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Invasive plants accelerate nitrogen cycling: evidence from experimental woody monocultures

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Summary

1. Although it is widely believed that non-native invasive species threaten the functional integrity of forest ecosystems, their impact on important ecosystem processes such as nitrogen (N) cycling is not well understood.

2. To examine how invasive species alter ecosystem N dynamics, we established monocultures of five phylogenetic pairs of native and non-native invasive understory woody species common to Eastern U.S. forests.

3. After 3 years, we found invaders increased N cycling by enhancing the flow of N to the soil through greater litter N production and litter N content, and increased the uptake of available soil N, via greater fine root production and specific root length.

4. *Synthesis*. Our results highlight the importance of linking above- and below-ground processes to better understand invader impacts on ecosystem nutrient processes. The rapid shifts in soil N processes as a result of invader dominance observed in our study suggest that invaders may be an important driver of forest ecosystem functioning.

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

Introduction

Non-native invasive plant species tend to grow faster than co-occurring native species, even in low resource habitats (Leishman *et al.* 2007; Liao *et al.* 2008; Funk 2013; Fridley & Craddock 2015; Heberling & Fridley 2016). This fast growth of invasive species is often associated with a suite of plant traits that can increase photosynthetic capacity and nutrient uptake, including high leaf nitrogen (N), specific leaf area and specific root length (SRL) (van Kleunen, Weber & Fischer 2010; Jo, Fridley & Frank 2015). To the extent that these same traits influence ecosystem functioning, such as greater leaf decomposition rates and accelerated nutrient cycling, faster growing invaders should also have large ecosystem impacts (Ehrenfeld 2003; Vilà *et al.* 2011; Castro-Diez *et al.* 2014; Reich 2014). However, it remains unclear how traits of invaders may be mechanistically linked to soil N dynamics, and, consequently, how invaders affect soil N processes.

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 by roots (Binkley & Hart 1989; Chapin, Matson & Vitousek 2011). Patterns of this plant–soil feedback vary among species (Wedin & 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 plant-mediated changes in soil N cycling in turn influence plant performance, plant community composition and ecosystem function (Vitousek *et al.* 1987; Wedin & Tilman 1990; Craine *et al.* 2002; Ehrenfeld 2003; Bezemer *et al.* 2006).

Compared to co-occurring native shrubs in the Eastern United States, invading non-native shrub species exhibit higher leaf production of greater N concentration, and higher root production that is biased towards fine diameter (i.e. SRL) (Heberling & Fridley 2013; Fridley & Craddock 2015; Jo, Fridley & Frank 2015). Enhanced litter production that is potentially of greater quality (e.g. lower C : N), coupled with faster growth of fine roots, should increase both the mineralization and root uptake rate of soil N. Although we have a good understanding of these differences for native and non-native, invasive species at the trait level, and have established that such differences remain after accounting for phylogenetic differences between native and non-native species (Jo, Fridley & Frank 2015, 2016), it remains to be tested whether and

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how such traits alter ecosystem N cycling (Ehrenfeld, Kourtev & Huang 2001). Further, efforts to determine how invaders affect soil N processes to date have confounded variation in initial soil conditions and the influence of coexisting species on soil processes (Ehrenfeld, Kourtev & Huang 2001; Evans *et al.* 2001; Mack, D'Antonio & Ley 2001; MacDougall & Turkington 2005; Stricker, Hagan & Flory 2015), such that it has not yet been possible to attribute changes in ecosystem N cycling solely to the dominance of invasive plant species.

In this study, we used a monoculture approach in a common garden to provide evidence for coordinated above- and below-ground behaviours of invasive plants that accelerate plant–soil N cycling, suggesting a strong shift in ecosystem functioning with the increasing dominance of non-native plant species. We hypothesized that invaders enhance N cycling by increasing the rate of N mineralization and plant N uptake. We tested this hypothesis using a hierarchical model (Fig. 1) that incorporated various processes and plant attributes that affect soil N availability and plant N uptake, measured in the monoculture experiment and in concurrent studies on the same species in an adjacent experimental garden (Jo, Fridley & Frank 2015, 2016).

Materials and 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*, *Lonicera sempervirens* and *Lonicera villosa*) and five congener invasive species (*Celastrus orbiculatus*, *Frangula alnus*, *Lonicera fragrantissima*, *Lonicera japonica* and *Lonicera morrowii*). The pairing of native and invasive congeneric species provided a built-in control for phylogenetic effects that were further modelled at the genus level (see *Statistical analyses*, below). In 2011, plants were propagated in a greenhouse using cuttings (10–15 cm) 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. The size of the *L. canadensis* plants was comparable to that of the propagated plants.

In spring 2012, we established three blocks of 11 plots ($2{\cdot}5 \times 2{\cdot}5$ m^2) per block, including three bare (control) plots within an enclosed experimental garden at Syracuse, NY, USA. The site, which previously was a mown field, was tilled and cleared of rocks and large plant debris. 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, three 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 weed growth. The shade cloth was removed in spring 2013 to allow for above–belowground 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 budbreak, we harvested above-ground biomass in each plot. Total fresh biomass per plot was measured. Total dry

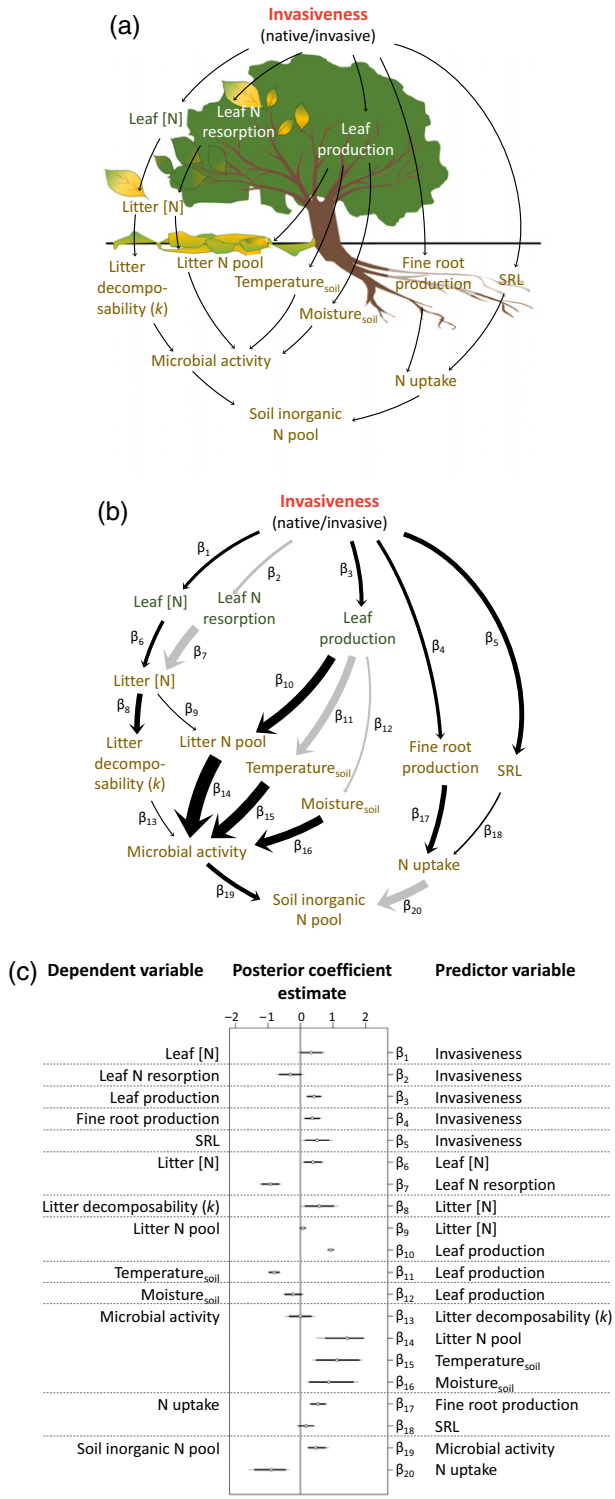

Fig. 1. Hypothesized relationships between the soil inorganic N pool and potential invasive species-induced changes in plant and soil attributes (a). Estimated posterior parameter values (β coefficients) for the relationships in (a) are displayed in (b) and (c). Arrow thickness is proportional to the mean posterior value; black arrows represent a positive mean posterior value and grey arrows represent negative values (b). The circles represent means and the lines represent 95% (thin lines) and 90% (thick lines) credible intervals of the parameters (c). [Colour figure can be viewed at wileyonlinelibrary.com]

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 the 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 >100 leaves collected from the parent plants of the cuttings at the adjacent experimental garden in October 2013. Total leaf production (kg per plot) 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 × 10 cm height) were collected at random locations in each plot to determine standing root biomass in 0–10 cm soil (kg per plot). Roots were picked immediately after collecting each core and were kept on ice in a cooler 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 three additional cores at random locations in four plots when no roots were found in the nine 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 × 10 cm height) were constructed with plastic (1 × 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. All roots were picked at the field site immediately after each ingrowth core was pulled from the soil, and the ingrowth cores were refilled to the approximate field-level bulk density conditions with the soil after all roots were picked; nearby additional soil was used to fill the core, if needed. 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 (first to third 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 were 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 three cores 15 cm from the main stem of each plant, for a total of nine cores per plot. We aggregated the cores by plot and 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 analyser (NC2100 Soil; CE Elantech Inc., Lakewood, NJ, USA).

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, Saskatchewan, Canada) in 2014. PRS probes adsorb mineralized N (NO_3^--N and NH_4^+-N) 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 × 10 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 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 plant impact on soil N concentration, we sampled nine soil cores (10 cm top soil) around the plants (15 cm from the main stem) for each plot in November, 2014. After removing organic debris and roots, we determined total soil N concentration using the CN elemental analyser. To determine how plants affect soil microclimate, soil moisture content (%) and temperature (°C) of 0–10 cm soil were measured in each plot, using time domain reflectometry (HydroSense Soil Water Measurement System; Campbell Scientific, Logan, UT, USA) and a soil thermometer (Rapitest Digital Soil Thermometer; Luster Leaf Products, Inc., Woodstock, IL, USA), five times, June to November 2014. We took four measurements in each plot. Analyses were performed on plot-averaged values.

STATISTICAL ANALYSES

We modelled the effects of invaders on plant–soil N processes using a hierarchical Bayesian approach summarized in Fig. 1. Our model included 13 sub-models to examine the independent effects of plant traits and soil microclimate on the soil inorganic N pool, and, simultaneously, whether those factors are influenced by invader-associated differences in plant functional traits (Table S1, Supporting Information). Fourteen variables were incorporated in the model, including one categorical variable, species invasiveness (non-native invasive = 1, native = 0) and one latent variable, microbial activity. The latent variable was added to capture microbial N mineralization processes in the model by measures of litter N pool and soil temperature and moisture contents. Plant functional traits included in the model (Fig. 1, Table S1) were collected from previous studies performed by our research group. We used leaf and litter N concentration ($[N]_{leaf}$ and $[N]_{litter}$) and leaf N resorption rate (%) from Jo, Fridley & Frank (2015) and SRL (m g^{-1}, SRL) from Jo, Fridley & Frank (2016). A random block intercept was included in the sub-model for soil inorganic N pool, and phylogenetic autocorrelation was incorporated in the invasiveness predictor sub-models to account for correlated variation in measurements contributed by shared phylogeny, following de Villemereuil *et al.* (2012). The phylogenetic tree of the study species was created using Phylomatic (ver. 3; Webb & Donoghue 2005) with additional information (Rehder 1903; Theis, Donoghue & Li 2008) to resolve the Lonicera polytomy. Branch lengths were estimated using the BLADJ algorithm in Phylocom (ver. 4.2) based on the node ages from the file 'agescl3' (Gastauer & Meira-Neto 2013) (Fig. S1). 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 with binary variables (Gelman & Hill 2006). The posterior values for the regression coefficients (βs) were estimated to determine the relative effects of parameters on the dependent variables 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; Su & Yajima 2015). R model code is available in Appendix S1. We used non-

informative uniform priors for β regression coefficients in the model, except for positive and negative priors for β_{19} (N supply) and β_{20} (N uptake), respectively (Table S1). 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 with the Wilcoxon rank-sum test.

Results

Leaf and root production were greater for invaders compared to native species (Fig. 1, $\beta_{3,4}$; Fig. 2a). Invaders had greater leaf N concentration (Fig. 1, $P(\beta_1 > 0) = 0{\cdot}91$) and lower leaf N resorption rate (Fig. 1, $P(\beta_2 < 0) = 0{\cdot}89$), which were associated with higher litter N concentration (Fig. 1, $\beta_{6,7}$). The combination of greater leaf production and leaf N content was associated with a greater litter N pool size for invading species (Fig. 1, $P(\beta_9 > 0) = 0{\cdot}87$, β_{10}; Fig. 2a and b). The effect size of litter N concentration on litter N pool was relatively small compared to that of leaf production (Fig. 1, $\beta_{9,10}$). Litter N pool, in turn, had a large facilitating effect on estimated soil microbial activity, which increased the soil inorganic N pool (Fig. 1, $\beta_{14,19}$). Litter N concentration increased litter decomposability (Fig. 1, β_8), but the litter decomposability did not have a strong impact on estimated soil microbial activity (Fig. 1, β_{13}).

Invader-driven changes in leaf and fine root production and SRL affected the soil inorganic N pool negatively by way of reducing soil temperature and moisture content (Fig. 1, β_{11}, P ($\beta_{12} < 0$) = 0·87) and increasing plant N uptake (Fig. 1, β_{17}, $P(\beta_{18} > 0) = 0{\cdot}84$; Fig. 2b). Leaf production was negatively associated with soil temperature (Fig. 1, β_{11}) and soil moisture content (Fig. 1, β_{12}), which can reduce soil microbial activity (Fig. 1, $\beta_{15,16}$). 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 (Fig. 1, $\beta_{14–16}$).

Soil N concentration was not significantly different between plots with native and invasive species (Fig. 2d); however, the soil inorganic N pool was weakly smaller for plots with invaders (Fig. 2c, $P = 0{\cdot}07$), in part due to their greater capacity to take up the available N with a greater production of finer roots than natives (Fig. 1, $\beta_{4,5}$, β_{17}, $P(\beta_{18} > 0) = 0{\cdot}84$; Fig. 2a and b).

Discussion

Results of our 3-year monoculture experiment using five native and five invasive forest understory woody species of the Eastern United States support the hypothesis that invaders facilitate N cycling by increasing soil N availability and plant N uptake. We found that the greater above-ground production of invaders resulted in greater litter biomass and N input to the soil as a substrate for soil microbes. Greater production of fine roots with high SRL increased the capacity of invaders to take up soil N that was mineralized at accelerated rates compared to those rates in the soil of native species plots. Litter decomposability (decomposition rate on a mass basis) had no effect on soil N availability and the inhibitory influence of above-ground production on soil microclimate was outweighed by the facilitating effects of greater invasive litter production on soil N availability.

There has been considerable interest in comparing litter decomposition rates between native and invasive species due to the presumably close link between decomposition rate and soil N availability (Scott & Binkley 1997; Allison & Vitousek 2004; Ashton *et al.* 2005). Although we found that invaders increased soil N availability in our monoculture plots, the

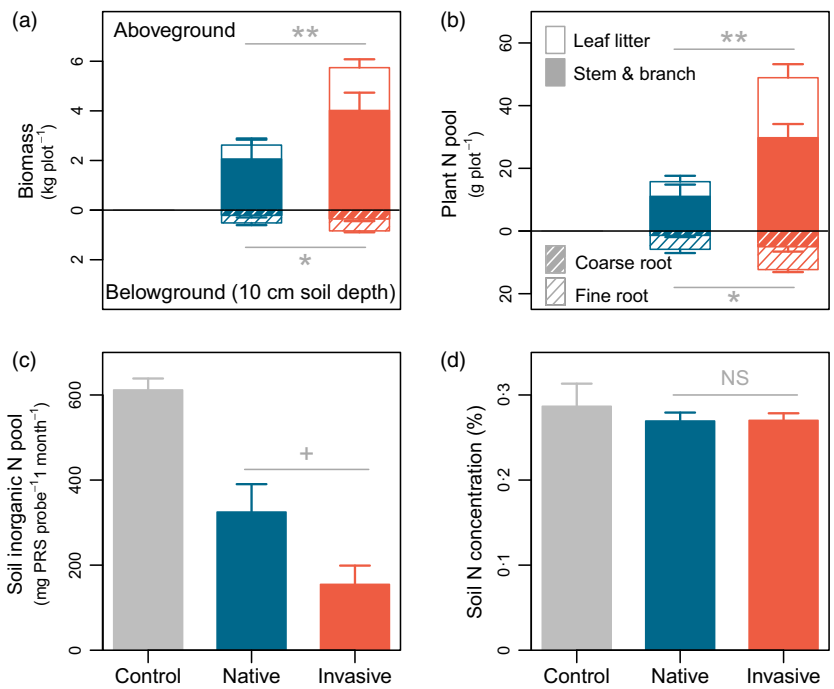

Fig. 2. Biomass (a), plant N pool (b), soil inorganic N pool (c) and soil N concentration (d) for five native and five invasive species examined in the monoculture experiment after three growing seasons. Soil inorganic N pool and soil N concentration for bare (control) plots are also plotted in (c) and (d). Error bars represent standard error. Statistical significance for overall native vs. non-native invasive comparisons was tested with Wilcoxon's rank-sum test. NS, not significant; $^{+}P < 0{\cdot}1$; $^{*}P < 0{\cdot}05$; $^{**}P < 0{\cdot}01$. [Colour figure can be viewed at wileyonlinelibrary.com]

main effect of invaders on soil N availability was due to their greater production of leaf litter rather than litter decomposability (Fig. 1, β_{13-14}). Along with a previous decomposition study of 80 forest understory species that found leaf and root decomposition rates did not differ between invasive and native species in our study system (Jo, Fridley & Frank 2016), results of the present experiment suggest that soil N availability is primarily driven by the quantity rather than the quality of plant litter. These effects were measured during the 2-year period after plants were established in the monoculture plots. Considering the greater productivity of invaders compared to the natives, we expect that invader effects would strengthen with time.

Plants also affect the microbial activity of N transformations (e.g. mineralization and nitrification) by altering soil microclimate (Binkley & Hart 1989; Knoepp & Swank 2002; Chapin, Matson & Vitousek 2011). In this study, plant leaf production reduced soil temperature and moisture (Fig. 1, $\beta_{11,12}$), likely due to greater shade cast and transpirational loss as shrub canopy size increased. Thus, although the larger canopies of invasive shrubs altered soil microclimate in a way less conducive for microbial activity, the stimulatory effects of a greater input of plant litter to the soil outweighed effects of invaders on soil microclimate (Fig. 1, β_{14-16}).

The soil inorganic N pool size measured in this study was a function of mineral N production and plant N uptake. Although invasive species stimulated N mineralization, with greater fine root production, and thus a greater capacity for N uptake, invaders still reduced the size of the soil inorganic N pool compared to natives. The increased N mobility through rapid N cycling may cause increasing N loss from leaching (Gundersen, Schmidt & Raulund-Rasmussen 2006). We did not find a difference in soil N concentration between native and invasive plots (Fig. 2d). Although the short 3-year duration of this experiment makes it difficult to draw a conclusion about how the accelerated N cycle of invaders affects N leaching in the field, greater nutrient uptake by invaders may reduce N leaching, immobilizing N in plant biomass.

Our results partially support the common view that plant functional traits influence ecosystem functioning (Lavorel & Garnier 2002; De Deyn, Cornelissen & Bardgett 2008; Orwin *et al.* 2010; Reich 2014). For example, we showed that leaf N concentration and leaf N resorption rate were related to litter N concentration, litter decomposability and total litter N pool (Fig. 1, β_{6-9}), which in turn were both linked to soil N availability. In addition, greater SRL was associated with greater N uptake that reduced the soil inorganic N pool (Fig. 1, $\beta_{18,20}$). However, compared to those functional traits, leaf and root production were more directly associated with the litter N pool and plant N uptake, which in turn were closely related to soil N availability (Fig. 1, $\beta_{8,12}$). Our results thus support the argument that plant biomass dynamics, mediated by functional traits, drive ecosystem functioning (Lohbeck *et al.* 2014).

Our study suggests that invasive shrubs and lianas of Eastern U.S. forests accelerate soil N cycling by promoting the rates of both soil N mineralization and plant uptake, which can further support higher invader productivity (Loreau 2010). We found that invasive plants increased soil N availability by producing more litter that was N enriched, and decreased the soil N pool through greater plant N uptake compared to native shrubs. However, impacts of invasive shrubs on soil N dynamics in unshaded field monoculture plots may differ from those occurring under a forest canopy. In forests, the effect of invasive shrubs on ecosystem processes will be influenced by other co-occurring understory and canopy plants competing for limiting resources such as light and mineral nutrients (Breshears *et al.* 1998; Reich *et al.* 1998; Ellsworth, Harrington & Fownes 2004). Nevertheless, considering the significant impacts of invaders on plant–soil N dynamics after only three growing seasons, and that invaders often occupy open habitats (e.g. roadsides, forest edges) under conditions similar to those in our study, invading shrubs and lianas are likely major agents of ecosystem change in the Eastern United States.

Authors' contributions

I.J., J.D.F. and D.A.F. designed the study. I.J. performed the experiments and analysed data. I.J. wrote the first draft of the manuscript and all authors contributed substantially in discussions and revisions. All authors gave final approval for publication.

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Data accessibility

Data used for hierarchical Bayesian model deposited in the Dryad Digital Repository https://doi.org/10.5061/dryad.tt8v6 (Jo, Fridley & Frank 2017).

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Supporting Information

Details of electronic Supporting Information are provided below.

Fig. S1. Phylogenetic tree of the species used.

Table S1. Regression sub-models used in the hierarchical model illustrated in Fig. 1.

Appendix S1. R code for hierarchical Bayesian model used in this study.