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Region-wide assessment of fine-scale associations between invasive plants and forest regeneration

Adrián Lázaro-Lobo [a,*], Rima D. Lucardi [b], Carlos Ramirez-Reyes [c], Gary N. Ervin [a]

[a] Department of Biological Sciences, Mississippi State University, MS 39762, United States
[b] Center for Forest Disturbance, Invasive Plants, Southern Research Station, United States Dept. of Agriculture, Forest Service, Athens, GA 30602, United States
[c] Department of Wildlife, Fisheries, and Aquaculture, Mississippi State University, MS 39762, United States

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ABSTRACT

Invasive plants are widely spread throughout the forests of the southern United States (US) and are expected to rapidly increase their distributional ranges over the next few decades. Multiple studies have shown that invasive plants pose great challenges to forest regeneration at local spatial scales; however, little is known about how those local-scale impacts of invasive plants may collectively influence forest regeneration at a regional scale. In this study, we hypothesized that invasive plants influence forest regeneration across southern US forests by altering tree seedling and sapling abundance and diversity. We used a total of 52,690 southern US forestland plots surveyed between 2015 and 2019 by the Forest Inventory and Analysis (FIA) program of the US Department of Agriculture Forest Service. We compiled presence/absence data from 16 major invasive plant taxa and calculated the number, richness, and diversity of seedlings and saplings for all major tree species present in the dataset. We used Generalized Linear Models to examine the relationship of the selected invasive plants to tree seedlings and saplings. We then used principal component analysis to evaluate whether negative relationships appeared to be related to niche differences. We found that the presence of invasive plants generally was negatively associated with tree seedling and sapling abundance, and that these negative interactions appeared to be independent of niche associations. Moreover, fast-growing hardwood tree species had the fewest negative species-wise associations with invasive plants, which suggests that the influence of plant invasions on forest regeneration may be partly mediated by the functional traits of regenerating tree species. We also found that the invasive plants evaluated in this study differentially influenced seedling versus sapling abundance and diversity, which could have complex implications for decision-making related to forest management strategies. Ultimately, the potential impact of these invasive plants on tree regeneration is likely to hamper the sustainable management of southern US forests (natural and managed) by the reduction of extant biodiversity. Thus, invasive plants should be incorporated into management strategies to help ensure the persistence of native forest communities and the ecological services they provide.

1. Introduction

Invasive species are one of the leading causes of biodiversity loss around the world and cause many environmental, economic and social problems (Gordon, 1998; Villamagna and Murphy, 2010; Vilà et al., 2011), including altering the structure and function of invaded ecosystems (Doren et al., 2009; Vilà et al., 2011). Southern forests of the United States (US, hereafter) are areas of primary concern with regards to the spread of invasive nonnative/exotic/alien plant species ("invasive plants" hereafter; Oswalt and Oswalt, 2011). These forests are highly productive due to favorable climate conditions, such as warm temperatures and abundant rainfall (USDA Forest Service, 2020). Southern forests are also economically important and a popular recreation destination for the human population of the region, and provide habitat for multiple organisms, including wildlife, game, and endangered species (USDA Forest Service, 2020). Most of the invasive plants were introduced in the southern US during the 1800 s and early 1900 s for multiple reasons: 1) as forage food for game species and livestock, 2) for ornamental and aesthetic purposes, and/or 3) for erosion control (Miller et al., 2013; EDDMapS, 2020). Since their introduction, invasive plants have undergone demographic explosions and rapidly dispersed to new areas, including forested lands, where their spread has possibly

* Corresponding author at: 295 Lee Blvd, Department of Biological Sciences, Mississippi State University, MS 39762, USA.
E-mail address: adrianlalobo@gmail.com (A. Lázaro-Lobo).

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been facilitated by forest management practices such as timber thinning and harvesting activities, which can disperse propagules and cause disturbance that creates favorable environmental conditions for successful establishment (Didham et al., 2007; Kerns and Day, 2017).

As an example of the prevalence of invasive plants in southern US forests, Oswalt et al. (2015) found that over 40% of the 0.4-ha plots surveyed in this region as part of the US Department of Agriculture (USDA) Forest Service National Forest Inventory and Analysis (FIA) program were occupied by one or more invasive plants. Moreover, Miller et al. (2013) highlighted that the annual spread of invasive plants in southern forests is conservatively estimated at over 58,000 ha. Such rapid spread of invasive plants has the potential to cause negative impacts on species diversity, native woody species density, forest understory species, tree regeneration, and plant community structure through competition and allelopathic interactions (Oswalt et al., 2007; Oswalt and Oswalt, 2011). Furthermore, invasive plants threaten human economic and cultural activities in southern forests by impacting forest productivity, ecosystem services, and human use potential of forested lands (Miller et al., 2013). Based on a continuation of historical development intensities, Wear (2013) forecasted that southern forests will lose 7–13% of their area due to urban development from 1997 to 2060. Similarly, characteristics related to climate change in southern forests, such as warmer temperatures, drier conditions, increased variability in precipitation, and increased severity of wildfire events could hinder successful forest regeneration and drive shifts in vegetation structure over time (McNulty et al., 2013; Stanturf and Goodrick, 2013). Invasive plants represent yet an additional threat to future sustainability of southern US forests, through their association with changes in land use and changes in regional climate, and their impacts not only on extant forest communities, but also on future forests via altered tree regeneration.

Multiple biotic, abiotic, and landscape factors drive forest regeneration by dispersing tree propagules (primarily seeds) and creating suitable conditions for seedling establishment (Hooper et al., 2004; Bose et al., 2016; Arenas et al., 2017). Invasive plants can have direct negative effects on forest regeneration through competition with tree seedlings and saplings for light, nutrients, and water (Merriam and Feil, 2002; Standish et al., 2002; Boyce, 2009; Marod et al., 2012; Johnson et al., 2015), as well as through alteration of disturbance regimes (Mack and D'Antonio, 1998; Levine et al., 2003). Moreover, invasive plants may indirectly influence tree regeneration by changing the abundance or behavior of a third species, and therefore altering biological and trophic interactions (Johnson et al., 2015). In this sense, invasive plants can increase consumption rates of native plants by attracting herbivores and seed predators (a.k.a. apparent competition; Meiners, 2007; Flory and Clay, 2010; Orrock and Witter, 2010). However, invasive plants can also act as nurse plants and protect tree seedlings from consumers when forming dense herbaceous or thorny vegetation (Malizia and Greslebin, 2000; Horsley et al., 2003; Johnson et al., 2015), although tree seedlings will still compete with invasive plants for resources, which can cause a negative net effect of invasive plants on tree regeneration (Gorchov and Trisel, 2003; Meiners, 2007). Also, invasive plants can facilitate the regeneration of tree species in harsh habitats through amelioration of environmental conditions, such as water stress, heat, nutrient cycling, soil stabilization, and environmental fluctuations. For example, Becerra and Montenegro (2013) found that invasive *Pinus radiata* trees facilitated regeneration of native woody species in a semi-arid ecosystem in central Chile when compared to open sites.

Because invasive plants may have either positive or negative effects on tree regeneration at local spatial scales, we were interested in understanding these relationships at a regional scale, such as the entirety of inventoried sites across the southern US. Here, we hypothesized that invasive plants of multiple growth forms influence forest regeneration in southern US forests, by altering tree seedling and sapling abundance and diversity. We predicted that invaded plots would generally have fewer seedlings and saplings of the major tree species generally present in southern US forests, and that slow-growing tree species would be more negatively impacted by invasive plants. We also predicted that invaded plots would have lower tree seedling and sapling diversity because the invasive plants would influence both the richness of tree species and their relative abundances. Finally, we evaluated the degree to which correlations among desirable forest trees and invasive plants were likely to have been driven by environmental niche preference vs. biotic interactions among species. We hypothesized that a lack of overlap in the environmental niche space between forest trees and invasive plants would suggest that these species simply tend to occupy different habitats and any observed negative correlations in their abundances probably were not driven by biotic interactions. On the other hand, if there is substantial overlap in their environmentally defined niche space, the species would be expected to co-occur and any observed negative correlations between forest trees and invasive plants may well be driven by negative biotic interactions. We predicted that the forest tree seedlings and saplings would have similar environmentally defined niche space as invasive plants, suggesting biotic interactions were responsible for observed correlations in their abundances.

2. Materials and methods

2.1. Study region

The study area corresponded to the continental part of the Southern Region (Region 8) of the USDA Forest Service, which manages more than 5 million hectares of forests and grasslands (USDA Forest Service, 2020; Fig. 1).

2.2. Species data

We obtained data for a total of 52,690 plots (51,194 with seedlings and 47,079 with saplings) surveyed by and in cooperation with the USDA Forest Service, Forest Inventory and Analysis (FIA, hereafter) program between 2015 and 2019. All of the selected plots were classified as "forestland" by the FIA program, which includes those plots with at least 10% canopy cover by trees of any size. Such plots have a width of at least 36.6 m, and continuous length of at least 110.6 m. FIA sampling is hierarchical in some plots. The largest FIA plots are 0.4 ha and are systematically located throughout the US. Each FIA plot consists of four circular 7.3-m radius subplots on which all trees with a Diameter at Breast Height (DBH, ~1.3 m height) of at least 12.7 cm are identified and measured (USDA Forest Service, 2018). One subplot is placed at the center and the remaining three subplots are located 36.6 m away at azimuths of 120°, 240°, and 360° (USDA Forest Service, 2018). Within each of these subplots is nested a circular 2.07-m radius microplot, of increased data collection intensity, where all tree seedlings and saplings are registered (USDA Forest Service, 2018). Tree seedlings are individuals with a DBH $<$ 2.54 cm that are either $\geq$ 15.24 cm tall for conifer species or $\geq$ 30.48 cm tall for hardwood species, whereas tree saplings are individuals with a DBH between 2.54 and 12.7 cm (USDA Forest Service, 2018). Additionally, the FIA program registers the presence of multiple invasive plants that can out-compete native species within the plots, causing ecological and economic problems.

In this study, we used presence/absence data from 16 invasive plant taxa of different growth forms with high rates of spread throughout southern US forests (Miller et al., 2013; Table 1). For each invasive plant, we selected all the plots where it was present between 2015 and 2019, and 10,000 plots (also sampled between 2015 and 2019) where the species has been absent since the FIA program started collecting data on invasive plants in 2002, to avoid possible ecological legacies derived from invasive plants. The absence plots were selected within the distributional range of the corresponding invasive plant to exclude the possibility that external factors, such as different climatic or edaphic conditions, influence the analyses and interpretation in this study.

Within the selected plots, we calculated the number of seedlings and

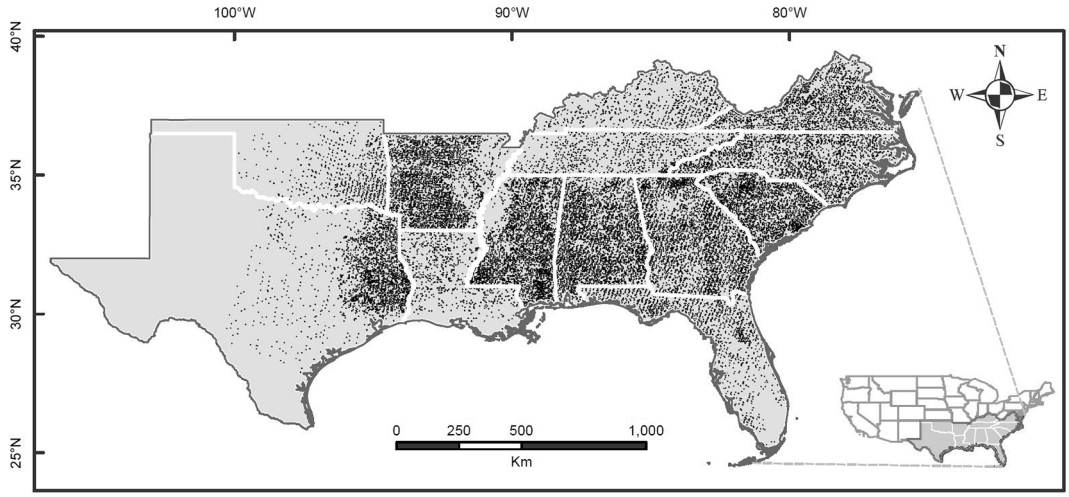

Fig. 1. Study region. Continuous lines delimitate U.S. states. The shaded area corresponds to the Southern Region of the USDA Forest Service (Region 8). The black dots indicate the location of the Forest Inventory and Analysis (FIA) plots used in this study.

Table 1
Invasive taxa evaluated in this study. Common names are based on the PLANTS Database (USDA, 2020), whereas information regarding introduction of extensive planting date, average annual rate of spread, and projected cover in 2060 were taken from Miller et al. (2013).

Growth form	Invasive taxa (common name)	Invasive taxa (scientific name)	Date of introduction of extensive planting	Average annual rate of spread (ha)	Projected cover 2060 (ha)	No. presence plots
Tree	Tree of heaven	*Ailanthus altissima*	1784	435	1,201,450	485
	Silktree	*Albizia julibrissin*	1785	162	44,543	517
	Chinaberrytree	*Melia azedarach*	1830	228	52,447	433
	Callery pear	*Pyrus calleryana*	–	–	–	330
	Chinese tallow	*Triadica sebifera*	About 1900	2,193	350,966	1,105
Shrub	Thorny olive	*Elaeagnus pungens*	1939*	488*	63,408 *	114
	Sericea lespedeza	*Lespedeza cuneata*	1863*	1,465*	288,649*	1,829
	Japanese privet	*Ligustrum japonicum*	1875*	9,534*	1,763,801 *	505
	Privet	*Ligustrum* spp. (≠*L. japonicum*)	1875*	9,534*	1,763,801 *	6,637
	Rose	*Rosa* spp. (non-natives)	1877*	2,110*	386,223*	1,799
Vine	Japanese honeysuckle	*Lonicera japonica*	About 1850	26,158	5,493,168	2,445
	Japanese climbing fern	*Lygodium japonicum*	About 1918	1,384	196,605	1,502
	Kudzu	*Pueraria montana* var. *lobata*	About 1920	1,020	142,829	185
Graminoid	Cogongrass	*Imperata cylindrica*	About 1935	324	40,541	121
	Nepalese browntop	*Microstegium vimineum*	1919	4,161	586,614	670
	Tall fescue	*Schedonorus phoenix*	1940	4,435	532,248	177

*Average data for all the registered invasive plants within the corresponding genus.

saplings for all major tree species present in southern forestlands (Table 2). Lastly, from the number of tree species and individuals within each plot, we calculated three measures of diversity (species richness, exponential of Shannon-Wiener index, and inverse Simpson index). Species richness indicates the number of tree seedling or sapling species within each plot, whereas the other two transformed indices of diversity (exponential of Shannon-Wiener index and inverse Simpson index) consider both the number of species present and their relative abundances in units of species richness, which is appropriate for analyzing biological diversity (Jost, 2006; Gotelli and Chao, 2013).

2.3. Environmental variables for niche evaluation

We compiled a broad range of environmental variables to compare niche requirements between focal invasive plants and tree seedlings and saplings. All environmental variables were resampled, if needed, to a grid of 30-m pixel size using the bilinear resample technique. This resampling method averages (weighted for distance) the values of the four nearest pixels (ESRI, 2018) and has been broadly implemented in ecological studies (Arif and Akbar, 2005; Chapman et al., 2005).

We obtained digital elevation data from the US Geological Survey database (U.S. Geological Survey, 2020) and calculated slope using ArcGIS 10.5.1 (ESRI, 2018). Biologically relevant bioclimatic variables were obtained from the WorldClim database (Fick and Hijmans, 2017). Species thermal tolerance was evaluated with minimum temperature of coldest month and maximum temperature of warmest month, whereas the lowest water availability that the species can tolerate was assessed with precipitation of driest quarter.

We used the National Land Cover Database 2016 (NLCD 2016; Multi-Resolution Land Characteristics Consortium, 2019) to obtain land cover data and, then, calculated Euclidean distance to the nearest developed and pasture/cultivated area from the plots using ArcGIS 10.5.1 as surrogates of human land-use influence. Percent tree canopy cover data was also downloaded from NLCD (2016) as a surrogate of light availability in

Table 2
Tree species evaluated in this study. For each tree species, we show the number of plots that contain seedlings and saplings, as well as their minimum (min.), maximum (max.), and mean abundance. Tree growth rates are based on the PLANTS Database (USDA, 2020).

	Tree taxa (common name)	Tree taxa (scientific name)	Seedling				Sapling				Growth rate
			Plots	Min.	Max.	Mean	Plots	Min.	Max.	Mean	
Softwoods	Cypresses	*Taxodium* spp.	248	1	102	6.4	275	1	28	3.1	Slow-Rapid
	Eastern hemlock	*Tsuga canadensis*	155	1	33	2.9	138	1	10	1.9	Slow
	Eastern redcedar	*Juniperus virginiana*	3,390	1	73	3.3	1,731	1	18	2.0	Slow
	Eastern white and red pines	*Pinus strobus* and *P. resinosa*	440	1	119	6.3	281	1	21	2.2	Rapid
	Loblolly and shortleaf pines	*Pinus taeda* and *P. echinata*	4,852	1	793	10.8	4,609	1	74	4.0	Rapid
	Longleaf and slash pines	*Pinus palustris* and *P. elliottii*	678	1	220	6.3	850	1	30	2.8	Rapid
	Other yellow pines	*Pinus* spp.	670	1	115	4.2	642	1	38	3.3	Moderate-Rapid
Hardwoods	American beech	*Fagus grandifolia*	1,341	1	89	3.3	831	1	12	1.7	Slow
	American sycamore	*Platanus occidentalis*	175	1	29	2.6	150	1	22	2.0	Rapid
	Ashes	*Fraxinus* spp.	3,777	1	143	4.9	1,559	1	20	2.1	Moderate-Rapid
	Basswood	*Tilia americana*	65	1	11	2.4	66	1	10	1.7	Moderate
	Black walnut	*Juglans nigra*	131	1	7	1.7	83	1	6	1.3	Rapid
	Cottonwood and aspen	*Populus* spp.	41	1	34	3.7	31	1	7	2.0	Rapid
	Elms	*Ulmus* spp.	5,442	1	104	3.9	3,531	1	24	2.1	Moderate -Rapid
	Hackberries	*Celtis* spp.	1,651	1	55	3.6	681	1	20	1.8	Moderate- Rapid
	Hickories	*Carya* spp.	5,821	1	51	3.0	2,902	1	14	1.7	Slow
	Magnolias	*Magnolia* spp.	1,453	1	67	3.3	998	1	20	2.6	Moderate-Rapid
	Maples	*Acer* spp.	7,461	1	134	4.9	5,479	1	31	2.7	Slow-Rapid
	Red oaks	*Quercus* spp.	11,386	1	95	4.2	5,946	1	40	2.5	Moderate-Rapid
	Sweetgum	*Liquidambar styraciflua*	7,559	1	96	5.1	6,086	1	38	3.2	Rapid
	Tupelos and blackgum	*Nyssa* spp.	3,500	1	1.5	3.0	3,204	1	51	2.0	Moderate
	White oaks	*Quercus* spp.	6,222	1	310	4.5	3,099	1	32	1.9	Slow-Moderate
	Willows	*Salix* spp.	115	1	43	5.5	137	1	30	3.0	Rapid
	Yellow poplar	*Liriodendron tulipifera*	1,595	1	158	4.9	1,461	1	48	2.5	Rapid

the plots. The normalized difference vegetation index (NDVI), which indicates plant greenness, was obtained from remote sensing measurements taken from NASA's Landsat 8 and included the average values from May to August between 2015 and 2017.

Soil properties in the top 50-cm of soil at each plot location were extracted from the US Department of Agriculture Soil Survey Geographic (SSURGO) database (Soil Survey Staff, 2020). Such properties included organic matter, pH, effective cation exchange capacity (CEC), available water capacity (AWC), and percent of sand, silt and clay. We also extracted depth to soil restrictive layer from the SSURGO

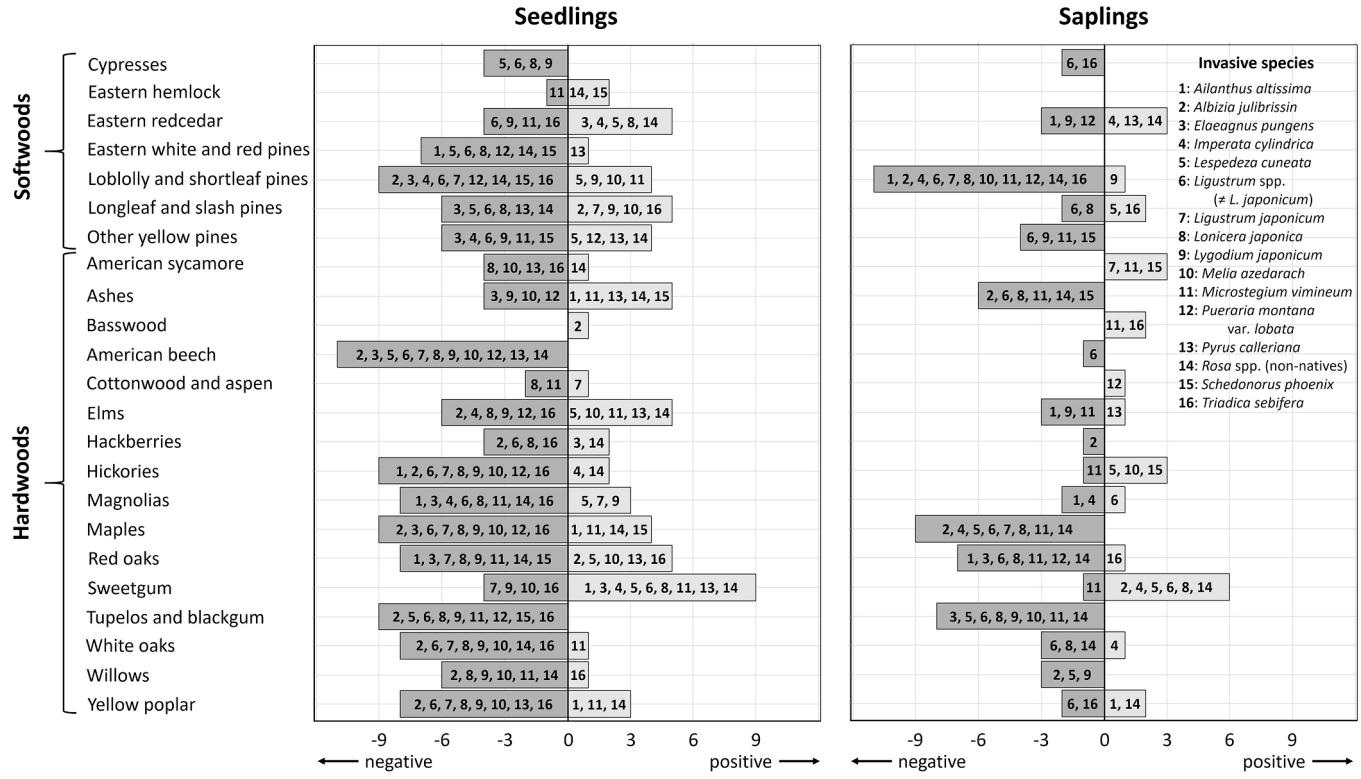

Fig. 2. Number of significant relationships (with $p < 0.05$) between invasive taxa presence and tree seedling and sapling abundance. Values to the left of the x-axis (negative sign) represent the number of negative relationships, whereas values to the right indicate the number of positive associations. The invasive taxa responsible for the significant relationships are included inside the bars of each tree taxon. For each tree taxa and size (seedling or sapling), we performed a total of 16 statistical analyses (one from each invasive taxa).

database.

2.4. Statistical analyses

All statistical analyses were performed in the program R (version 3.6.1; R Core Team, 2019). We used Generalized Linear Models (GLMs) to examine the influence of the selected invasive plants presence on abundance and diversity of tree seedlings and saplings. Some of the tree species were grouped following FIA guidelines for reporting purposes. Abundance and richness of tree seedling and saplings were evaluated with the Poisson distribution, whereas exponential of Shannon-Wiener and inverse Simpson indices were tested with the Gamma distribution due to the skewness of their data distributions. We also obtained lower AIC values with Gamma distribution when compared to the models with Gaussian distribution.

We used principal component analysis (PCA) to compare the niche associations between invasive plants and tree seedlings and saplings and, thus, evaluate whether the negative relationships appeared to have resulted from niche differences (i.e., the species occupied different environmentally defined ordination space) or from true-negative interactions between invasive plants and tree seedlings and saplings resulting from sharing similar ecological requirements. This technique arranges the data along multiple axes in order to summarize complex ecological relationships (McCune et al., 2002). In this sense, we conducted PCAs inclusive of the environmental information from occurrence points for invasive plants and tree seedlings and saplings, and then evaluated their overlap in ordination space. Because the environmental variables were measured at different scales, we standardized such variables before conducting the PCAs so that the analyses were not biased by those variables with the biggest scales and variances.

3. Results

Tree seedlings had more significant negative relationships with invasive plants than tree saplings (Fig. 2). Approximately two-thirds of the tree taxa were negatively correlated with six or more of the focal invasive plants. In contrast, seedlings from eastern hemlock (*Tsuga canadensis*), eastern red cedar (*Juniperus virginiana*), ashes (*Fraxinus* spp.), basswood (*Tilia Americana*), and sweetgum (*Liquidambar styraciflua*) had more positive than negative relationships with the focal invasive plants (Fig. 2). As for tree saplings, there were many fewer tree species that were negatively correlated with six or more invasive plants. These included loblolly and shortleaf pines (*Pinus taeda* and *Pinus echinata*), ashes (*Fraxinus* spp.), maples (*Acer* spp.), red oaks (*Quercus* spp.), and tupelos and blackgum (*Nyssa* spp.). Again, we saw a small suite of hardwood species that exhibited more positive than negative associations with the selected invasive plants (American sycamore (*Platanus occidentalis*), basswood (*Tilia americana*), cottonwood and aspen (*Populus* spp.), hickories (*Carya* spp.), and sweetgum (*Liquidambar styraciflua*); Fig. 2). The PCA results showed that invasive plants and tree seedlings and saplings that were negatively correlated with one another were similarly distributed in ordination space, indicating their negative correlations were not the result of having different environmental niche associations (Fig. 3).

Over half of the invasive taxa evaluated had at least twice as many negative relationships than positive relationships with tree seedlings and/or saplings (Fig. 4). The invasive plants *Albizia julibrissin*, *Triadica sebifera, Ligustrum* spp., *Lonicera japonica*, and *Lygodium japonicum* had the highest number of negative relationships with tree seedlings (≥10; Fig. 4). In contrast, a few invasive plants had more positive than negative relationships with tree seedlings (*Pyrus calleryana*, *Lespedeza cuneata*, and *Rosa* spp.). Moreover, *Ligustrum* spp., *Rosa* spp., *Lonicera japonica*, and *Microstegium vimineum* had the highest number of negative associations with tree saplings (≥7; Fig. 4). However, as with tree seedlings, *Pyrus calleryana* had more positive than negative relationships with tree saplings.

Tree seedling and sapling richness and diversity were reduced in the presence of *Melia azedarach*, *Triadica sebifera*, *Lygodium japonicum*, and *Imperata cylindrica* (Table 3). Furthermore, plots invaded by *Ligustrum japonicum* had lower tree seedling richness and diversity, whereas plots invaded by *Pyrus calleryana* and *Schedonorus phoenix* had lower tree sapling richness and diversity. However, other invasive taxa were

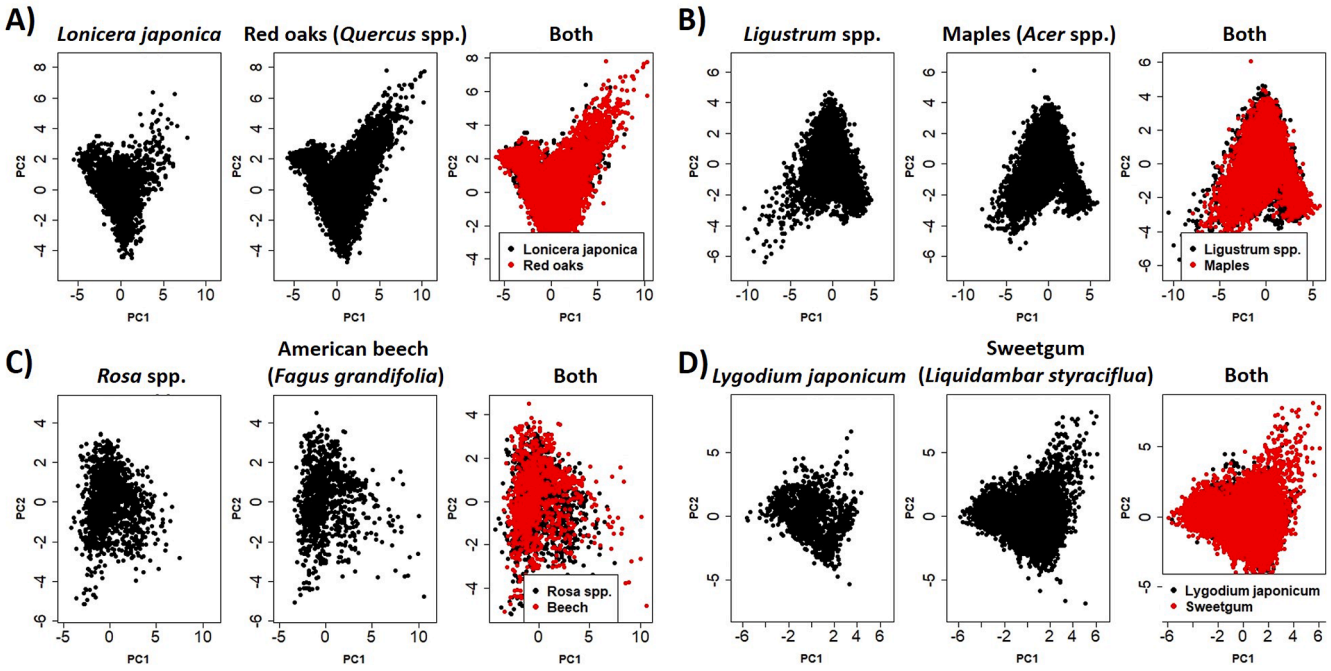

Fig. 3. Examples of Principal Component Analysis (PCA) showing similarities in niche requirements between negatively correlated invasive plants and tree seedlings and saplings. The more the points from both taxa overlap in the ordination space defined by the PCA axes, the more similar their ecological niches are. The ordination space was defined by multiple environmental variables, including climate, canopy cover, topography, land use, and soil properties. A) *Lonicera japonica* and read oak seedlings, B) *Ligustrum* spp. and maple seedlings, C) *Rosa* spp. and beech seedlings, and D) *Lygodium japonicum* and sweetgum seedlings.

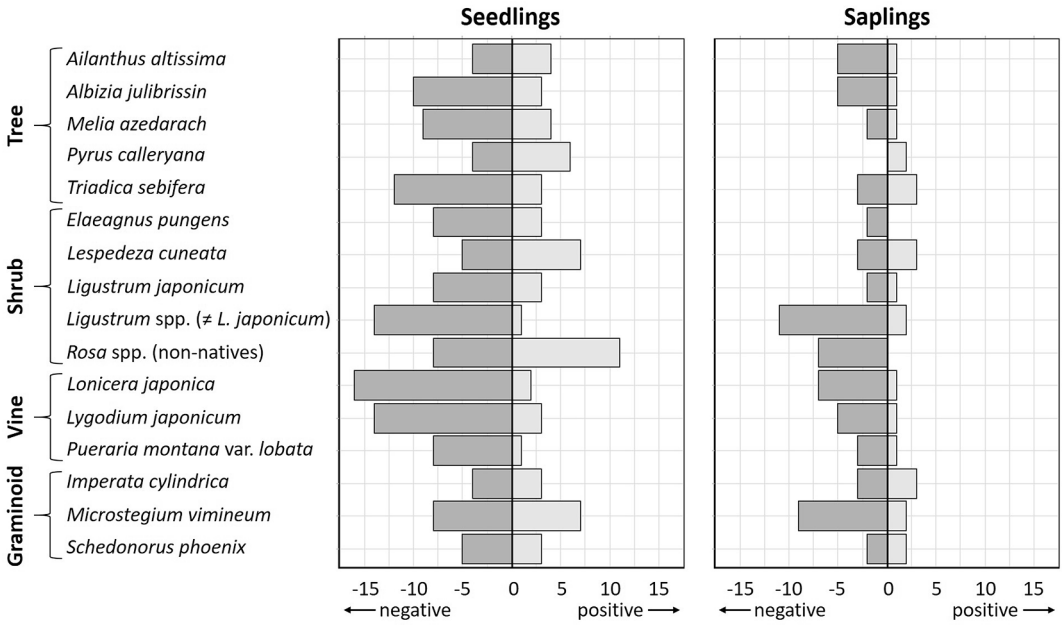

Fig. 4. Number of significant relationships (with $p < 0.05$) between invasive taxa presence and tree seedling and sapling abundance. Values to the left of the x-axis (negative sign) represent the number of negative relationships, whereas values to the right indicate the number of positive associations. For each tree taxa and size (seedling or sapling), we performed a total of 16 statistical analyses (one from each invasive taxa).

Table 3
Relationships between invasive taxa presence and tree seedling and sapling diversity. Positive (+), negative (-), and neutral (0) relationships were reported considering the model estimate signs and *p*-values. Invasive plants with *p*-values greater than 0.05 were considered to have neutral relationships. The symbols (+) or (-), (++) or (–), and (+++) or (– – –) refer to relationships with *p*-values < 0.05, < 0.01, and < 0.001, respectively.

Growth form	Invasive taxa	Seedling			Sapling		
		Richness	Exponential Shannon	Inverse Simpson	Richness	Exponential Shannon	Inverse Simpson
Tree	*Ailanthus altissima*	+++	+++	+++	+	++	++
	Albizia julibrissin	+++	+++	+++	+++	++	++
	Melia azedarach	—	–	–	–	–	–
	Pyrus calleryana	0	0	0	–	–	—
	Triadica sebifera	—	—	—	—	—	—
Shrub	*Elaeagnus pungens*	+++	+++	++	++	++	++
	Lespedeza cuneata	+++	+++	+++	0	0	0
	Ligustrum japonicum	—	—	–	0	0	0
	Ligustrum spp. (≠*L. japonicum*)	0	0	0	+++	+++	+++
	Rosa spp. (non-natives)	+++	+++	+++	0	0	0
Vine	*Lonicera japonica*	+++	+++	+++	+++	+++	+++
	Lygodium japonicum	—	—	—	—	—	—
	Pueraria montana var. *lobata*	0	0	0	0	0	0
Graminoid	*Imperata cylindrica*	—	–	–	–	–	–
	Microstegium vimineum	+++	+++	+++	0	0	0
	Schedonorus phoenix	0	0	0	—	—	—

positively related with tree seedling and sapling richness and diversity (Table 3). Curiously, significant relationships between invasive shrubs and tree sapling richness and diversity were always positive, in spite of there being numerous negative correlations between invasive shrubs and sapling abundance (Table 3 vs. Fig. 4). Similarly, significant correlations between invasive graminoids and tree sapling richness and diversity were always negative. In contrast, vines and trees had mixed results as expected, based on the resulting seedling and sapling abundance data (Table 3).

4. Discussion

Our results showed that invasive plants were, in general, negatively associated with multiple tree species across southern US forests, and that specific attributes of these relationships varied among tree species. This finding suggests that future forest community composition has the potential to be highly influenced by invasive plants, possibly through direct competition or through changes in the biotic and abiotic environment, as shown by previous research (e.g., Merriam and Feil, 2002; Oswalt et al., 2007; Boyce, 2009; Johnson et al., 2015; Pile et al., 2019). We also found that the invasive plants evaluated in this study differentially influenced seedling and sapling abundance and diversity, which has timely implications for strategic decision-making and forest management plans in this region. These are a few of the practical applications in the region-wide effort to manage and/or contain plant invasions as well as secondary spread from established populations based on existing inventory data.

Our results also showed that many of the invasive plants that were negatively associated with seedlings and saplings of desirable tree species occupy similar niche spaces as did the trees (Fig. 3). For example, the invasive vine *Lonicera japonica* (Japanese honeysuckle) had a negative relationship with red oak seedlings (genus *Quercus*); however,

both were similarly distributed in the environmentally defined abiotic ordination space (based on climate, canopy cover, topography, land use, and soil properties; Fig. 3). The assumption, then, is that the negative associations were not simply the result of these species occupying different habitats. A potential consequence of these shared environmental associations is that the spread of invasive plants throughout southern forests could decrease the availability of suitable habitat within which desirable tree species can persist *via* regeneration after accounting for biotic interactions (a.k.a., their realized niche; Soberón and Arroyo-Peña, 2017). This could have consequences not only for tree population growth, but also for tree propagule dispersal, and subsequent establishment in response to climate change, anthropogenic habitat modifications, and stochastic natural disasters and other unpredictable disturbance events, including wind.

Seedlings and saplings of pine (*Pinus* spp.) had a large number of negative relationships with the analyzed invasive plants. Several species within *Pinus* provide the most significant economic market for the southern US region; this timber market, commonly known as the "woodbasket" of the nation, results in forest products from dimensional lumber to wood pellets for domestic use and international export. Heavy management activities on all forestlands, such as thinning and harvesting, dramatically impact site conditions *via* disturbance, and also increase the probability of human-assisted plant propagule dispersal, thereby facilitating nascent invasive plant establishment in novel spaces (Didham et al., 2007). However, silvicultural practices that enhance the vigor of the planted trees and control competition with invasive species can decrease the chances of invasive plant establishment (Burns and Miller, 2004; Gan et al., 2009). Our results also suggest that, once invasive plants are established, they can influence the recovery of pine forests and plantations following timber extraction or other disturbances (i.e., fire, tornado, hurricane). Specifically, loblolly pine (*Pinus taeda*) and shortleaf pine (*Pinus echinata*) saplings, which are among the most important commercial conifers in the Southern Region (USDA Forest Service Southern Research Station, 2020), also exhibited the strongest negative correlations among the impacted tree species in our analyses (Fig. 2). Thus, invasive plant presence has significant potential to impact regional regeneration of economically important pine species.

Similarly to the economically important pine species, slower growing hardwood tree seedlings and saplings were negatively correlated with invasive species occurrence; these included American beech (*Fagus grandifolia*), elms (*Ulmus* spp.), hickories (*Carya* spp.), magnolias (*Magnolia* spp.), maples (*Acer* spp.), red and white oaks (*Quercus* spp.), and tupelos and blackgum (*Nyssa* spp.; Figs. 2 and 3). These species are among the most ecologically and economically important trees of the southern US hardwood forests and provide refuge and food for wildlife, including game and endangered species (USDA Forest Service Southern Research Station, 2020). Lack of hardwood tree regeneration (e.g., oak, hickory) in this region is one of several major concerns resulting from long-term fire suppression and increase in white-tailed deer populations (Hicks et al., 2004). Thus, the regional proliferation of invasive plants could further hinder the regeneration of more desirable hardwood tree species and, ultimately, reduce carbon storage, forest productivity, and suitable wildlife habitat availability. Special attention should be paid to those silviculture practices that increase resource availability that promotes hardwood regeneration, such as canopy tree removal (for shade-intolerant species) and prescribed fire (Brose et al., 2013). Such silviculture practices can also reduce biotic resistance and facilitate the establishment of invasive plants in the presence of invading propagules, which, in turn, could reduce the available niche space for desirable tree species (Davis et al., 2000).

On the contrary, seedlings from fast-growing, early-mid successional hardwood tree species such as American sycamore (*Platanus occidentalis*), the ashes (*Fraxinus* spp.), cottonwood and aspen (*Populus* spp.), hackberries (*Celtis* spp.), and sweetgum (*Liquidambar styraciflua*) were least impacted by invasive plants. This could suggest that these tree species are better able to compete with other fast-growing species and therefore, have more opportunities to become established in the presence of invasive plants. Thus, the influence of plant invasions on forest regeneration may be mediated by the functional traits of regenerating tree species (Flory and Clay, 2010). This also could have implications for succession and future forest community composition in invaded plots, which could shift towards fast-growing trees dominating the landscape, to the disadvantage of the often more desirable slow-growing species.

Most of the evaluated invasive taxa are widely distributed in Southern forests and are also expected to continue expanding within the southern US over the next 40 years (Wang et al., 2011; Miller et al., 2013; Lázaro-Lobo et al., 2020). However, previous research suggests that *Elaeagnus pungens* is in its early "lag" phase of forest invasion with scattered occurrences and low population sizes (Miller et al., 2013), suggesting that its negative effects on forest regeneration could be accentuated in the near future due to continued horticultural sales and propagule rain into natural forest systems due to escape from cultivation. Moreover, even though the invasive perennial C_4 grass *Imperata cylindrica* is one of the worst invasive species (Holm et al., 1977) impacting the southern US, it is rarely observed within FIA plots. This is generally due to its infrequent occurence in deep forest understories (Ervin and Holly, 2011). As a result, the potential future impacts of this species may be greatly underestimated in our present work, which was derived solely on data from forested plots (FIA and Georgia Forestry Commission, personal communication). Since *I. cylindrica* establishment and occurrence is so related to soil disturbances, the roads created for harvest are known to facilitate the invasion of this aggressive species deeper into forest interiors and target forest regeneration sites (Ervin and Holly, 2011). Our results here show that *I. cylindrica* is likely to decrease tree seedling and sapling richness and diversity.

Shrubs belonging to the genus *Ligustrum* (nonnative, invasive privets) and the vines, *Lonicera japonica* and *Lygodium japonicum,* were among the most impactful invasive plants, resulting in negative associations with more than half of the tree taxa evaluated. Previous research also found that *Ligustrum* spp. significantly reduced herbaceous species and almost completely suppressed tree regeneration in a mixed hardwood forest (Merriam and Feil, 2002). The fast-growing vines, *L. japonica* and *L. japonicum*, form dense infestations that can completely cover trees and occupy the forest ground layer (Miller et al., 2013). Previous research indicated that *L. japonica* interferes with tree regeneration not only through above- and belowground competition, but also through allelopathic interactions (Dillenburg et al., 1993; Skulman et al., 2004). Similarly, *L. japonicum* negatively impacts forests *via* resource competition and crown fire promotion (Wyatt and Wyatt, 2013). From our analyses, the presence of *L. japonicum* also decreased tree seedling and sapling richness and diversity, which would be expected to negatively influence future forest community composition across the invasive distribution of this species. Among the invasive tree species we investigated, *Albizia julibrissin*, *Melia azedarach*, and *Triadica sebifera*, had the greatest potential to cause substantial harm to forest regeneration due to their negative effects on tree seedling and sapling abundance, richness, and diversity.

Invasive roses (*Rosa* spp.) and the annual warm-season (C_4) grass *Microstegium vimineum* had a high number of positive relationships with tree seedlings and also increased tree seedling richness and diversity; however, they were among the most potentially harmful invasive plants for tree saplings. *Rosa* spp. are widely spread thorny shrubs that occur along forest margins, within interior forests, and along stream banks across the southern US, whereas the shade and moisture tolerant *M. vimineum* mainly occurs on the alluvial floodplains and streamsides in the Appalachian-Cumberland and Piedmont subregions of the southern US (Touchette and Romanello, 2010; Miller et al., 2013). Our findings suggest that the thorny *Rosa* spp. shrubs and the dense herbaceous *M. vimineum* cover may initially protect tree seedlings from herbivory (Meiners, 2007; Johnson et al. 2015). However, the seedlings that benefitted from cover must now grow under dense *Rosa* spp. or *M. vimineum* thickets, which would decrease resource availability (e.g.,

light, nutrients) and therefore, hinder tree development into the sapling stage (Meiners, 2007). Also, tree saplings may be suppressed when growing along with *M. vimineum* due to higher herbivory by small mammals than seedlings (Flory and Clay, 2010). Light availability could have also influenced the relationship between *M. vimineum* and tree regeneration. Previous research suggests that the presence of shade reduces survivorship and reproduction of this invasive grass (Schramm and Ehrenfeld, 2010). Tree saplings provide more shading than seedlings, which could increase resistance to invasion by *M. vimineum*.

The results discussed above all suggest that the 16 invasive plant species examined here have significant potential to impact forest regeneration and future forest composition in similar ways and to a similar degree across the Southern Region's forested lands. However, further research is needed to deepen our understanding of the mechanisms and consequences of these biological invasions on forest regeneration for both short- and long-term management plans and goals. For example, little is known about how invasive plant abundance and variable propagule availability can also influence forest regeneration at regional scales. Furthermore, there are other factors influencing the ultimate outcomes of interactions among these species, including forest type, stand characteristics (e.g., stand age, successional status, tree layer, understory, forest floor), and disturbance characteristics (e.g., type, intensity, timing, duration, and extent). We should also note that forest regeneration can be driven by factors other than, or in addition to, plant invasions, such as site disturbances, adequate native tree reproduction, climate change, and fragmentation (MacDougall and Turkington, 2005; McNulty et al., 2013; Stanturf and Goodrick, 2013; Link et al., 2019; Vickers et al., 2019).

5. Conclusions

This research analyzed the relationships between desirable forest tree species and some of the most environmentally and economically impactful invasive plants in the Southern Region of the USDA Forest Service. Our results provide broad insight into the region-wide potential impact of plant invasion on forest regeneration, and consequently, the impacts of these plant invaders on forest sustainability. The relationships that we observed between invasive plants and desirable tree seedlings and saplings could ultimately result in diminished nativity and biodiversity loss within regional forests, or loss of forest-types entirely. These substantial consequences would likely lead to reduced capacity for the region's forests to provide ecosystem services such as biomass production, carbon storage, wildlife habitat, and potential forest adaptability to climate change.

Albizia julibrissin, *Ligustrum* spp., *Lonicera japonica*, *Lygodium japonicum*, *Microstegium vimineum*, *Rosa* spp., and *Triadica sebifera* were the most harmful invasive plants influencing desirable tree seedlings and/or saplings at the regional scale. Further, the niche spaces of both invasive plants and desirable tree species frequently overlapped, contributing to likely increases in resource competition after establishment. Richness and diversity of desirable tree seedlings and saplings were also reduced in the presence of *Melia azedarach*, *T. sebifera, L. japonicum*, and *Imperata cylindrica*, which would influence forest community composition in the southern region of the US over time. We also found that plant invasions' influence on forest regeneration may be mediated by the functional traits of the regenerating tree species. For example, multiple fast-growing hardwood tree species were found to exhibit fewer overall negative associations with the invasive plants included in this research.

Based on our analyses, invasive plants should always be incorporated into forest management strategies that aim to protect and improve the abundance and diversity of native and desirable forest communities. Along these lines, data repositories such as those available through the FIA program are an invaluable tool in understanding relationships among plant species and, thus, monitoring the ever-changing impact of introduced species on native ecosystems and economically important managed systems.

CRediT authorship contribution statement

Adrián Lázaro-Lobo: Conceptualization, Methodology, Software, Validation, Formal analysis, Investigation, Data curation, Writing - original draft, Writing - review & editing, Visualization, Funding acquisition. **Rima D. Lucardi:** Conceptualization, Methodology, Validation, Resources, Writing - review & editing, Visualization, Supervision, Funding acquisition. **Carlos Ramirez-Reyes:** Conceptualization, Methodology, Software, Validation, Formal analysis, Data curation, Writing - review & editing, Visualization. **Gary N. Ervin:** Conceptualization, Methodology, Validation, Resources, Writing - review & editing, Visualization, Supervision, Funding acquisition.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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References

Arenas, J.M., Lázaro-Lobo, A., Mola, I., Escudero, A., Casado, M.A., 2017. The influence of site factors and proximity of adjacent vegetation on tree regeneration into roadslopes. Ecol. Eng. 101, 120–129.

Arif, F., Akbar, M., 2005. Resampling air borne sensed data using bilinear interpolation algorithm. IEEE ICM. 2005, 62–65.

Becerra, P.I., Montenegro, G., 2013. The widely invasive tree *Pinus radiata* facilitates regeneration of native woody species in a semi-arid ecosystem. Appl. Veg. Sci. 16, 173–183.

Bose, A.K., Weiskittel, A., Wagner, R.G., Kuehne, C., 2016. Assessing the factors influencing natural regeneration patterns in the diverse, multi-cohort, and managed forests of Maine. USA. J. Veg. Sci. 27, 1140–1150.

Boyce, R.L., 2009. Invasive shrubs and forest tree regeneration. J. Sustain. For. 28, 152–217.

Brose, P.H., Dey, D.C., Phillips, R.J., Waldrop, T.A., 2013. A meta-analysis of the fire-oak hypothesis: does prescribed burning promote oak reproduction in eastern North America? For. Sci. 59, 322–334.

Burns, J.H., Miller, T.E., 2004. Invasion of Chinese tallow (*Sapium sebiferum*) in the Lake Jackson area, northern Florida. Am. Midl. Nat. 152, 410–417.

Chapman, A.D., Muñoz, M.E., Koch, I., 2005. Environmental information: placing biodiversity phenomena in an ecological and environmental context. Biodivers. Inform. 2, 24–41.

Davis, M.A., Grime, J.P., Thompson, K., 2000. Fluctuating resources in plant communities: a general theory of invasibility. J. Ecol. 88, 528–534.

Didham, R.K., Tylianakis, J.M., Gemmell, N.J., Rand, T.A., Ewers, R.M., 2007. Interactive effects of habitat modification and species invasion on native species decline. Trends Ecol. Evol. 22, 489–496.

Dillenburg, L.R., Whigham, D.F., Teramura, A.H., Forseth, I.N., 1993. Effects of below- and aboveground competition from the vines *Lonicera japonica* and *Parthenocissus quinquefolia* on the growth of the tree host *Liquidambar styraciflua*. Oecologia 93, 48–54.

Doren, R.F., Richards, J.H., Volin, J.C., 2009. A conceptual ecological model to facilitate understanding the role of invasive species in large-scale ecosystem restoration. Ecol. Indic. 9S, S150–S160.

EDDMapS., 2020. Early Detection and Distribution Mapping System. The University of Georgia – Center for Invasive Species and Ecosystem Health. http://www.eddmaps.org/. Accessed 2 June 2020.

Environmental Systems Research Institute (ESRI), 2018. ArcGIS Desktop ArcGIS 10.5.1. Redlands, CA.
Ervin, G.N., Holly, D.C., 2011. Examining local transferability of predictive species distribution models for invasive plants: An example with cogongrass (Imperata cylindrica). Invasive Plant Sci. Manag. 4, 390–401.
Fick, S.E., Hijmans, R.J., 2017. Worldclim 2: New 1–km spatial resolution climate surfaces for global land areas. Int. J. Climatol. 37, 4302–4315.
Flory, S.L., Clay, K., 2010. Non-native grass invasion suppresses forest succession. Oecologia 164, 1029–1038.
Gan, J., Miller, J.H., Wang, H., Taylor, J.W., 2009. Invasion of tallow tree into southern US forests: influencing factors and implications for mitigation. Can. J. For. Res. 39, 1346–1356.
Gorchov, D.L., Trisel, D.E., 2003. Competitive effects of the invasive shrub, *Lonicera maackii* (Rupr.) Herder (Caprifoliaceae), on the growth and survival of native tree seedlings. Plant Ecol. 166, 13–24.
Gordon, D.R., 1998. Effects of invasive, non–indigenous plant species on ecosystem processes: lessons from Florida. Ecol. Appl. 8, 975–989.
Gotelli, N.J., Chao, A., 2013. Measuring and estimating species richness, species diversity, and biotic similarity from sampling data. The Encyclopedia of Biodiversity 5, 195–211.
Hicks, R.R., Conner, W.H., Kellison, R.C., Van Lear, D., 2004. Silviculture and management strategies applicable to southern hardwoods. General Technical Report SRS–75. USDA-Forest Service, Southern Research Station. Asheville, North Carolina, pp. 51–62.
Holm, L.G., Pucknett, D.L., Pancho, J.B., Herberger, J.P., 1977. The World's Worst Weeds. Distribution and Biology. Univ, Press of Hawaii, Honolulu, HI.
Hooper, E.R., Legendre, P., Condit, R., 2004. Factors affecting community composition of forest regeneration in deforested, abandoned land in Panama. Ecology 85, 3313–3326.
Horsley, S.B., Stout, S.L., DeCalesta, D.S., 2003. White-tailed deer impact on the vegetation dynamics of a northern hardwood forest. Ecol. Appl. 13, 98–118.
Johnson, D.J., Flory, S.L., Shelton, A., Huebner, C., Clay, K., 2015. Interactive effects of a non-native invasive grass *Microstegium vimineum* and herbivore exclusion on experimental tree regeneration under differing forest management. J. Appl. Ecol. 52, 210–219.
Jost, L., 2006. Entropy and diversity. Oikos 113, 363–375.
Kerns, B.K., Day, M.A., 2017. The importance of disturbance by fire and other abiotic and biotic factors in driving cheatgrass invasion varies based on invasion stage. Biol. Invasions 19, 1853–1862.
Lázaro-Lobo, A., Evans, K.O., Ervin, G.N., 2020. Evaluating landscape characteristics of predicted hotspots for plant invasions. Invasive Plant Sci. Manag. 13, 163–175.
Levine, J.M., Vila, M., D'Antonio, C.M., Dukes, J.S., Grigulis, K., Lavorel, S., 2003. Mechanisms underlying the impacts of exotic plant invasions. P. Roy. Soc. B-Biol. Sci. 270, 775–781.
Link, A.F., Johnson, L.M., Utz, R.M., 2019. To manage or not? Successful native tree seedling restoration despite a dense, invasive shrub. *Berberis thunbergii*. Plant Ecol. 220, 577–593.
Mack, M.C., D'Antonio, C.M., 1998. Impacts of biological invasions on disturbance regimes. Trends Ecol. Evol. 13, 195–198.
Malizia, L.R., Greslebin, A., 2000. Reclutamiento de especies arbóreas bajo arbustos exóticos en la Sierra de San Javier, Tucumán Argentina. In: Grau, H.R., Aragón, R. (Eds.), Ecología de árboles exóticos en las Yungas Argentinas. LIEY-UNT, Tucumán, pp. 47–58.
Marod, D., Duengkae, P., Kutintara, U., Sungkaew, S., Wachrinrat, C., Asanok, L., Klomwattanakul, N., 2012. The influences of an invasive plant species (*Leucaena leucocephala*) on tree regeneration in Khao Phuluang Forest, northeastern Thailand. J. Agric. Nat. Resour. 46, 39–50.
MacDougall, A.S., Turkington, R., 2005. Are invasive species the drivers or passengers of change in degraded ecosystems? Ecology 86, 42–55.
McCune, B., Grace, J.B., Urban, D.L., 2002. Analysis of ecological communities. MjM software design, Gleneden Beach, Oregon, USA.
McNulty, S., Myers, J.M., Caldwell, P., Sun, G., 2013. Climate change summary. In: Wear, D.N., Greis, J.G. (Eds.), The Southern Forest Futures Project: technical report. General Technical Report 178. USDA-Forest Service, Southern Research Station, Asheville, North Carolina, pp. 27–43.
Meiners, S.J., 2007. Apparent competition: an impact of exotic shrub invasion on tree regeneration. Biol. Invasions 9, 849–855.
Merriam, R.W., Feil, E., 2002. The potential impact of an introduced shrub on native plant diversity and forest regeneration. Biol. Invasions 4, 369–373.
Miller, J.H., Lemke, D., Coulston, J., 2013. The invasion of southern forests by nonnative plants: current and future occupation, with impacts, management strategies, and mitigation approaches. In: Wear, D.N., Greis, J.G. (Eds.), The Southern Forest Futures Project: technical report. General Technical Report 178. USDA-Forest Service, Southern Research Station, Asheville, North Carolina, pp. 397–456.
Multi-Resolution Land Characteristics Consortium, 2019. NLCD 2016 (CONUS). Available at. https://www.mrlc.gov/data.
Orrock, J.L., Witter, M.S., 2010. Multiple drivers of apparent competition reduce re-establishment of a native plant in invaded habitats. Oikos 119, 101–108.
Oswalt, C.M., Oswalt, S.N., Clatterbuck, W.K., 2007. Effects of *Microstegium vimineum* (Trin.) A. Camus on native woody species density and diversity in a productive mixed-hardwood forest in Tennessee. For. Ecol. Manag. 242, 727–732.
Oswalt, S.N., Oswalt, C.M., 2011. The extent of selected nonnative invasive plants on southern forest lands, in: Fei, S., Lhotka, J.M., Stringer, J.W., Gottschalk, K.W., Miller, G.W. (Eds.), Proceedings, 17th central hardwood forest conference, Gen. Tech. Rep. NRS-P-78. US Department of Agriculture, Forest Service, Northern Research Station, Lexington, KY, pp 447–459.
Oswalt, C.M., Fei, S., Guo, Q., Iannone III, B.V., Oswalt, S.N., Pijanowski, B.C., Potter, K. M., 2015. A subcontinental view of forest plant invasions. NeoBiota 24, 49–54.
Pile, L.S., Vickers, L., Stambaugh, M., Norman, C., Wang, G.G., 2019. The tortoise and the hare: A race between native tree species and the invasive Chinese tallow. For. Ecol. Manag. 445, 110–121.
R Core Team., 2019. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria https://www.R–project.org/.
Schramm, J.W., Ehrenfeld, J.G., 2010. Leaf litter and understory canopy shade limit the establishment, growth and reproduction of *Microstegium vimineum*. Biol. Invasions 12, 3195–3204.
Skulman, B.W., Mattice, J.D., Cain, M.D., Gbur, E.E., 2004. Evidence for allelopathic interference of Japanese honeysuckle (*Lonicera japonica*) to loblolly and shortleaf pine regeneration. Weed Sci. 52, 433–439.
Soberón, J., Arroyo-Peña, B., 2017. Are fundamental niches larger than the realized? Testing a 50-year-old prediction by Hutchinson. PLoS One 12, e0175138.
Soil Survey Staff, 2020. The Gridded Soil Survey Geographic (gSSURGO) Database. United States Department of Agriculture, Natural Resources Conservation Service. Available online at https://www.nrcs.usda.gov/.
Standish, R.J., Robertson, A.W., Williams, P.A., 2002. The impact of an invasive weed *Tradescantia fluminensis* on native forest regeneration. J. Appl. Ecol. 38, 1253–1263.
Stanturf, J.A., Goodrick, S.L., 2013. In: The Southern Forest Futures Project: technical report. General Technical Report 178. USDA-Forest Service, Southern Research Station, Asheville, North Carolina, pp. 509–542.
Touchette, B.W., Romanello, G.A., 2010. Growth and water relations in a central North Carolina population of *Microstegium vimineum* (Trin.) A. Camus. Biol. Invasions 12, 893–903.
Geological Survey, U.S., 2020. The National Map. U.S, Department of the Interior. Available at https://www.nationalmap.gov.
USDA Forest Service., 2018. FIA Database Description and User Guide for Phase 2 (version: 8.0). USDA Forest Service, Forest Inventory and Analysis National Office.
USDA Forest Service., 2020. United States Forest Service. United States Department of Agriculture. https://www.fs.usda.gov/r8. Accessed on May 5th, 2020.
USDA, NRCS., 2020. The PLANTS Database. National Plant Data Team, Greensboro, NC 27401–4901 USA. http://plants.usda.gov. Accessed on May 31st, 2020.
USDA Forest Service Southern Research Station, 2020. United States Forest Service. United States Department of Agriculture. https://www.srs.fs.usda.gov/. Accessed on June 3rd, 2020.
Vickers, L.A., McWilliams, W.H., Knapp, B.O., D'Amato, A.W., Dey, D.C., Dickinson, Y.L., Kabrick, J.M., Kenefic, L.S., Kern, C.C., Larsen, D.R., Royo, A.A., Saunders, M.R., Shifley, S.R., Westfall, J.A., 2019. Are current seedling demographics poised to regenerate Northern US forests? J. For. 117, 592–612.
Vilà, M., Espinar, J.L., Hejda, M., Hulme, P.E., Jarošík, V., Maron, J.L., Pergl, J., Schaffner, U., Sun, Y., Pyšek, P., 2011. Ecological impacts of invasive alien plants: a meta–analysis of their effects on species, communities and ecosystems. Ecol. Lett. 14, 702–708.
Villamagna, A.M., Murphy, B.R., 2010. Ecological and socio-economic impacts of invasive water hyacinth (*Eichhornia crassipes*): a review. Freshw. Biol. 55, 282–298.
Wang, H.H., Grant, W.E., Swannack, T.M., Gan, J., Rogers, W.E., Koralewski, T.E., Miller, J.H., Taylor Jr, J.W., 2011. Predicted range expansion of Chinese tallow tree (*Triadica sebifera*) in forestlands of the southern United States. Divers. Distrib. 17, 552–565.
Wear, D.N., 2013. Forecasts of land uses. In: Wear, D.N., Greis, J.G. (Eds.), The Southern Forest Futures Project: technical report. General Technical Report 178. USDA-Forest Service, Southern Research Station, Asheville, North Carolina, pp. 45–71.
Wyatt, R., Wyatt, G.E., 2013. *Lygodium japonicum* (Thunberg) Swartz in the Piedmont of Georgia. Am. Fern J. 103, 188–190.