

LETTER

Dominant forest tree mycorrhizal type mediates understory plant invasions

Insu Jo,¹ Kevin M. Potter,² Grant M. Domke³ and Songlin Fei^{1*}

¹Department of Forestry and Natural Resources, Purdue University, West Lafayette, IN 47907, USA

²Department of Forestry and Environmental Resources, North Carolina State University, Research Triangle Park, NC 27709, USA

³Northern Research Station, United States Department of Agriculture, Forest Service, St. Paul, MN 55108, USA

*Correspondence: E-mail: sfei@purdue.edu

Abstract

Forest mycorrhizal type mediates nutrient dynamics, which in turn can influence forest community structure and processes. Using forest inventory data, we explored how dominant forest tree mycorrhizal type affects understory plant invasions with consideration of forest structure and soil properties. We found that arbuscular mycorrhizal (AM) dominant forests, which are characterised by thin forest floors and low soil C : N ratio, were invaded to a greater extent by non-native invasive species than ectomycorrhizal (ECM) dominant forests. Understory native species cover and richness had no strong associations with AM tree dominance. We also found no difference in the mycorrhizal type composition of understory invaders between AM and ECM dominant forests. Our results indicate that dominant forest tree mycorrhizal type is closely linked with understory invasions. The increased invader abundance in AM dominant forests can further facilitate nutrient cycling, leading to the alteration of ecosystem structure and functions.

Keywords

Eastern USA, forest mycorrhizal type, nutrient cycling, plant-soil feedback, temperate forests, understory invasions.

Ecology Letters (2017)

INTRODUCTION

Plant-fungal symbiosis is common to flowering plants and plays an important role in plant nutrition (Brundrett 2009). Through this mutualistic relationship, host plants receive mineral nutrients via their root system associated with fungal hyphae, and in return fungi gain a substantial amount of energy (carbon [C]) assimilated from photosynthesis (Smith & Read 2008; van der Heijden *et al.* 2015). The plant-fungal interactions, which differ depending on the dominant mycorrhizal types, can have substantial impacts on soil nutrient dynamics and community structure in forest ecosystems (Phillips *et al.* 2013; Bennett *et al.* 2017; Wurzbürger *et al.* 2017). For example, in arbuscular mycorrhizal (AM) tree dominant forests, higher litter decomposition rate and soil nitrogen (N) mineralisation associated with the higher litter quality of AM trees can result in rapid N cycling than those in ectomycorrhizal (ECM) tree dominant forests (Lin *et al.* 2017).

If dominant forest mycorrhizal type (e.g. AM or ECM tree dominant forests) mediates soil nutrient dynamics, how does it affect understory plant invasions? Although invaders often accelerate nutrient cycling, such as N, and are known to have more efficient resource-use strategies than natives to maintain their high productivity (Ehrenfeld 2003; Funk & Vitousek 2007; Liao *et al.* 2008; Jo *et al.* 2017), nutrient demands of invasive species will likely be met from sites where nutrients are less limiting (Davis *et al.* 2000). However, it remains unclear whether the mycorrhizal mediated variations in soil nutrient cycling can facilitate non-native plant invasions.

In this study, we hypothesised that AM tree dominant forests are more prone to understory invasions than ECM tree dominant forests. Because many non-native invasive species

are fast-growing and often have a greater capacity to take up soil nutrients than co-occurring native counterparts (Fridley & Craddock 2015; Jo *et al.* 2017), fast nutrient cycling in AM forests will benefit understory invaders (Lin *et al.* 2017). Higher litter decomposition rates in AM tree dominant forests can result in thinner forest floor layers than in ECM dominant forests (Cornelissen *et al.* 2001; Averill *et al.* 2014), which may further facilitate invader establishment, as a thick litter layer inhibits emergence and survival of understory seedlings (Beatty & Sholes 1988; Facelli & Pickett 1991; Sayer 2006; Schramm & Ehrenfeld 2010).

Here, we evaluated the hypothesis with the consideration of forest floor and soil attributes and forest community structure using national forest inventory data from the Forest Inventory and Analysis (FIA) program (USDA, Forest Service) in the eastern United States (US), modelled in a hierarchical Bayesian framework (Fig. 1). Although many understory invaders are shade-tolerant (Martin *et al.* 2008), light availability, moderated by forest overstory structure, is an important limiting factor of forest understory invasions (Valladares & Niinemets 2008). In addition, high richness and abundance for the native community can assist the resistance to plant invasions through competitive exclusion (Guo *et al.* 2015; Iannone *et al.* 2015, 2016). Including forest community structure of native species (i.e. overstory and understory species abundance and richness) in the model, therefore, allows comparisons of the impacts of forest mycorrhizal type and forest structure on understory invasions.

We have two primary objectives in this paper. First, to better understand the relationship between dominant forest tree mycorrhizal type and understory plant invasions. Second, to determine how forest floor and soil attributes and understory native community structure, mediated by forest tree

mycorrhizal type and overstory abundance, affect forest understory invasions in temperate forests in the eastern US.

METHODS

Data collection

Vegetation and soil data were extracted from a forest inventory database populated and maintained by the FIA Program. The FIA database includes forest inventory information for permanent plots located across the US. Each permanent ground plot comprises four smaller fixed-radius (7.32 m) plots (i.e. subplots) spaced 36.6 m apart in a triangular arrangement with one subplot in the centre. Tree- and site-level attributes – such as diameter at breast height (dbh) and tree height – are measured at regular temporal intervals on plots that have at least one forested condition defined in a prefield process (USDA Forest Service 2017a). Litter and soil samples are collected along with other non-standing tree ecosystem attributes on every 1/16th base intensity plot – where at least one forested condition exists – distributed approximately every 38 848 ha (USDA Forest Service 2017b). Since we aimed to test the relationships between plant species and soil properties, we included only the FIA plots in the study region where both vegetation and soil attributes were collected ($n = 524$).

The plots included in this study were located in temperate forests in the eastern US (Fig. S1). Mean annual temperature ranged from 2.4 to 14°C and mean annual precipitation from 630 to 1300 mm (PRISM Climate Group 2012). The major soil types of the study sites were alfisols (42%), followed by

ultisols (17%), spodosols (16%), inceptisols (14%) and mollicsols (7%) (Schwarz & Alexander 1995; USDA-NRCS 1999).

To describe soil and forest floor attributes, we used forest floor C and N concentrations and thickness; and mineral soil C and N concentrations, and pH for 0–20 cm mineral soil depth for each plot, which were compiled from the FIA database (O'Neill *et al.* 2005; Domke *et al.* 2016, 2017; USDA Forest Service 2017b). Forest floor includes litter and humus above the mineral soil. Plots with missing values for any of the forest floor and mineral soil properties were not included in the analyses ($n = 68$). Soil and forest floor summary statistics are provided in Table 1.

To describe overstory and understory structure, we utilised total basal area (> 2.54 cm dbh) of trees and understory species cover (%) and richness. Understory species include shrub, vine and herbaceous species. Non-native invasive understory species have been defined as those that are weedy and invasive in the contiguous US according to the USDA Plants database (USDA-NRCS, 2016). To minimise the uncertainty due to the lack of species level identification of understory plants for certain plots, we excluded plots from the analyses if a cumulative cover of understory species with only a genus-level identification and no native/non-native status information was > 10% ($n = 131$). We also excluded plots if N-fixing trees ($n = 6$) or non-native trees were present ($n = 2$) or if the basal area of evergreen trees was > 66.7% of total basal area ($n = 29$) because plant traits and soil properties associated with N-fixation, nativity, and evergreen species can confound the effects of tree mycorrhizal type on the analyses. As a result, a total of 288 plots were included in the final analyses (Fig. S1).

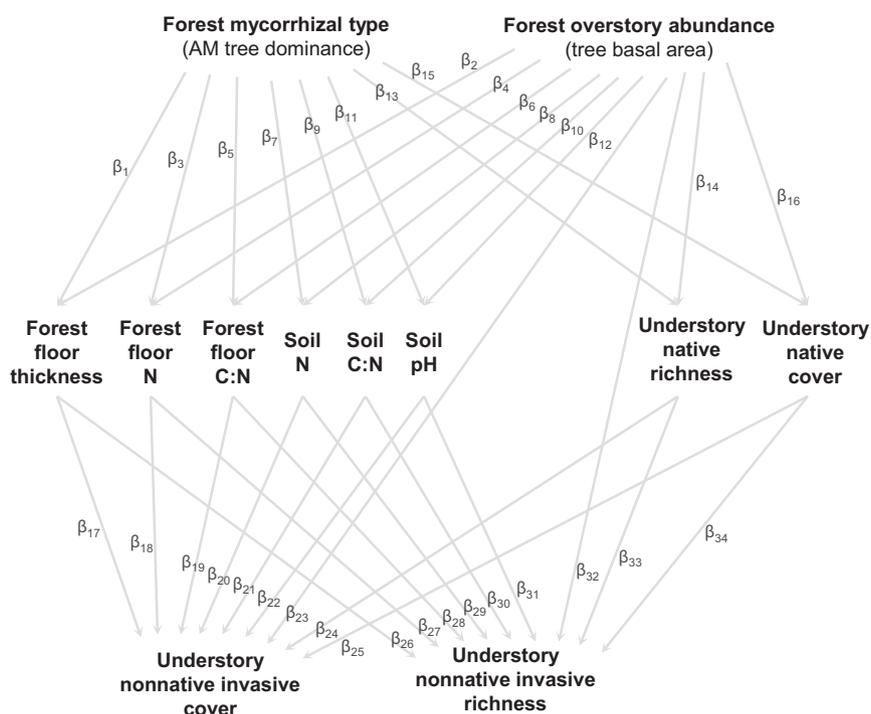


Figure 1 Hypothesised relationships between understory invasions and forest community structure and soil attributes mediated by dominant forest tree mycorrhizal type and overstory abundance. Relative effect sizes (posterior distribution of estimated coefficient, β s) for the relationships are plotted in Fig. 4.

Table 1 Summary of vegetation inventory and soil attributes used in this study. Mean \pm standard error (SE)

	All plots (<i>n</i> = 288)	AM dominant plots (<i>n</i> = 101)	Mixed plots (<i>n</i> = 75)	ECM dominant plots (<i>n</i> = 112)
Forest floor and soil attributes				
Forest floor thickness (cm)	4.6 \pm 0.2	4.3 \pm 0.3	4.8 \pm 0.4	4.7 \pm 0.2
Forest floor C (%)	31.8 \pm 0.7	31.5 \pm 1.3	31.0 \pm 1.4	32.7 \pm 1.1
Forest floor N (%)	1.23 \pm 0.03	1.20 \pm 0.05	1.25 \pm 0.06	1.23 \pm 0.04
Forest floor C:N ratio	26.5 \pm 0.4	26.8 \pm 0.7	25.2 \pm 0.7	27.0 \pm 0.6
Soil C (% 0–20 cm mineral soil)	3.04 \pm 0.15	3.25 \pm 0.2	3.60 \pm 0.42	2.47 \pm 0.14
Soil N (% 0–20 cm mineral soil)	0.19 \pm 0.01	0.22 \pm 0.01	0.22 \pm 0.02	0.15 \pm 0.01
Soil C:N ratio (0–20 cm mineral soil)	16.1 \pm 0.3	14.9 \pm 0.4	16.6 \pm 0.5	16.8 \pm 0.6
Soil pH	5.2 \pm 0.1	5.2 \pm 0.1	5.4 \pm 0.1	5.0 \pm 0.1
Overstory tree				
AM tree dominance (0–1; based on basal area)	0.48 \pm 0.02	0.92 \pm 0.01	0.48 \pm 0.01	0.09 \pm 0.01
Tree species richness	3.3 \pm 0.1	2.9 \pm 0.1	3.5 \pm 0.2	3.5 \pm 0.1
Tree basal area (m ² ha ⁻¹)	21.6 \pm 0.8	21.7 \pm 1.4	21.9 \pm 1.8	21.3 \pm 1.3
Understory plants				
Understory native species richness	14.1 \pm 0.4	13.3 \pm 0.7	14.9 \pm 0.9	14.2 \pm 0.7
Understory non-native invasive species richness	0.9 \pm 0.1	1.3 \pm 0.2	0.8 \pm 0.2	0.7 \pm 0.1
Cumulative cover of native species (%)	61.6 \pm 3.1	61.4 \pm 5.9	64.9 \pm 5.3	59.5 \pm 5.0
Cumulative cover of non-native invasive species (%)	6.6 \pm 1.1	10.8 \pm 2.4	4.4 \pm 1.6	4.2 \pm 1.4

AM dominant plots: AM tree dominance > 0.667; Mixed plots: 0.333 < AM tree dominance < 0.667; ECM dominant plots: AM tree dominance < 0.333.

Species mycorrhizal type information was extracted from Brundrett *et al.* (1990), Wang & Qiu (2006), Akhmetzhanova *et al.* (2012) and Bueno *et al.* (2017). If the species level mycorrhizal type was not available, we assigned the most frequent mycorrhizal type within genus (or family) (see Appendices S2 and S3 for species list with mycorrhizal type information). We then calculated the AM tree dominance (based on basal area) for each plot by dividing total AM tree basal area by the sum of AM and ECM mycorrhizal tree basal area. If a species is both AM and ECM, we assigned a half of the basal area each to AM and ECM.

Statistical analyses

Using a Bayesian modelling approach, we tested bivariate relationships between the AM tree dominance and understory species cover and richness for native species and non-native invaders (Fig. 2). Native species cover and richness were modelled using a Poisson distribution with a log link, and invasive species were modelled using a zero-inflated Poisson model due to many zero invasive species cover and richness observations for the uninvaded plots (Ghosh *et al.* 2006; Rathbun & Fei 2006). We also tested differences between the proportion of each mycorrhizal type of understory non-native invader separately for AM and ECM dominant plots using a Wilcoxon Rank-Sum test (Fig. 3).

We used a Bayesian hierarchical model to examine how forest mycorrhizal type and overstory tree abundance are related to soil properties and understory native species structure (cover and richness) and, simultaneously, how these factors influence understory invasions. First, we modelled forest floor and soil attributes as response variables with AM tree

dominance and tree basal area as predictor variables to examine how the forest tree mycorrhizal type and forest overstory abundance are associated with forest floor and soil properties and understory native species structure (Fig. 1). Then we tested how these forest floor and soil attributes and understory native community structure, along with overstory abundance, influence understory invader cover and richness (Fig. 1). Our model contained ten dependent variables (Fig. 1), including eight variables (the six forest floor and soil property attributes along with understory native richness and understory native cover) with normal distributions and two zero-inflated variables (understory invasive cover and understory invasive richness) with either a Bernoulli or a Poisson distribution. We included ecoregions (based on Cleland *et al.* 2007) as a random intercept for each of the regression sub-models to account for spatial autocorrelation within the response variables. All independent variables were log-transformed (except AM tree dominance) and standardised to make effect sizes comparable among different variables via subtracting their mean and dividing by two standard deviations (Gelman & Hill 2006). Regression components and specifications of the model are listed in Appendix S1.

We fitted the models to estimate posterior coefficients (β s) to determine the relative effects of parameters on dependent variables using Markov chain Monte Carlo methods (MCMC) in JAGS in R 3.3.1 with the package 'R2jags' (Plummer 2003; Su & Yajima 2012; R Development Core Team 2014). We ran three parallel MCMC chains for 50 000 iterations with a 10 000-iteration burn-in and evaluated model convergence using the Gelman-Rubin convergence diagnostic (Gelman *et al.* 2014).

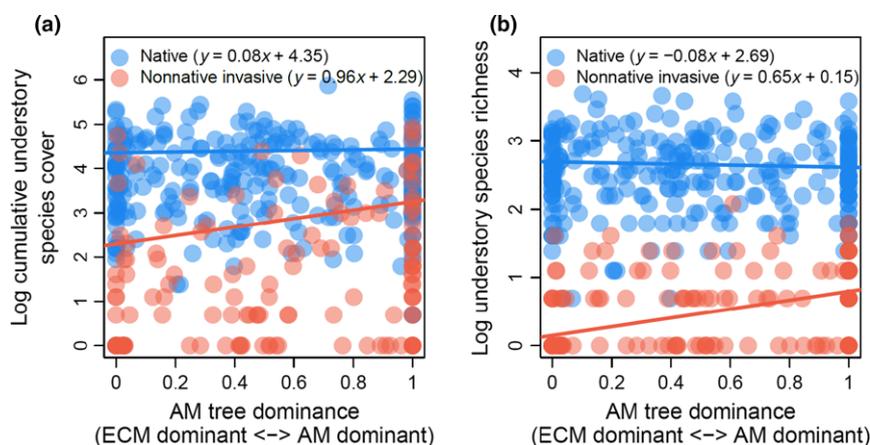


Figure 2 Relationships between AM tree dominance (based on basal area) and understory species cover (a) and richness (b). Red fitted line is for non-native invasive species and blue line is for native species.

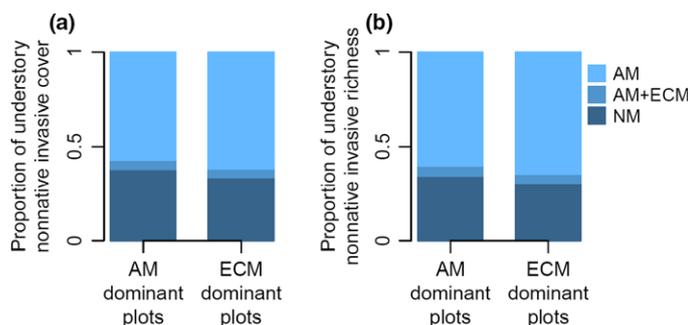


Figure 3 Proportions of understory non-native invasive species mycorrhizal type by cover (a) and richness (b) for AM and ECM dominant forests where invaders were present. No significant differences were found between the proportion of each mycorrhizal type of understory invaders for AM and ECM dominant plots based on Wilcoxon Rank-Sum test ($P > 0.1$). No ECM understory invaders were present in the study plots. AM, arbuscular mycorrhizal; ECM, ectomycorrhizal; AM+ECM, both AM and ECM; NM, non-mycorrhizal.

RESULTS

Summary of the studied plots

The plots included in this study were located in temperate broadleaf and mixed forests (Fig. S1). Mean plot forest floor thickness was 4.6 cm and forest floor C and N concentrations and C : N ratio were 31.8%, 1.2%, and 26.5 respectively (Table 1). Mean soil C and N concentrations, C : N ratio, and pH in 0–20 cm mineral soil depth were 3.0%, 0.2%, 16.1 and 5.2 respectively (Table 1). Mean tree richness was 3.3 species per plot and basal area was 21.6 m² ha⁻¹. About half (48%) of the basal area was contributed by AM trees (Table 1). Among the 86 tree species found in the plots, common AM tree species included *Acer rubrum* L., *A. saccharum* Marsh., *Prunus serotina* Ehrh., *Ulmus Americana* L., *Fraxinus Americana* L. and *Sassafras albidum* (Nutt.) Nees (Appendix S2). The most abundant ECM tree species in the plots included *Quercus alba* L., *Q. rubra* L., *Q. velutina* Lam., *Betula papyrifera* Marsh., *Fagus grandifolia* Ehrh. and *Carya ovata* (Mill.) K. Koch (See Appendix S2 for the full list of the tree species).

The understory was dominated by native species (cumulative cover [plot⁻¹], 61.6%; mean richness [plot⁻¹], 14 species) compared to non-native invaders (6.6%, 1 species) (Table 1 and Fig. 2). Non-native invasive species were present on 128 out of 288 plots. In total, 75 non-native invasive species were recorded across the plots, with *Rosa multiflora* Thunb., *Lonicera japonica* Thunb. and *Alliaria petiolata* (M. Bieb.) Cavara & Grande being the most abundant (See Appendix S3 for the full list of the invasive species).

Relationship between forest mycorrhizal type and understory invasions

Invasion of non-native plants was strongly related to the dominance of forest mycorrhizal type (Fig. 2; Table 1). Understory species cover for both native and non-native invasive species was positively associated with the AM tree dominance (Fig. 2a). However, invasive species cover increased at a rate 12 times greater at a log-scale than native species as AM tree dominance increased (Fig. 2a; slope estimate [95% credible intervals] for invasive, 0.963 [0.824, 1.101] and for native, 0.083 [0.041, 0.125]). Species richness of understory invasive species also had a positive association with AM tree dominance; however, native species richness had a negative but weak association with AM tree dominance (Fig. 2b; slope estimate for invasive, 0.651 [0.282, 1.026] and for native, -0.079 [-0.161, 0.003]). Forest mycorrhizal type was more strongly associated with invasive cover than with invasive richness, suggesting forest mycorrhizal type may be more closely related to the invader dominance than invader establishment. Overall, both invader cover and richness were positively related to AM tree dominance regardless of their growth form, except shrub cover (Appendix S4).

Mycorrhizal type of understory invasive species

The most dominant mycorrhizal type of understory invaders was AM (Fig. 3). In AM dominant forests, 57% of invasive cover and 60% of invader richness were contributed by AM invaders, followed by non-mycorrhizal invaders (NM, 38% in

cover and 34% in richness) (Fig. 3). Similarly, AM invaders were also the most dominant mycorrhizal type in ECM dominant forests, contributing 62% of invasion cover and 65% of invader richness. NM invaders contributed 33% of invasion cover and 31% of invader richness in ECM dominant forest (Fig. 3). The proportions of each mycorrhizal type between AM dominant plots and ECM dominant plots were not significantly different for both cover and richness (Fig. 3).

Effects of overstory tree mycorrhizal type and abundance on soil and understory native community

Overall, forest mycorrhizal type had stronger impacts on forest floor and soil attributes than overstory abundance (Fig. 4, β_{1-12}). AM tree dominance had significant positive associations with soil N and pH (Fig. 4, $\beta_{7,11}$; Table 1) and negative associations with forest floor thickness and soil C : N ratio (Fig. 4, $\beta_{1,9}$; Table 1). Tree basal area was negatively related to soil pH, but the effect size was small (Fig. 4, β_{12}). Understory native species cover and richness were not related to AM tree dominance (Fig. 4, $\beta_{13,15}$; Table 1), but understory native species cover was negatively associated with tree basal area (Fig. 4, β_{16}).

Factors associated with understory invasions

The forest floor and soil attributes and forest community structure had significant associations with understory invasions, particularly for invasive cover (Fig. 4, β_{17-34}). Among the forest floor and soil attributes that were significantly associated with AM tree dominance, forest floor thickness and soil C : N ratio had strong associations with invasive cover and richness (Fig. 4, $\beta_{17,21,26,30}$), suggesting that AM tree dominance may facilitate understory invasions by decreasing forest floor thickness and soil C : N ratio. Soil N and pH had a significant positive association with invasive cover but not with invasive richness (Fig. 4, $\beta_{20,22,29,31}$). Contrasting with soil N and C : N ratio (Fig. 4, $\beta_{20,21,29,30}$), forest floor N had no significant associations with invader cover and richness, while forest floor C : N ratio was positively associated with invader cover and richness (Fig. 4, $\beta_{18,19,27,28}$). Native plant community structure attributes (tree basal area and understory native species richness but not native species cover) were negatively associated with invasive cover, with the strongest effect size of tree basal area (Fig. 4, β_{23-25}); however, invasive richness was positively associated with understory native richness (Fig. 4, β_{33}). Tree basal area and native species cover had no significant associations with invasive richness (Fig. 4, $\beta_{32,34}$).

DISCUSSION

Dominant trees in forest ecosystems are an important driver of nutrient dynamics (Binkley & Giardina 1998; Finzi *et al.* 1998), but their role, particularly that of their mycorrhizal type, on the invasion of understory plants was not clear. We demonstrated that AM tree dominant forests are more vulnerable to understory invasions, likely due to increased nutrient availability and decreased forest floor, resulting from more open nutrient cycling than in ECM dominant forests. AM

understory invaders may get more benefits than other mycorrhizal type invaders, in part, by foraging for mineral nutrients using AM hyphal networks in AM dominant forests (Selosse *et al.* 2006). However, we found no difference in the mycorrhizal type composition of understory invaders between AM and ECM dominant forests (Fig. 3).

Our study supports the idea of tree mycorrhizal-associated nutrient economy in forest ecosystems (Phillips *et al.* 2013). Consistent with previous findings (Averill *et al.* 2014; Midgley & Phillips 2014; Lin *et al.* 2017), our study shows that AM tree dominant forests have more soil N and lower soil C : N ratio and forest floor thickness than in ECM tree dominant forests (Table 1; Fig. 4, $\beta_{1,7,9}$), suggesting that AM dominant forests have faster nutrient cycling than ECM tree dominant forests. In addition, we note that AM tree dominance was positively associated with soil pH, which in turn increase invader cover (Fig. 4, $\beta_{11,22}$). Low pH in ECM dominant forests may decrease soil organic matter decomposition (Augusto *et al.* 2002), resulting in low nutrient availability. While it is necessary to test whether the mineralised nutrient pools differ between AM and ECM dominant forests in our study sites, the significant association between forest tree mycorrhizal type and forest floor and soil attributes suggests the important role of dominant forest tree mycorrhizal type in forest mineral nutrient cycling. It is also notable that, overall, tree basal area had a smaller effect size on soil and forest floor attributes than mycorrhizal type, reaffirming the important role of dominant tree mycorrhizal type in forest nutrient economy.

The differing forest floor and soil properties associated with different forest mycorrhizal types, in turn, affect forest understory invasions. A greater abundance and richness of invasive species was related to less forest floor and lower soil C:N ratio that were linked to AM dominant forests (Fig. 4, $\beta_{17,21,26,30}$). High soil N and low soil C:N ratio are related to high decomposition rates of organic materials that can increase soil nutrient availability (Finzi *et al.* 1998), and then favour fast-growing invaders. Less forest floor depth further enables invaders to easily establish or expand. Although forest mycorrhizal type was not associated with forest floor C:N ratio (Fig. 4, β_5), it is notable that forest floor C:N ratio had an opposite effect on understory invasions as compared to soil C : N ratio (Fig. 4, $\beta_{19,28}$). In our study, the forest floor included both humus and litter layers; therefore, low forest floor C:N ratio may imply a thick humus and litter layer that can inhibit the establishment of understory invaders.

Our study provided evidence of biotic resistance to understory invasions in forests. We showed that overstory abundance and understory native species richness were negatively associated with understory invader cover, although some other native species community structure measures also had varying impacts on invader cover and richness (Fig. 4, $\beta_{23-25,32-34}$). More understory native species may be related to higher competition levels in resource uptake by native species and higher niche occupancy (Muller 2003). Although forest understory invaders are often shade-tolerant and have more efficient resource-use strategies than co-occurring native species (Martin *et al.* 2008; Heberling & Fridley 2013; Jo *et al.* 2015), resource competition for light and nutrients between overstory trees and understory species is an important factor

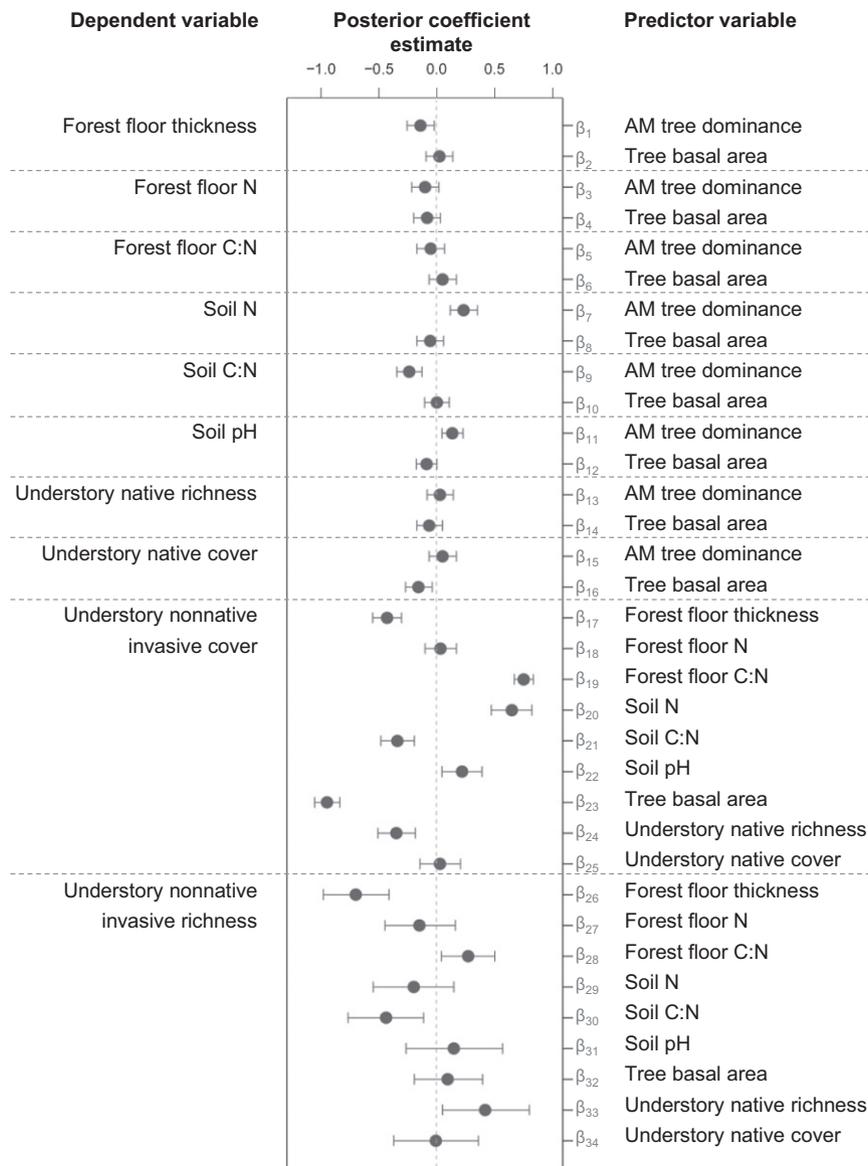


Figure 4 Estimated posterior coefficient values (β s) with 95% credible intervals (CIs) for relationships in Fig. 1.

for resisting understory invasions (Meiners *et al.* 2002; Schramm & Ehrenfeld 2010).

Previous studies of mycorrhizal associated plant invasions were mostly focused on mycorrhizal type (and status) of invaders (Stampe & Daehler 2003; Menzel *et al.* 2017). Utilising extensive forest inventory data compiled across the eastern US, our study underscores the role of overstory mycorrhizal type on understory plant invasions. We note that the data lack detailed belowground tissue traits and soil biota (e.g. fine root and litter production and turnover rate, fungal and bacterial compositions and enzyme activities), including pathogens, which can influence forest structure and functions (Wardle *et al.* 2004; McCormack *et al.* 2014). For example, ECM trees can inhibit pathogenic damage and facilitate conspecific tree seedlings (Bennett *et al.* 2017), although it is an open question whether the pathogen-associated feedback also relates to invasions of understory species (e.g. shrubs, herbaceous). These detailed fine-scale data

will help to better understand mycorrhizal mediated invasion patterns and processes. Nevertheless, our study demonstrated the strong correlation between the forest AM-ECM mycorrhizal gradient and understory plant invasions, indicating that dominant forest mycorrhizal type mediates plant invasions.

We acknowledge that it is difficult from this study, using observational field data, to address a causal relationship between AM tree dominant forests and understory plant invasions. Controlled experiments (or repeated inventory data) testing the relative impacts of understory invasions and the dominant forest mycorrhizal type on soil nutrients dynamics will be useful to tease out the causal relationships. We further suggest evaluation of our results by investigating whether the dominant forest mycorrhizal type and understory invasion relationships exist at a larger scale (e.g. continental USA or global scale). More complete vegetation inventory database information (e.g. clear species ID) paired with soil attributes

will be able to help address those relationships across broader scales.

Non-native invasive plants are an important driver of ecosystem function and stability (Liao *et al.* 2008; Ehrenfeld 2010; Vilà *et al.* 2011; Fei *et al.* 2014; Jo *et al.* 2017). Our findings on the linkage between forest mycorrhizal type and plant invasions suggest that forest mycorrhizal type is an important indicator of plant invasions. As forests in the eastern USA shifting from ECM dominated oak-hickory (*Quercus* & *Carya* Spp.) forests to AM dominated maple (*Acer* Spp.) forests (Fei & Steiner 2007; Fei *et al.* 2011), more invasion by exotic plants will likely occur. Given that invaders often facilitate nutrient cycling and have more efficient resource-use strategies, the increased invader abundance in AM tree dominant forests can further alter ecosystem structure and functions.

ACKNOWLEDGEMENTS

This work was partially supported by a postdoc fellowship by Department of Forestry and Natural Resources at Purdue University to IJ and National Science Foundation Macrosystems Biology to SF and KMP (grant number 1638702). We thank E. McCallen, G. Nunez-Mir, L. Tedersoo, and three anonymous reviewers for valuable comments that improved the manuscript.

AUTHORSHIP

IJ and SF conceived the study. IJ, KMP, and GMD provided data. IJ performed the analyses and drafted the manuscript. All authors contributed substantially to revisions and confirmed the final version of the manuscript.

DATA ACCESSIBILITY STATEMENT

Vegetation inventory and soil data used in this study is available at an open data repository (Purdue University Research Repository, <https://doi.org/10.4231/r73f4msb>).

REFERENCES

- Akhmetzhanova, A.A., Soudzilovskaia, N.A., Onipchenko, V.G., Cornwell, W.K., Agafonov, V.A., Selivanov, I.A. *et al.* (2012). A rediscovered treasure: mycorrhizal intensity database for 3000 vascular plant species across the former Soviet Union: Ecological Archives E093-059. *Ecology*, 93, 689–690.
- Augusto, L., Ranger, J., Binkley, D. & Rothe, A. (2002). Impact of several common tree species of European temperate forests on soil fertility. *Ann. For. Sci.*, 59, 233–253.
- Averill, C., Turner, B.L. & Finzi, A.C. (2014). Mycorrhiza-mediated competition between plants and decomposers drives soil carbon storage. *Nature*, 505, 543–545.
- Beatty, S.W. & Sholes, O.D.V. (1988). Leaf litter effect on plant species composition of deciduous forest treefall pits. *Can. J. For. Res.*, 18, 553–559.
- Bennett, J.A., Maherali, H., Reinhart, K.O., Lekberg, Y., Hart, M.M. & Klironomos, J. (2017). Plant-soil feedbacks and mycorrhizal type influence temperate forest population dynamics. *Science*, 355, 181–184.
- Binkley, D. & Giardina, C. (1998). Why do tree species affect soils? The warp and woof of tree-soil interactions. In: *Plant-induced soil changes: Processes and feedbacks* (ed. van Breemen, Nico). Dordrecht Netherlands, Springer, pp. 89–106.
- Brundrett, M.C. (2009). Mycorrhizal associations and other means of nutrition of vascular plants: understanding the global diversity of host plants by resolving conflicting information and developing reliable means of diagnosis. *Plant Soil*, 320, 37–77.
- Brundrett, M., Murase, G. & Kendrick, B. (1990). Comparative anatomy of roots and mycorrhizae of common Ontario trees. *Can. J. Bot.*, 68, 551–578.
- Bueno, C.G., Moora, M., Gerz, M., Davison, J., Öpik, M., Pärtel, M. *et al.* (2017). Plant mycorrhizal status, but not type, shifts with latitude and elevation in Europe. *Glob. Ecol. Biogeogr.*, 26, 690–699.
- Cleland, D., Freeouf, J., Keys, J., Nowacki, G., Carpenter, C. & McNab, W. (2007). Ecological subregions: sections and subsections for the conterminous United States.
- Cornelissen, J.C., Aerts, R.A., Cerabolini, B.C., Werger, M.W. & van der Heijden, M. (2001). Carbon cycling traits of plant species are linked with mycorrhizal strategy. *Oecologia*, 129, 611–619.
- Davis, M., Grime, J. & Thompson, K. (2000). Fluctuating resources in plant communities: a general theory of invasibility. *J. Ecol.*, 88, 528–534.
- Development Core Team, R. (2014). *R: A language and environment for statistical computing*. Austria, Vienna.
- Domke, G.M., Perry, C.H., Walters, B.F., Woodall, C.W., Russell, M.B. & Smith, J.E. (2016). Estimating litter carbon stocks on forest land in the United States. *Sci. Total Environ.*, 557–558, 469–478.
- Domke, G.M., Perry, C.H., Walters, B.F., Nave, L.E., Woodall, C.W. & Swanston, C.W. (2017). Toward inventory-based estimates of soil organic carbon in forests of the United States. *Ecol. Appl.*, 27, 1223–1235.
- Ehrenfeld, J. (2003). Effects of exotic plant invasions on soil nutrient cycling processes. *Ecosystems*, 6, 503–523.
- Ehrenfeld, J.G. (2010). Ecosystem Consequences of Biological Invasions. *Annu. Rev. Ecol. Evol. Syst.*, 41, 59–80.
- Facelli, J.M. & Pickett, S.T.A. (1991). Plant litter: its dynamics and effects on plant community structure. *Bot. Rev.*, 57, 1–32.
- Fei, S. & Steiner, K. (2007). Evidence for increasing red maple abundance in the eastern United States. *For. Sci.*, 53, 473–477.
- Fei, S., Kong, N., Steiner, K.C., Moser, W.K. & Steiner, E.B. (2011). Change in oak abundance in the eastern United States from 1980 to 2008. *For. Ecol. Manag.*, 262, 1370–1377.
- Fei, S., Phillips, J. & Shouse, M. (2014). Biogeomorphic impacts of invasive species. *Annu. Rev. Ecol. Evol. Syst.*, 45, 69–87.
- Finzi, A.C., Van Breemen, N. & Canham, C.D. (1998). Canopy tree-soil interactions within temperate forests: species effects on soil carbon and nitrogen. *Ecol. Appl.*, 8, 440–446.
- Fridley, J.D. & Craddock, A. (2015). Contrasting growth phenology of native and invasive forest shrubs mediated by genome size. *New Phytol.*, 207, 659–668.
- Funk, J.L. & Vitousek, P.M. (2007). Resource-use efficiency and plant invasion in low-resource systems. *Nature*, 446, 1079–1081.
- Gelman, A. & Hill, J. (2006). *Data Analysis Using Regression and Multilevel/Hierarchical Models*. Cambridge University Press, Cambridge.
- Gelman, A., Carlin, J.B. & Stern, H.S. (2014). *Bayesian Data Analysis*. Taylor & Francis, Abingdon, UK.
- Ghosh, S.K., Mukhopadhyay, P. & Lu, J.-C. (2006). Bayesian analysis of zero-inflated regression models. *J. Stat. Plann. Inference*, 136, 1360–1375.
- Guo, Q., Fei, S., Dukes, J.S., Oswald, C.M., Iii, B.V.I. & Potter, K.M. (2015). A unified approach for quantifying invasibility and degree of invasion. *Ecology*, 96, 2613–2621.
- Heberling, J.M. & Fridley, J.D. (2013). Resource-use strategies of native and invasive plants in Eastern North American forests. *New Phytol.*, 200, 523–533.
- van der Heijden, M.G.A., Martin, F.M., Selosse, M.-A. & Sanders, I.R. (2015). Mycorrhizal ecology and evolution: the past, the present, and the future. *New Phytol.*, 205, 1406–1423.

- Iannone, B.V., Oswalt, C.M., Liebhold, A.M., Guo, Q., Potter, K.M., Nunez-Mir, G.C. *et al.* (2015). Region-specific patterns and drivers of macroscale forest plant invasions. *Divers. Distrib.*, 21, 1181–1192.
- Iannone, B.V., Potter, K.M., Hamil, K.-A.D., Huang, W., Zhang, H., Guo, Q. *et al.* (2016). Evidence of biotic resistance to invasions in forests of the Eastern USA. *Landscape Ecol.*, 31, 85–99.
- Jo, I., Fridley, J.D. & Frank, D.A. (2015). Linking above- and belowground resource use strategies for native and invasive species of temperate deciduous forests. *Biol. Invasions*, 17, 1545–1554.
- Jo, I., Fridley, J.D. & Frank, D.A. (2017). Invasive plants accelerate nitrogen cycling: evidence from experimental woody monocultures. *J. Ecol.*, 105, 1105–1110. In press.
- Liao, C., Peng, R., Luo, Y., Zhou, X., Wu, X., Fang, C. *et al.* (2008). Altered ecosystem carbon and nitrogen cycles by plant invasion: a meta-analysis. *New Phytol.*, 177, 706–714.
- Lin, G., McCormack, M.L., Ma, C. & Guo, D. (2017). Similar belowground carbon cycling dynamics but contrasting modes of nitrogen cycling between arbuscular mycorrhizal and ectomycorrhizal forests. *New Phytol.*, 213, 1440–1451.
- Martin, P., Canham, C. & Marks, P. (2008). Why forests appear resistant to exotic plant invasions: intentional introductions, stand dynamics, and the role of shade tolerance. *Front. Ecol. Environ.*, 7, 142–149.
- McCormack, M.L., Lavelly, E. & Ma, Z. (2014). Fine-root and mycorrhizal traits help explain ecosystem processes and responses to global change. *New Phytol.*, 204, 455–458.
- Meiners, S.J., Pickett, S.T.A. & Cadenasso, M.L. (2002). Exotic plant invasions over 40 years of old field successions: community patterns and associations. *Ecography*, 25, 215–223.
- Menzel, A., Hempel, S., Klotz, S., Moora, M., Pysek, P., Rillig, M.C. *et al.* (2017). Mycorrhizal status helps explain invasion success of alien plant species. *Ecology*, 98, 92–102.
- Midgley, M.G. & Phillips, R.P. (2014). Mycorrhizal associations of dominant trees influence nitrate leaching responses to N deposition. *Biogeochemistry*, 117, 241–253.
- Muller, R.N. (2003). Nutrient relations of the herbaceous layer in deciduous forest ecosystems. In: *The Herbaceous Layer in Forests of Eastern North America* (ed. Frank, Gilliam.) Oxford University Press, New York, pp. 15–37.
- O'Neill, K.P., Amacher, M.C. & Perry, C.H. (2005). Soils as an indicator of forest health: a guide to the collection, analysis, and interpretation of soil indicator data in the Forest Inventory and Analysis program. *Gen. Tech. Rep. NC-258. St. Paul, MN: U.S. Department of Agriculture, Forest Service, North Central Research Station*. 53p.
- Phillips, R.P., Brzostek, E. & Midgley, M.G. (2013). The mycorrhizal-associated nutrient economy: a new framework for predicting carbon-nutrient couplings in temperate forests. *New Phytol.*, 199, 41–51.
- Plummer, M. (2003). JAGS: A program for analysis of Bayesian graphical models using Gibbs sampling. *Proceedings of the 3rd international workshop on distributed statistical computing*, Vienna, p. 125.
- PRISM Climate Group (2012). Oregon State University. Available at: <http://prism.oregonstate.edu>. Last accessed 31 August 2017.
- Rathbun, S.L. & Fei, S. (2006). A spatial zero-inflated poisson regression model for oak regeneration. *Environ. Ecol. Stat.*, 13, 409.
- Sayer, E.J. (2006). Using experimental manipulation to assess the roles of leaf litter in the functioning of forest ecosystems. *Biol. Rev.*, 81, 1–31.
- Schramm, J. & Ehrenfeld, J. (2010). Leaf litter and understory canopy shade limit the establishment, growth and reproduction of *Microstegium vimineum*. *Biol. Invasions*, 12, 3195–3204.
- Schwarz, G.E. & Alexander, R. (1995). State soil geographic (STATSGO) data base for the conterminous United States, US Geological Survey Publication No. 95-449. Available at: <https://pubs.er.usgs.gov/publication/ofr95449>. Last accessed 31 August 2017.
- Selosse, M.A., Richard, F., He, X. & Simard, S.W. (2006). Mycorrhizal networks: des liaisons dangereuses? *Trends Ecol. Evol.*, 21, 621–628.
- Smith, S.E. & Read, D. (2008). *Mycorrhizal Symbiosis*. Academic Press, Cambridge, MA.
- Stampe, E.D. & Daehler, C.C. (2003). Mycorrhizal species identity affects plant community structure and invasion: a microcosm study. *Oikos*, 100, 362–372.
- Su, Y.-S. & Yajima, M. (2012). R2jags: A Package for Running jags from R.R package version 0.03-08. Available at: <http://CRAN.R-project.org/package=R2jags>. Last accessed 11 October 2017.
- USDA Forest Service (2017a) The Forest Inventory and Analysis Database: Database Description and User Guide for Phase 2 (version 7.0). Available at: https://www.fia.fs.fed.us/library/database-documentation/current/ver70/FIADB%20User%20Guide%20P2_7-0_ntc.final.pdf. Last accessed 9 May 2017.
- USDA Forest Service (2017b). The Forest Inventory and Analysis Database: Database Description and User Guide for Phase 3 (version 6.0.1). Available at: https://www.fia.fs.fed.us/library/database-documentation/current/ver60/FIADB%20User%20Guide%20P3_6-0-1_final.pdf. Last accessed 9 May 2017.
- USDA-NRCS (1999). *Soil taxonomy—a basic system of soil classification for making and interpreting soil surveys: by Soil Survey Staff, 2nd edition, Natural Resources Conservation Service, US Department of Agriculture Handbook number 436*.
- USDA-NRCS (2016). The PLANTS database. Available at: <http://plants.usda.gov>. Last accessed 9 March 2017.
- Valladares, F. & Niinemets, Ü. (2008). Shade Tolerance, a Key Plant Feature of Complex Nature and Consequences. *Annu. Rev. Ecol. Evol. Syst.*, 39, 237–257.
- Vilà, M., Espinar, J.L., Hejda, M., Hulme, P.E., Jarošík, V., Maron, J.L. *et al.* (2011). Ecological impacts of invasive alien plants: a meta analysis of their effects on species, communities and ecosystems. *Ecol. Lett.*, 14, 702–708.
- Wang, B. & Qiu, Y.L. (2006). Phylogenetic distribution and evolution of mycorrhizas in land plants. *Mycorrhiza*, 16, 299–363.
- Wardle, D.A., Bardgett, R.D., Klironomos, J.N., Setälä, H., van der Putten, W.H. & Wall, D.H. (2004). Ecological Linkages Between Aboveground and Belowground Biota. *Science*, 304, 1629–1633.
- Wurzburger, N., Brookshire, E.N.J., McCormack, M.L. & Lankau, R.A. (2017). Mycorrhizal fungi as drivers and modulators of terrestrial ecosystem processes. *New Phytol.*, 213, 996–999.

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

Editor, Montserrat Vila

Manuscript received 12 June 2017

First decision made 23 July 2017

Second decision made 7 October 2017

Manuscript accepted 24 October 2017