regulating microbial activity (Binkley and Hart 1989; Knoepp and Swank 2002; Chapin et al. 2011). Although we didn't measure soil microbial activity directly, the positive association between soil temperature and moisture contents and soil inorganic N pool in this study suggests that soil microclimate affected microbial activities associated with soil N mineralization. In this study, we showed that plant leaf and root production were negatively related to soil temperature and moisture contents, likely due to evapotranspiration and shade from the leaf canopy and root water uptake. Invaders had significant inhibitory effects on soil microclimate due to their greater leaf and root production; however, the stimulatory effects of a greater flow of plant litter (substrate) to the soil appeared to overwhelm any negative effects.

Our results partially support the view that plant functional traits influence ecosystem function (Lavorel and Garnier 2002; De Deyn et al. 2008; Reich 2014). For example, we showed that leaf N and leaf N resorption rate were positively and negatively, respectively, related to litter N concentration and total litter N pool, both of which are linked to soil N availability. In addition, greater SRL was associated with greater N uptake that reduced the soil inorganic N pool. However, tissue traits were not necessarily linked to N processes (e.g. litter decomposition rates) and leaf and root production were more directly associated with the litter N pool and plant N uptake that are closely related to soil N processes. It is thus likely that the relationship between functional traits and ecosystem function is more complex than previously thought.

Despite our finding that invaders had large impacts on soil N dynamics in an open-field monoculture study, whether the similar mechanisms can explain invader impacts on soil N processes in forest ecosystems remains an open question. It should be noted that the impacts of

invasive shrubs that we measured in an open field may differ than those occurring under a forest canopy. Under the forest canopy, limited plant growth by shade and canopy tree roots and litter input will have different consequences on invader litter production, soil microclimate, and plant N uptake than we have observed in our experiment, potentially reducing the plant-soil feedback rate (Breshears et al. 1998; Reich et al. 1998; Ellsworth et al. 2004). We also note that we have not examined mycorrhizal associations and the deep soil N concentration (below 10 cm) which might affect soil N cycling. Nevertheless, our results merit further experimental investigation in situ, given our poor understanding of invader impacts on soil N processes for understory woody species.

In summary, our results suggest that invasive shrubs and lianas of Eastern U.S. forests accelerate soil N cycling by promoting both N mineralization and uptake. We found that invaders increased soil N availability by producing more litter biomass with greater N concentration, and decreased the soil N pool through a greater plant N uptake, with smaller but significant impacts on soil temperature and moisture-mediated microbial activity. Although multiple plant and soil properties drive soil N cycling, we demonstrated that a common garden, monoculture approach is able to quantify direct and indirect impacts of invasive species on ecosystem processes.

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Figure Legends

Figure 1. Hypothesized relationships between the soil inorganic N pool and potential invasive species-induced changes in plant and soil attributes. Beta (β) coefficients represent posterior parameter values estimated in Fig. 3. Asterisks on β coefficient indicate > 90% of posterior values are greater than/less than zero. Arrow thickness is proportional to the mean posterior value. A black arrow represents a positive mean posterior value and a gray represents negative. Variables in shaded boxes are from other studies (Jo et al. 2015; Jo et al. in review).

Figure 2. Biomass (a), plant N pool (b), and soil inorganic N pool (c) for 5 native and 5 non-native species examined in the monoculture experiment. Statistical significance for overall native vs. non-native invasive comparisons were tested with Wilcoxon's rank-sum test. NS, not significant; *, $P < 0.5$; **, $P < 0.01$. Root biomass and N pools were estimated for 0-10 cm soil.

Figure 3. Estimated posterior parameter values for the relationships in Fig. 1. The circles represent means and the lines represent 95% (thin lines) and 90% (thick lines) credible intervals of the parameters.

Figure 1

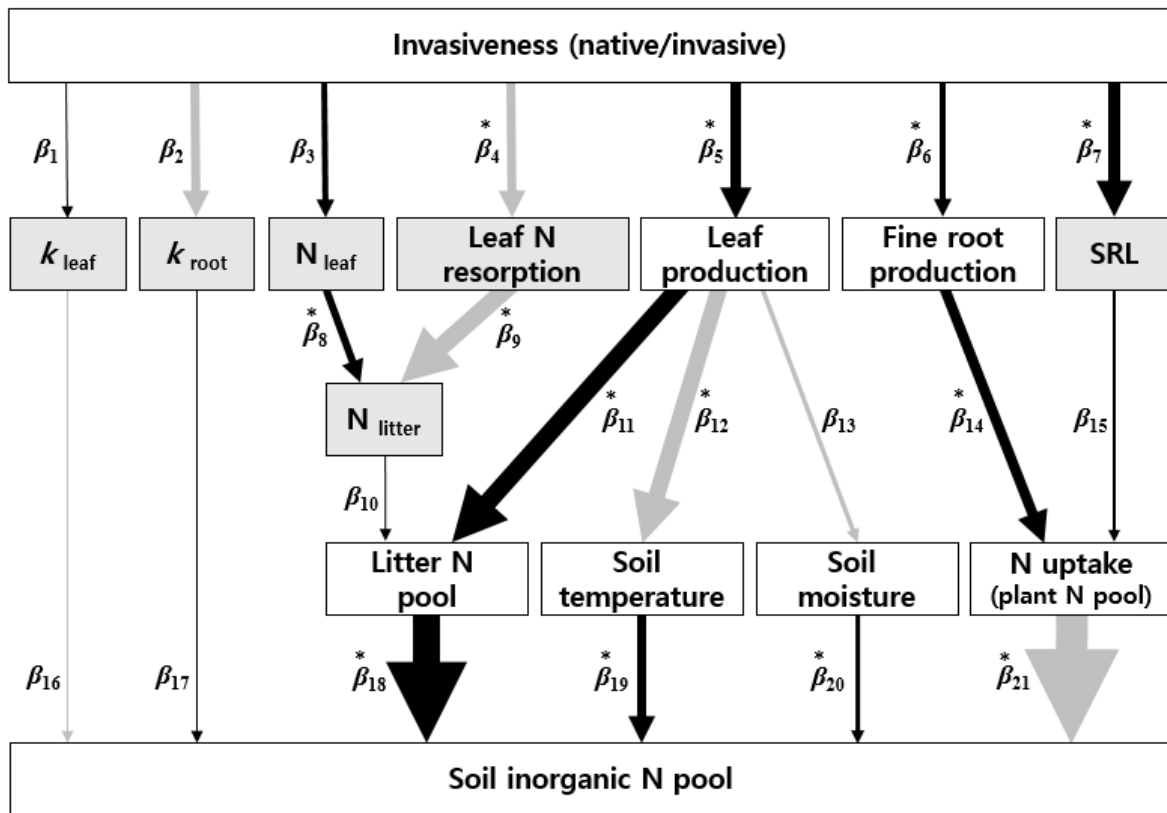


Figure 2

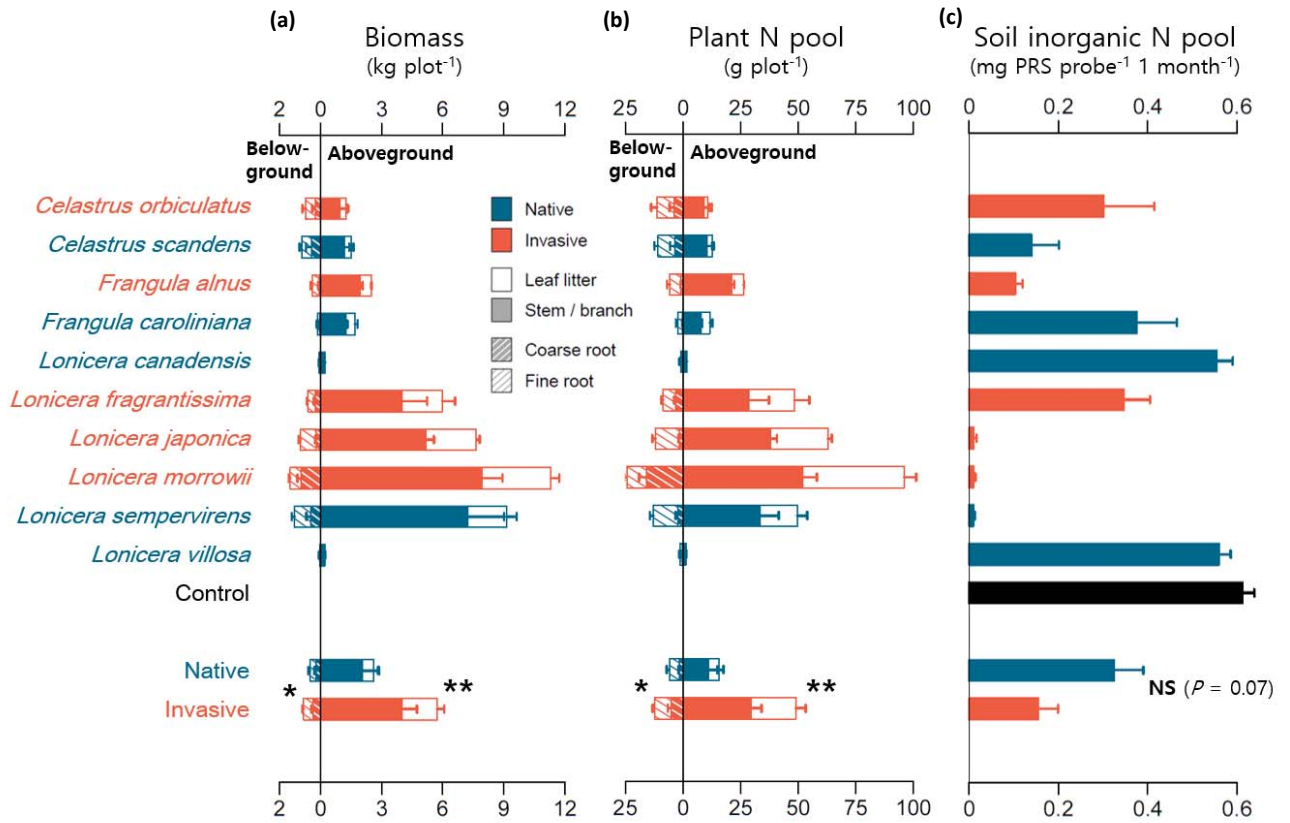
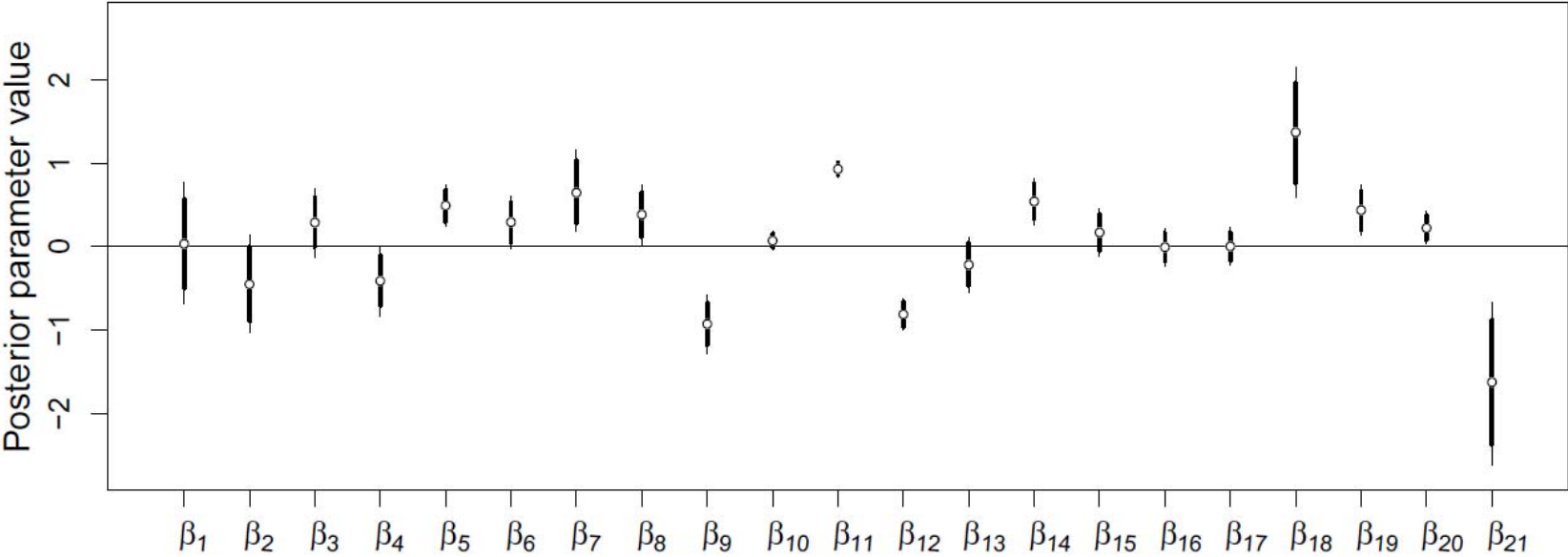


Figure 3



CHAPTER 5

Synthesis

Why are non-native invasive species successful and what are the impacts of invaders on ecosystems? Despite the many studies that have examined the mechanisms that promote successful invasion and the impacts that invaders have on ecosystems, our general understanding of invasion strategies and how invaders may alter ecosystem processes remains poor (Mack et al. 2000; Hulme et al. 2013). With the recent development of a trait-based approach, which links traits to plant performance and ecosystem function (Westoby et al. 2002), many studies have compared leaf traits associated with plant growth strategy (e.g. photosynthetic rate, leaf nitrogen [N], specific leaf area) to explain successful invaders (Baruch and Goldstein 1999; Funk and Vitousek 2007; Leishman et al. 2007, 2010; Osunkoya et al. 2010; Ordonez and Olff 2013). Although those studies suggest that some invaders have different aboveground resource-use traits associated with a greater carbon (C) gain strategies compared to the co-occurring natives, most studies have ignored roots, which comprise a large proportion of the total plant biomass and play an important role in nutrient uptake (Vogt et al. 1995; Jackson et al. 1997; Wilson 2014). Consequently, our understanding of the linkage between plant traits and invader-driven changes in soil properties remains rudimentary.

To maintain greater aboveground productivity, invaders must take up soil nutrients at a rate sufficient to support their greater aboveground demands compared to native species. Although invaders can be more efficient in utilizing nutrients at the leaf level than natives (Baruch and Goldstein 1999; Funk and Vitousek 2007), invaders still need to acquire more nutrients, considering their greater plant N pool associated with their greater biomass (Liao et al.

2008; Castro-Diez et al. 2014). If no external N is supplied to the system (e.g., atmospheric deposition), invaders need to facilitate N cycling, the plant-soil feedback rate, to maintain their greater productivity (Laungani and Knops 2009). In this dissertation, I investigated the potential mechanisms that can facilitate greater N uptake by non-native forest understory species in the Eastern U.S. In the first study (Chapter 2), I found that (1) greater aboveground productivity of invaders was linked to greater leaf N concentration, (2) lower leaf N resorption, and (3) greater fine root production and specific root length. Together these results suggested that greater productivity of non-native shrub species may be an inextricable function of a greater rate of N becoming available in the soil due to higher litter quality and/or rate of litter decomposition and a greater capacity to take up that available N from the soil. The subsequent experiments tested these hypotheses.

In the second experiment (Chapter 3), I compared litter decomposition rates between invasive vs native Eastern U.S. forest understory species. I determined leaf decomposition rates for 42 native and 36 non-native species, and root decomposition rates for 23 native and 25 non-native species. I found that native and non-native species did not differ in leaf and root decomposition rates. The different leaf and root traits of native and non-native species were not significantly associated with decomposition rates, except leaf N. These results suggest that differences in litter decomposition rates through litter quality is not a pathway by which invasive species affect soil N processes in Eastern U.S. forests. Whether leaf and root phenology and lifespan of invaders are associated with the decomposer activity need to be tested. In the last experiment (Chapter 4), I tested whether invaders change soil N processes. I isolated the plant-soil systems in a replicated monoculture experiment that included five invasive and five native woody understory species. The results indicated that invaders promoted plant-soil N cycling by

increasing soil N availability, due to greater litter-N input, and accelerating root uptake of that available N, due to their more extensive and finer root systems.

Overall, the results of my research suggest that invaders have different above-and belowground resource-use strategies and the greater productivity of invaders is the major driver that changes ecosystem processes. This study provides a comprehensive framework for studying invasive plant strategies and the impacts of invaders by examining how shoot and root linkages differ between invasive and native forest understory species. Although common garden studies, including monocultures, are helpful to test how different resource-use strategies of invaders compared to the natives affect nutrient cycling, invader effects need to be studied within the context of intact forest communities to understand the extent to which non-native species can shift forest ecosystem processes. Long-term invader impact studies of experimental manipulations in forests would further contribute to an understanding of invader impacts on the functional organization and stability of forest ecosystems in a changing environment.

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