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BRIEF COMMUNICATION

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Woody invaders are more highly colonized by arbuscular mycorrhizal fungi than congeneric native species

Louis J. Lamit[1,2] | Amy S. Giovati[1,2] | Insu Jo[3] | Doug A. Frank[1] | Jason D. Fridley[1]

[1]Department of Biology, Syracuse University, 107 College Place, Syracuse, NY 13244, USA

[2]Department of Environmental Biology, State University of New York College of Environmental Science and Forestry, 1 Forestry Drive, Syracuse, NY 13210, USA

[3]Manaaki Whenua—Landcare Research, 54 Gerald Street, Lincoln 7608, New Zealand

Correspondence

Louis J. Lamit, Department of Biology, Syracuse University, 107 College Place, Syracuse, NY 13244, USA.
Email: ljlamit@syr.edu

Abstract

Premise: Invasive species tend to possess acquisitive plant traits that support fast growth and strong competitive ability. However, the relevance of symbioses with arbuscular mycorrhizal fungi (AMF) to the fast growing, acquisitive strategy of invasive species is still unclear.

Methods: We measured AMF colonization in roots of five congeneric pairs of invasive and native eastern North American woody species (10 species total; 4 lianas, 6 shrubs) that were grown in a monoculture common garden experiment in Syracuse, NY. We then examined the relationships of AMF colonization to above and belowground traits of these species.

Results: Total AMF colonization and arbuscule colonization were greater in invasive compared to native woody species, a pattern that was more distinct in congeneric shrubs than congeneric lianas. The level of AMF colonization was also positively correlated with traits indicative of rapid plant growth and nutrient uptake.

Conclusions: The concordance of a resource-acquisitive strategy with higher AMF colonization suggests that symbioses with AMF may be part of the strategy by which invasive woody plants of eastern North America are able to maintain fast growth rates and outcompete their native counterparts.

KEYWORDS

arbuscular mycorrhiza, *Celastrus*, eastern North America, *Frangula*, invasive species, liana, *Lonicera*, shrub

Invasive plants can drive changes in ecosystem function and undermine native biodiversity (Webster et al., 2006; Castro-Diaz et al., 2014; Jo et al., 2017). The ability of invasive species to successfully establish and spread in novel habitats can in part be attributed to their functional traits (Guo et al., 2018). In addition to typically producing large quantities of easily dispersed propagules, invasive species often exhibit traits indicative of fast-growing, resource-acquisitive strategies that may give them a competitive advantage (Funk and Vitousek, 2007; Penuelas et al., 2010; Heberling and Fridley, 2013, 2016; Ordonez and Olff, 2013). For example, compared to co-occurring native species, woody understory invaders of eastern North American (ENA) forests tend to have higher photosynthetic rates and foliar nutrient content, and leaf phenology that increases their ability to photosynthesize late into autumn (Fridley, 2012; Heberling and Fridley, 2013). Belowground, ENA understory invaders exhibit higher fine root production, greater specific root length, and increased soil N uptake (Jo et al., 2015, 2017). However, it is unknown whether native and invasive species of ENA forests differ in their interactions with arbuscular mycorrhizal fungi (AMF), despite the importance of AMF to plant nutrient uptake.

Soil microorganisms such as AMF can play important roles in the process of invasion and ecosystem modification by non-native plants (Pringle et al., 2009; Dawson and Schrama, 2016; Grove et al., 2017). In some cases, invaders are nonmycorrhizal or have reduced dependence on AMF symbioses; this may allow invasive species to proliferate in disturbed environments with limited mycorrhizal inoculum potential (Owen et al., 2013; Menzel et al., 2017) and can lead to a depression in inoculum or shift in the AMF species pool available to native plants (Burke, 2008; Pringle et al., 2009; Vogelsang and Bever, 2009; Zubek et al., 2016). In contrast, some invasive species regularly form symbioses with AMF (e.g., Moora et al., 2011). These invaders may receive important growth and/or competitive benefits that facilitate the invasion process (e.g., Marler et al., 1999; Dong et al., 2021). AMF-dependent invaders can also modify AMF communities if they host AMF species that are distinct from those preferred by native plants (e.g., Hawkes et al., 2006; Moora et al., 2011). Irrespective of their mycorrhizal status, invaders can indirectly affect AMF and other soil microbes when their leaf litter and rhizosphere inputs modulate soil chemistry and nutrient cycling (e.g., Stinson et al., 2006; Arthur et al., 2012; Jo et al., 2017). To date, meta-analyses drawn primarily from studies with herbaceous species have not revealed systematic differences between how native and invasive species interact with AMF (e.g., Bunn et al., 2015; Reinhart et al., 2017). However, given the importance of woody invaders in habitats around the world (Richardson and Rejmanek, 2011), there is a clear need for more focus on plant–AMF interactions within the context of woody plant invasion.

We utilized a common garden containing monocultures of woody native and non-native invasive ENA forest species to investigate the relationship among AMF colonization, plant functional traits, and plant nativity. We addressed the following questions: (1) Does the level of AMF colonization in invasive species differ from those of congeneric native species? (2) Do above- and belowground plant functional traits covary with AMF colonization across species, and is this potential covariation related to whether species are native or invasive? AMF are dependent on plant host-derived energy in the form of carbon and assist plants in the uptake of limiting nutrients. Therefore, we predicted that the fast-growing, resource-acquisitive strategy of many invasive species allows them to support a greater abundance of AMF relative to native congeneric species. This prediction is motivated by the observation that some invasive species can be highly colonized by AMF (e.g., Zhang et al., 2010; Dong et al., 2021), although direct comparisons to congeneric native taxa are often lacking. Alternatively, AMF colonization might also be lower in invasive species compared to congeneric native species because traits often ascribed to a fast growth strategy (e.g., high production of fine, short-lived, thin roots with high specific root length) are associated with reduced AMF colonization and/or lower dependence on AMF (Hetrick, 1991; Wilson and Hartnett, 1998; Brundrett, 2002; Comas and Eissenstat, 2004; Eissenstat et al., 2015; Unger et al., 2017; McCormack and Iverson, 2019; but see Maherali, 2014). This link between functional traits and AMF is often examined outside the context of species invasions (e.g., Kong et al., 2014; Ma et al., 2018), despite the fact that the fast-growth strategy of many invasive species relative to native species offers a useful context to understand the connection between plant strategy and mycorrhizal symbioses.

MATERIALS AND METHODS

Study system

In spring of 2012, we established a common garden containing five native and five non-native species grown in monoculture plots (Jo et al., 2017). The garden included three genera of shrubs and lianas of ENA forests, with each genus represented by at least one native and one invasive species (Table 1). All non-native species included in the study are considered invasive in ENA forests (Fridley, 2008) and are hereafter referred to as invaders or invasive species. The common garden was established in an existing mowed field within an ~40 × 40 m area of homogenous flat topography that was evenly tilled. Each monoculture plot was 2.5 × 2.5 m and contained three clonally propagated conspecific individuals. Each species was represented by three monoculture plots that were divided evenly among three spatial blocks and assigned to random locations within each block, except *Frangula caroliniana*, which was only

TABLE 1 Plant species used in this study, with sample sizes by date.

Latin binomial	Species abbreviation	Family	Nativity	Growth form	May *N*	July *N*	September *N*
Celastrus orbiculatus Thunb.	CEOR	Celastraceae	Non-native	Liana	3	3	3
Celastrus scandens L.	CESC	Celastraceae	Native	Liana	3	3	3
Frangula alnus Mill.	FRAL	Rhamnaceae	Non-native	Shrub	2	0	3
Frangula caroliniana (Walter) A. Gray	FRCA	Rhamnaceae	Native	Shrub	1	0	2
Lonicera canadensis W. Bartram ex Marshall	LOCA	Caprifoliaceae	Native	Shrub	0	3	2
Lonicera sempervirens L.	LOSE	Caprifoliaceae	Native	Liana	3	2	3
Lonicera villosa (Michx.) Schult.	LOVI	Caprifoliaceae	Native	Shrub	0	3	0
Lonicera fragrantissima Lindl. & Paxton	LOFR	Caprifoliaceae	Non-native	Shrub	3	3	3
Lonicera japonica Thunb.	LOJA	Caprifoliaceae	Non-native	Liana	3	3	3
Lonicera morrowii A. Gray	LOMO	Caprifoliaceae	Non-native	Shrub	3	3	3
				N_{date} =	21	23	25
					$N_{\text{total}} = 69$		

represented by two plots, for a total of 29 plots. Root mixing among plots was prohibited by inserting plastic sheeting to 50-cm depth around their perimeters. To promote successful establishment in the first year, the soil surface of each plot was covered with landscape cloth and watered daily during the growing season. The cloth was removed in spring of 2013, and weeds were subsequently removed on a weekly basis during the growing season for the duration of the experiment. See Jo et al. (2017) for further details on the experimental design and plot preparation.

Root collection and AMF quantification

AMF colonization was measured in archived roots that were originally collected by Jo et al. (2017) for root productivity and chemistry measurements. Root samples were obtained from harvests of point-in-space ingrowth cores (Milchunas et al., 2005) installed in September 2013 and harvested in late May, late July, late September, and late November of 2014. Ingrowth cores (4 cm in diameter by 10 cm in height) were composed of 1 × 1 cm plastic mesh, installed at a depth of 0–10 cm, and filled with root-free soil from the site. Each plot contained 9–12 cores from which fine roots (including first to third order) were pooled to obtain one representative sample per plot at each harvest date. Collected roots were cleaned with deionized water and dried at 65°C for >2 days.

Roots from the May, July, and September 2014 harvest dates, which spanned the majority of the growing season, were used for AMF staining following a protocol modified from Vierheilig et al. (1998). Dried fine roots were rehydrated in water, cleared by submerging in 10% (mass/volume) potassium hydroxide at 90°C for 20 or more minutes, and then rinsed with tap water. During this process, the efficiency of clearing was checked under a microscope at 200× magnification. In some cases, after clearing, darker pigmented species (e.g., those in the Rhamnaceae) were briefly submerged in 3% H_2O_2, followed by a rinse with tap water. Roots were then acidified for 5 min in white vinegar (5% acetic acid, volume/volume), stained by heating in 5% Pelikan Blue ink (volume/volume) in white vinegar, rinsed twice with tap water to remove excess ink, and then destained overnight in tap water amended with a few drops of white vinegar.

AMF colonization was quantified using the magnified line intersect method (McGonigle et al., 1990) at 400× magnification. A minimum of 100 intersects were scored for each sample, with the exception of six samples whose ingrowth cores did not yield enough roots to reach 100 intersects. At each intersect, all AMF structures within roots were recorded, including hyphae, vesicles, arbuscules, and hyphal coils. For this paper, we focused on total AMF colonization (percentage of intersects with AMF structure of any kind) and colonization by arbuscules, the primary sites of resource exchange for the symbiosis. Aside from hyphae and arbuscules, other structures were present in an extremely small number of the intersects. In some cases, root material from a sample was consumed in previous measurements of root chemistry conducted by Jo et al. (2017) or roots were too difficult to sufficiently clear for visual inspection, reducing the sample size for some species. Each species was represented by three to nine replicates (median = 8.5) in the final data set, for a total sample size of 69 observations, with all but 1 species being represented in two or more sampling dates (Table 1).

Plant traits

Previously published data were incorporated into the analyses to link AMF colonization to plant resource-use strategy. One set of traits was measured during the 2014 growing season from each of the same monoculture plots in which roots for mycorrhizal work were collected. These included annual leaf production ($\mathrm{kg\,plot^{-1}}$), fine root production ($\mathrm{kg\,plot^{-1}}$ 10 cm soil depth), plant nitrogen uptake (plant N pool; $\mathrm{g\,plot^{-1}}$), and litter nitrogen pool ($\mathrm{g\,plot^{-1}}$) originally reported by Jo et al. (2017). Additional traits were measured on two to three individuals of each species in a common garden located at the same location. These included specific root length (SRL, $\mathrm{m\,g^{-1}}$) and root tissue density (RTD, $\mathrm{g\,cm^{-3}}$) from Jo et al. (2015), from which we also calculated average root diameter (RD, mm), and specific leaf area (SLA, $\mathrm{cm^2\,g^{-1}}$) and maximum photosynthetic rate ($A_{\max} = \mu\mathrm{mol\,CO_2\,m^{-2}\,s^{-1}}$) from Fridley (2012).

Statistical analyses

Total percentage AMF colonization and arbuscule percentage colonization were analyzed with linear mixed effects models. Models for each AMF variable included the fixed effects of plant nativity (native vs. invasive), plant-growth form (shrub vs. liana), plant genus, and a nativity-by-plant-growth form interaction, as well as the random effects of block, plant species, individual monoculture plot and harvest date. Harvest date was treated as a random effect because repeated sampling of ingrowth cores may produce trends that could confound seasonal effects; therefore, we refrained from interpreting differences among harvest dates. As a complementary analysis, a second set of mixed models were run with AMF data from the harvest date that had the largest sample size (September 2014); these models included plant nativity, plant-growth form, plant genus, and a nativity-by-plant-growth form interaction as fixed effects and block and plant species as random effects. All statistical analyses were conducted in R 4.03 (R Core Team, 2020). Models were fit using restricted maximum likelihood in the package lmerTest (Kuznetsova et al., 2017), with fixed effects tested using the Kenward–Roger approximation and type III sums of squares. The emmeans package (Lenth, 2020) was used to calculate marginal means.

A second set of analyses was aimed at identifying correlative relationships of total AMF colonization and arbuscule colonization with plant traits. These analyses utilized tests based on ranked data because some bivariate relationships were monotonic but nonlinear. Species-level estimates for each variable were obtained by averaging values from replicate plants. Individual bivariate relationships of AMF colonization variables with plant traits were examined with Spearman's rank correlations. Species values for plant traits and AMF variables were then ordinated together using principal component analysis (PCA) on ranked data, with the vegan package (Oksanen et al., 2020). A complementary set of Spearman's rank correlations was then run with AMF data averaged for each species from roots collected only in September 2014.

RESULTS

Variation in total AMF colonization was explained by nativity, growth form, and genus (Figure 1; Appendix S1: Table S1). The highest total colonization (~70 to 75% on average) was exhibited by the invaders *Frangula alnus* and *Lonicera japonica* and the native *Lonicera sempervirens*, which was approximately 3.5-fold greater than colonization in the species with the lowest total AMF colonization, the natives *Lonicera villosa* and *Lonicera canadensis* (~20 to 25% on average; Figure 1A). All main fixed effects in the linear mixed model were significant predictors of total AMF colonization (nativity, $F_{1,3.80} = 13.8$, $P = 0.023$; growth form, $F_{1,3.47} = 30.4$, $P = 0.008$; genus, $F_{2,3.93} = 10.7$, $P = 0.026$). Importantly, the influence of nativity on total AMF colonization was contingent on growth form (nativity × growth form, $F_{2,3.85} = 8.12$, $P = 0.048$). On average, total AMF colonization of native shrubs (marginal mean = 28.2%) was half the level of that for invasive shrubs (marginal mean = 57.9%; Figure 1A). In contrast, AMF colonization of native and invasive lianas was relatively high (marginal mean = 57.0% and 61.7%, respectively) and similar to invasive shrubs (Figure 1A). Mixed models using total AMF colonization data from only a single harvest date (September 2014) exhibited equivalent results to those with the full data set (Appendix S1: Table S2).

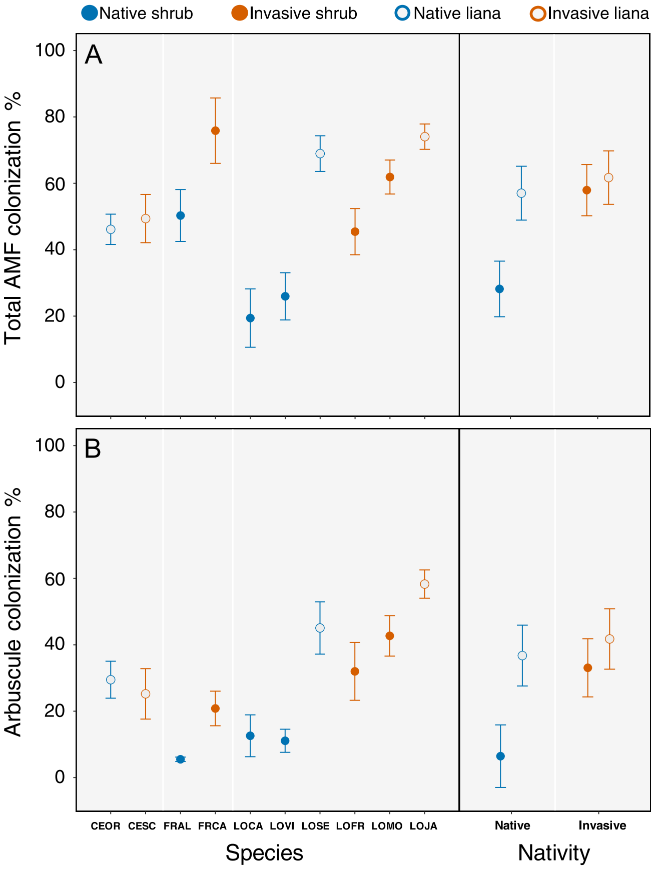

FIGURE 1 Total AMF (A) and arbuscule (B) colonization averages ± 1 SE for plant species and marginal means ± 1 SE for nativity by plant-growth form. See Table 1 for plant species name abbreviations.

Patterns of arbuscule colonization were similar to those of total AMF colonization, with some key differences (Figure 1; Appendix S1: Table S3). The invader *Lonicera japonica* had the highest average colonization of arbuscules (nearly 60%) and one of the highest total AMF colonization levels (Figure 1A, B). In contrast, the native *Frangula caroliniana* had the lowest average colonization of arbuscules (approximately 6%), despite having intermediate total AMF colonization (Figure 1A, B). All main fixed effects in the linear mixed model were significant predictors of arbuscule colonization (nativity, $F_{1,3.80} = 9.10$, $P = 0.042$; growth form, $F_{1,3.48} = 19.2$, $P = 0.016$; genus, $F_{2,3.92} = 7.35$, $P = 0.047$). Arbuscule colonization was elevated in lianas compared to shrubs for native and invasive species, leading to a lack of statistical significance for the nativity by growth form interaction (nativity × growth form, $F_{2,3.85} = 4.63$, $P = 0.100$). However, arbuscule colonization in invasive shrubs was on average greater than in native shrubs, and the difference in arbuscule colonization between invasive shrubs (marginal mean = 33.1%) and invasive lianas (marginal mean = 41.8%), was less than that between native shrubs (marginal mean = 6.4%) and native lianas (marginal mean = 33.1%; Figure 2B). Mixed models using arbuscule colonization data from only a single harvest date (September 2014) exhibited similar results to those with the full data set (Appendix S1: Table S4), although the nativity term was marginally significant.

AMF colonization correlated with the majority of plant traits (Figure 2; Appendix S2: Table S1). Of the plant traits measured in the monoculture plots (where AMF roots were also collected), total AMF and arbuscule colonization increased with leaf and fine root production, plant nitrogen uptake, and the litter nitrogen pool (Figure 2A). Of the plant traits measured in the adjacent common garden, total AMF colonization showed distinct positive relationships with specific leaf area and specific root length, although the relationship with specific root length was not statistically significant (Figure 2B).

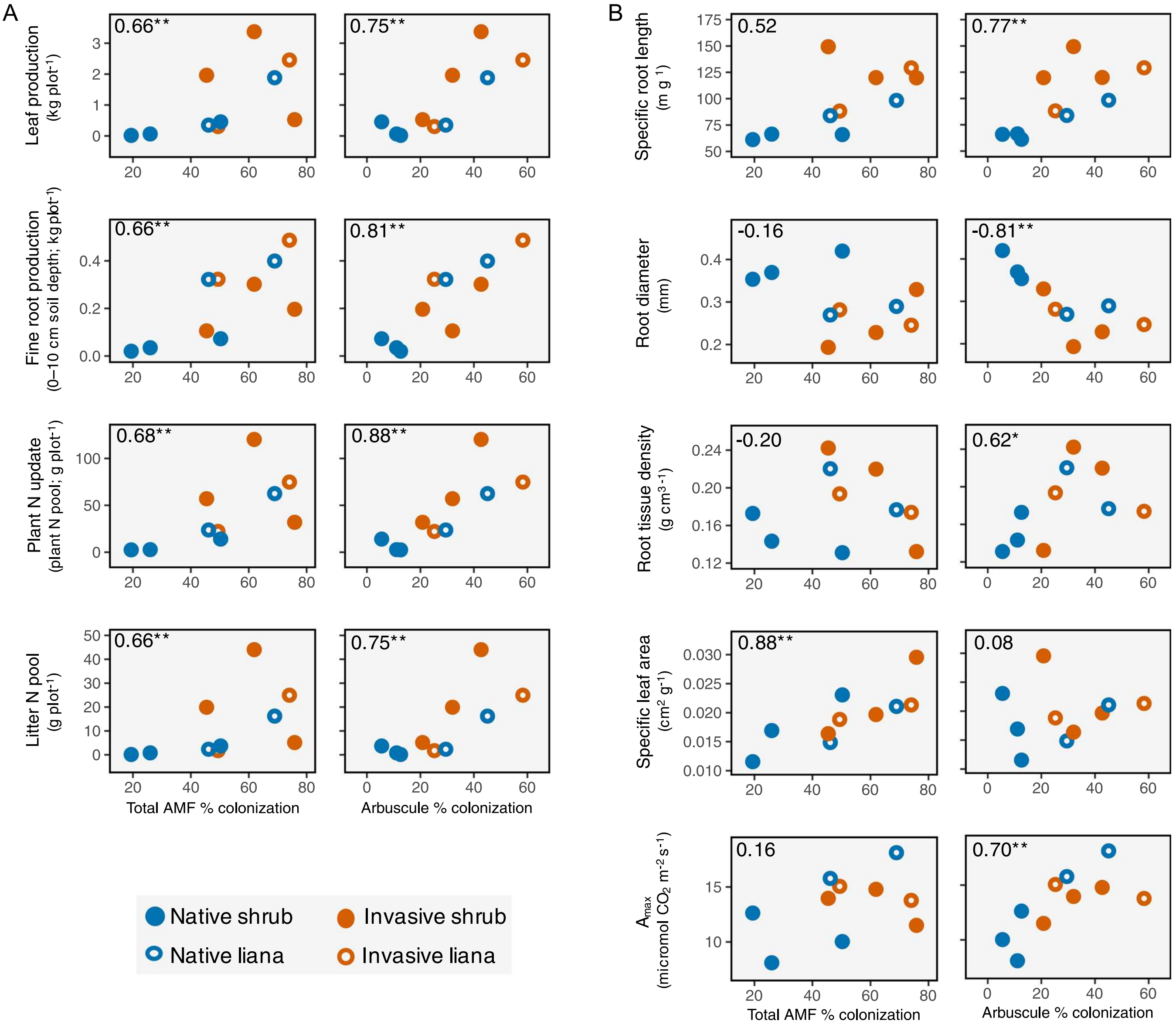

FIGURE 2 Bivariate plots of total AMF colonization and arbuscule colonization with traits measured on plants growing (A) in monocultures and (B) in an adjacent common garden. Numbers in the upper left of each plot are Spearman's rho. $^*P < 0.10$, $^{**}P < 0.05$. See Appendix S2 for precise *P*-values.

Arbuscule colonization showed increases with specific root length, root tissue density, and $A_{\max}$, and a negative relationship with root diameter (Figure 2B). Many of the observed relationships of total AMF and arbuscule colonization with plant traits were driven by greater colonization in lianas and invasive species (Figure 2A, B). Although there was a loss of power with the reduced sample size, correlations using AMF variables from only a single harvest date (September 2014) exhibited that same overall patterns as those with the full data set (Appendix S2: Table S2).

The first two axes of the PCA explained 86% of the variation in plant trait data, with the majority explained by PC1 (62%). Invaders and lianas tended to have low values on PC1 while native shrubs had high values (Figure 3). Mycorrhizal colonization variables and most plant traits were negatively correlated with PC1 (Figure 3), although some of these variables showed comparable or stronger loadings on PC2 (Figure 3). In contrast to other plant traits, root diameter increased along PC1 (Figure 3).

DISCUSSION

We found that the level of AMF colonization varied across woody species in relation to growth form (shrub vs. liana) and nativity status. These patterns were exhibited using all AMF data from the three sampling dates, and when using AMF data from only one sampling date, indicating that variation in species representation across ingrowth core harvest dates did

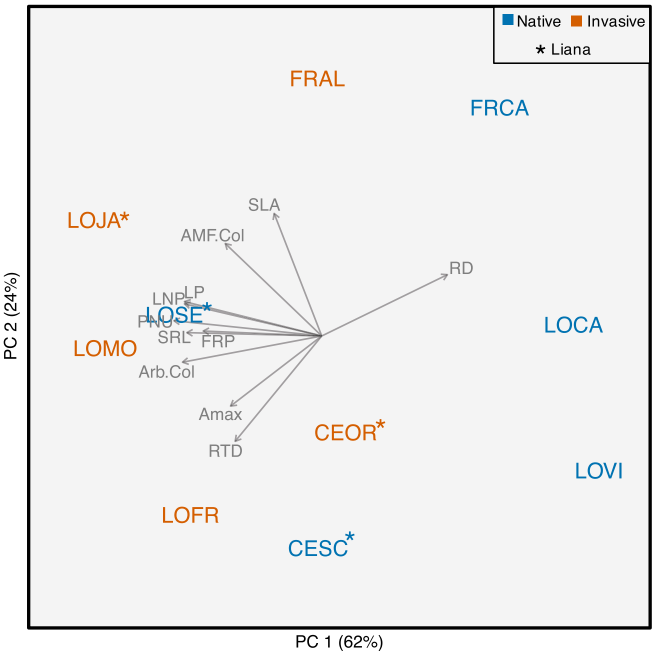

FIGURE 3 Principal component analysis of plant traits and AMF variables. See Table 1 for plant species name abbreviations. Abbreviations for variables and loadings on PC1 and PC2, respectively: LP = leaf production (−0.35, 0.15), FRP = fine root production (−0.30, 0.02), PNU = plant nitrogen uptake (−0.38, −0.07), LNP = litter nitrogen pool (−0.35, 0.15), SRL = specific root length (−0.34, 0.02), RD = root diameter (0.32, 0.28), RTD = root tissue density. (−0.22, −0.49), SLA = specific leaf area (−0.12, 0.57), A_{max} = maximum rate of photosynthesis (−0.23, −0.32). Asterisks indicate lianas, while all other species are shrubs.

not confound the overall results. For shrubs, AMF colonization was greater in invasive species compared to their native congeners. Because species were grown in a common garden, this difference in colonization levels was not driven by environment and points to the possibility of a general difference in how invasive understory ENA woody plants interact with AMF symbionts compared to congeneric native species. Other studies have found high colonization in invasive woody plants (e.g., Badalamenti et al., 2015; Yang et al., 2015), including some closely related to those we examined, such as *Lonicera maackii* (Alverson, 2013). Importantly, we systematically examined plant–AMF interactions for native and invasive woody plants paired within three plant genera. In a recent study involving phylogenetically paired native and invasive grassland species growing in monocultures, colonization was also greater in invaders compared to native species (Sielaff et al., 2019). In contrast, meta-analysis using a data set of primarily herbaceous species suggests that there is no general pattern in colonization between native and invasive species (Bunn et al., 2015). The discrepancy between our results and the findings from the meta-analysis points to the potential importance of accounting for relatedness when comparing native vs. invasive species interactions with AMF, since the shift in interaction can be obscured by other species-level attributes, including growth forms and phylogeny (Hinman et al., 2019).

The pattern of greater AMF colonization in invasive woody plants remained evident when only including arbuscules, the sites of resource exchange between symbionts. Although total colonization can be positively associated with plant benefit from AMF (Treseder, 2013), the connection with arbuscules is stronger evidence for a functional distinction in how the invasive species interact with AMF compared to native understory ENA woody species. Higher arbuscule colonization may benefit plant growth by increasing the uptake of limiting soil resources (Smith and Smith, 2011), which may contribute to the greater growth rates of invasive species in our study (Jo et al., 2017). Conversely, greater AMF colonization may be a fungal response to the fast growth rate of invasive species. The greater amount of aboveground biomass and root productivity observed for invasive taxa in these monocultures (Jo et al., 2017) may be due to a genetic predisposition of invasive taxa for fast growth that is independent of interactions with mycorrhizal fungi; invasive plants may support greater AMF in their roots even if they do not receive greater benefit from AMF than do natives. Our results highlight the need for controlled inoculation studies to elucidate how this distinction in colonization levels is related to a potential distinction in benefit between native and invasive shrubs from the AM symbiosis.

The strong relationships between AMF colonization and plant traits points to an important connection between the AM symbiosis and plant strategy. Highly AMF-colonized species tended to have combinations of aboveground (e.g., the highest A_{max}, leaf production) and belowground traits (e.g., the highest fine root productivity and specific root length, and the thinnest root diameters) indicative of a fast-growing, resource-acquisitive strategy. Similarly, the species with the greatest AMF colonization also had traits that were associated with faster overall plant–soil N cycling for the invasive species in this monoculture study (e.g., largest N uptake and litter N pools; Jo et al., 2017). The concordance of a fast-growing, resource-acquisitive strategy with faster N cycling and higher AMF colonization suggests that AMF may be part of the strategy by which these fast-growing species are able to maintain greater rates of N uptake even with depleted soil nutrient pools. Our results contrast the general expectation that species with resource-acquisitive fine root traits (e.g., small diameter, high SRL, high production) are less reliant on AMF (e.g., Hetrick, 1991; Reich, 2014; Ma et al., 2018; McCormack and Iverson, 2019, but see Maherali, 2014). Whether this pattern is the result of a smaller range of root trait values than seen in global studies or driven by the response of AMF to plant growth, rather than vice-versa, is unclear.

We observed a smaller difference in AMF colonization between native and invasive lianas compared to native and invasive shrubs. Plant-growth form is often cited as an important factor moderating mycorrhizal fungal interactions with plants (e.g., Hoeksema et al., 2010; Bunn et al., 2015); however, few studies to date have included lianas. Above- and belowground, lianas typically fall on the fast end of the plant strategy spectrum due to traits such as vigorous shoot growth, high specific leaf area and specific root length, and high branching intensity of fine roots (Ichihashi and Tateno, 2015; Collins et al., 2016). The similarity in functional strategy of native lianas to invaders, and the association of AMF colonization with functional traits, likely contributed to the growth form by nativity interaction in our study. Our findings contrast those of Collins et al. (2016), who observed that mycorrhizal fungi colonization (including AMF and ectomycorrhizal fungi pooled together) was generally lower in most tropical lianas compared to confamilial tropical tree species. The reasons for this contrast are unclear; however, other studies have found high levels of colonization in some of the lianas in our study (e.g., *Lonicera japonica*; Jiang et al., 2016).

CONCLUSIONS

In a monoculture common garden incorporating three woody plant genera, we found AMF colonization to be higher in invasive woody species that have more acquisitive resource-use strategies than congeneric native species. This pattern was more distinct for shrubs than for lianas in our data set, but the incorporation of more liana and shrub species in future studies is necessary to verify that this pattern is universal. Follow-up studies with a larger set of plant lineages will also be important for confirming that the correlations found here between AMF colonization and plant functional traits are evident across the whole ENA woody flora. Although the high AMF colonization in invaders was associated with a high proportion of arbuscules, possibly indicating higher rates of C-nutrient exchanges between invaders and AMF, it is unclear whether AMF in our study are drivers or passengers of the fast growth of invaders and the associated high rates of ecosystem N dynamics (Jo et al., 2017). The strong association between invasive plants and AMF colonization indicates that woody invaders are unlikely to significantly reduce the abundance of AMF communities in ENA forests. However, it is unknown whether invaders and natives associate with the same suite of AMF species, and it is possible that modification of the species pool by invaders could be detrimental to natives. Our results suggest that characterizing AMF community composition and controlled inoculations with AMF are important next steps to determine whether woody plant invasions are facilitated by AM fungi in ENA forests.

AUTHOR CONTRIBUTIONS

L.J.L., I.J., D.A.F., and J.D.F. were responsible for study conceptualization and funding acquisition. A.S.G., L.J.L., and I.J. conducted the research. L.J.L. conducted statistical analysis. L.J.L., A.S.G., D.A.F., and J.D.F. were responsible for writing the original draft and all authors participated in reviewing and editing the manuscript.

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DATA AVAILABILITY STATEMENT

AMF and root diameter data generated for this study are available in the Dryad Digital Repository at https://doi.org/10.5061/dryad.15dv41nzf (Lamit, 2022). See Fridley (2012) and Jo et al. (2015, 2017) for the previously published plant trait data utilized in this study.

ORCID

Louis J. Lamit http://orcid.org/0000-0002-0385-6010
Insu Jo http://orcid.org/0000-0002-1759-2319

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Appendix S1. ANOVA tables of mixed models for total arbuscular mycorrhizal fungal (AMF) root length colonization and only arbuscule colonization, for models that incorporate all three harvests dates, and for models run only with data from the September 2014 root harvest date.

Appendix S2. Bivariate Spearman's rho correlation analyses of plant traits with total arbuscular mycorrhizal fungal (AMF) root length colonization and only arbuscule colonization.

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