



Multivariate analysis of invasive plant species distributions in southern US forests

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Abstract

Context Invasive plants cause significant impacts in forested areas throughout the world. However, little is known about the relative importance of environmental drivers on the establishment and spread of invasive plants across forests at broader spatial scales.

Objectives We evaluated which factors are more closely associated with successful plant invasions across southern United States (US) forests and predicted regional susceptibility to invasion by 16 known major invasive plant taxa.

Methods We compiled environmental variables and presence-absence data for invasive plants across

52,690 southern US forestland plots surveyed by the Forest Inventory and Analysis (FIA) program of the USDA Forest Service. We used an ensemble species distribution modeling approach to model the potential distribution of the invasive plants and evaluated effects of the environmental predictors on species occurrences.

Results Invasive species presence was favored by proximity to land use such as pastures, croplands, and developed areas, as well as by high light availability and soil capacity to retain nutrients and water. Soil organic matter was negatively correlated with invasive species presence. However, the effect of climatic variables and other soil properties, such as pH and soil depth, was species-specific.

Conclusions Climate, land use, and soil organic matter were important but varied in their influence on invasive species distributions. Our results also indicate that most of our focal invasive plants are likely to occupy large forested areas throughout the study region. Thus, estimates of invasion risk should be incorporated into conservation strategies to prevent further establishment of invasive plants in forested areas.

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Introduction

Invasive plants cause significant ecological and economic harm in natural and managed forested areas throughout the world (Levine et al. 2003). Previous research has documented multiple ways in which invasive species alter the functioning of recipient forested ecosystems, including disturbance regimes, primary productivity, nutrient cycling, carbon sequestration, and tree regeneration (Levine et al. 2003; Peltzer et al. 2010; Lázaro-Lobo et al. 2021). Unfortunately, invasion events are likely to be more frequent in the future, as the rate of introduction of novel species continues to increase due to human-mediated dispersal through multiple trade networks (Capinha et al. 2015; Chapman et al. 2017; Lucardi et al. 2020). Consequently, limited resources to track species arrivals and their subsequent spread are being further stretched by an ever-increasing number of introductions (propagule pressure; Lockwood et al. 2005), underscoring the need for proactive and novel approaches to management, international border prevention and interception strategies, and inventory and monitoring programs to improve the efficiency with which invasions can be prevented and managed (Hulme 2009; Lucardi et al. 2020).

It is widely acknowledged that early detection of and rapid response (EDRR) to new infestations is key to reducing long-term impacts of individual species introductions, whether these new infestations represent novel species introductions or simply expansions of already established invaders (Kaiser and Burnett 2010; Reaser et al. 2020). Invasion risk maps are one tool that may be used in this respect, and many examples exist of species distribution models (SDMs) created for this purpose. However, although the establishment and spread of invasive species is affected by a combination of biotic, abiotic, and landscape factors (Theoharides and Dukes 2007; Catford et al. 2009; Milbau et al. 2009; Lázaro-Lobo and Ervin 2020), studies that integrate multiple types of environmental data in predicting invasive species distributions are scarce within the literature (Bradie and Leung 2017; Lázaro-Lobo et al. 2020). Many studies have used climate as the only environmental variable to predict future spread of plant species (Bradie and Leung 2017). Thus, in an effort to predict the potential regional spread of invasive plants in forested areas, we used a wide variety of

environmental variables that affect plant invasions at different spatial scales, as suggested by previous research (Ibáñez et al. 2009a, 2009b; Catford et al. 2011; Kelly et al. 2014; Walker et al. 2017; Lázaro-Lobo et al. 2020).

Landscape factors are especially important for the introduction and spread of invasive plants across a climatically suitable region (Catford et al. 2009). Previous work suggests that forest invasions are favored by landscape fragmentation and human land use (Iannone et al. 2015; Guo et al. 2018; Riitters et al. 2018). Invasive exotic species have been historically and frequently planted in developed and agricultural areas for soil stabilization, ornamental purposes, and cattle forage (Booth et al. 2003; Sämel and Kowarik 2010; Brown and Sawyer 2012). Once established in these human-modified areas, roadsides and other linear corridors can facilitate exotic plant species dispersal across the landscape and into less-impacted forest ecosystems (Lázaro-Lobo and Ervin 2019).

Once these species disperse into more remote areas of the landscape, local factors (e.g., resource availability and biotic community) can determine their survival and productivity (Diez and Pulliam 2007; Theoharides and Dukes 2007; Milbau et al. 2009). Nutrient availability, water availability, or both are greatly affected by soil properties, such as soil texture (composition of sand, silt, and clay), organic matter, and pH (Lucas and Davis 1961; Gurevitch et al. 2002). Soils with a high percentage of clay and organic matter have a great ability to retain water and minerals (Gurevitch et al. 2002), which could increase susceptibility to invasion (Davis et al. 2000). Nutrient availability in the soil solution can also increase with mild acidity (Gurevitch et al. 2002). Soil disturbance legacies from past agriculture also facilitate forest plant invasions, especially in young forests (Parker et al. 2010; Oswalt et al. 2015). Moreover, the recipient community can greatly determine invasion success. Some studies suggest that, at local scales, more diverse communities are more resistant to invasion because they use more resources and leave fewer empty niches for exotic species to occupy, generally known as the biotic-resistance hypothesis (Elton 1958; Shea and Chesson 2002; Beaury et al. 2019). Moreover, Iannone et al. (2016) found that native tree biomass and evolutionary diversity were negatively associated with invader establishment and dominance. Resistance to invasion also increases with

Table 1 Invasive taxa evaluated in this study (common names are based on the PLANTS Database; USDA, 2020) and percent of forested area within the study region that is at risk for species invasions (invasion risk > maximum training sensitivity plus specificity threshold). Forested areas are based on NLCD 2016 (Multi-Resolution Land Characteristics Consortium, 2019) and include deciduous, evergreen, and mixed forests, as well as woody wetlands

Growth form	Invasive taxa (scientific name)	Invasive taxa (common name)	Date of introduction of extensive planting	No. presence plots	% of forested area at risk of invasion
Tree	<i>Ailanthus altissima</i>	Tree of heaven	1784	485	6.2
	<i>Albizia julibrissin</i>	Silktree	1785	517	0.3
	<i>Melia azedarach</i>	Chinaberrytree	1830	433	1.4
	<i>Pyrus calleryana</i>	Callery pear	–	330	1.5
	<i>Triadica sebifera</i>	Chinese tallow	About 1900	1,105	9.7
Shrub	<i>Elaeagnus pungens</i>	Thorny olive	1939*	114	0.6
	<i>Lespedeza cuneata</i>	Sericea lespedeza	1863*	1,829	1.6
	<i>Ligustrum japonicum</i>	Japanese privet	1875*	505	7.8
	<i>Ligustrum</i> spp. (\neq <i>L. japonicum</i>)	Privet	1875*	6,637	38.5
Vine	<i>Rosa</i> spp. (non-natives)	Rose	1877*	1,799	23
	<i>Lonicera japonica</i>	Japanese honeysuckle	About 1850	2,445	37.2
	<i>Lygodium japonicum</i>	Japanese climbing fern	About 1918	1,502	13.4
Graminoid	<i>Pueraria montana</i> var. <i>lobata</i>	Kudzu	About 1920	185	0.2
	<i>Imperata cylindrica</i>	Cogongrass	About 1935	121	18.4
	<i>Microstegium vimineum</i>	Nepalese browntop	1919	670	7.9
	<i>Schedonorus phoenix</i>	Tall fescue	1940	177	5.2

*Average data for all the registered invasive species within the corresponding genus

the maturity of an ecosystem following disturbance, resulting in recently disturbed communities, such as pastures or local areas subjected to anthropogenic and natural disturbances, being more prone to be invaded than those that are further removed from disturbance (Planty-Tabacchi et al. 1996; Lázaro-Lobo and Ervin 2020).

In consideration of the above complexities in factors that may influence plant invasions of forested habitats, our aim was to determine those factors most closely associated with successful forest plant invasions across the southern United States (US), which is an area of primary concern with regard to the spread of invasive plant species (Oswalt and Oswalt 2011; Oswalt et al. 2015; USFS 2020). Along these lines, we hypothesized that susceptibility to invasion in forested

areas is affected by a combination of landscape and local factors. We predicted that human land use, light availability, and the soil capacity to retain nutrients and water would increase invasion susceptibility. We also predicted that climate would have the highest influence in those species whose distribution was restricted to specific areas of the study region. To test our hypothesis, we selected 16 major exotic plant taxa of different growth forms that are considered as invasive in the southern US (Table 1; Lázaro-Lobo et al. 2021), and evaluated the effect of predictor variables on invasion susceptibility. We further generated invasion risk maps of southern US forests, which can be used to assess the vulnerability of different areas to future plant species invasion(s), as

well as to inform which invasive species are most likely to spread across the region's forests.

Materials and methods

Study region

The study region corresponded to the mainland portion of the Southern Region of the United States Forest Service (USFS; Fig. 1). We excluded Puerto Rico and the US Virgin Islands to conduct this study to avoid possible island-related and substantial climatic difference effects on invasive species distributions. This resulted in 52,690 plots surveyed by the USFS Forest Inventory and Analysis (FIA) program as the dataset for our analysis and modeling. Forested area within the study region includes deciduous, evergreen, and mixed forests, as well as woody wetlands; based on NLCD 2016. Southern US forests are highly productive due to favorable climate conditions, such as warm temperatures and abundant rainfall (USFS 2020). Most of the parts of southern US have a relatively low topographic relief, except for the Appalachian Mountain chain, including the Blue Ridge, Ridge & Valley, and Piedmont ecophysiological regions. Invasive plants are widely established within the study region and are expected to increase their distribution over the next few decades (Miller et al. 2013; Lázaro-Lobo et al. 2020). There are over 380 recognized invasive plants in southern forests causing impacts on species diversity, tree regeneration, plant community structure, ecosystem services,

and human use potential of forested lands (Oswalt and Oswalt 2011; Miller et al. 2013; Lázaro-Lobo et al. 2021).

Species data

We used USFS FIA plots surveyed between 2015 and 2019 to obtain data on 16 invasive plant taxa of different growth forms with high rates of spread throughout southern forests (Miller et al. 2013). We worked directly with FIA personnel to match species data with georeferenced environmental variables from the precise locations of the FIA ground-truthed presence and absence data. We selected the years 2015–2019 to have the most recent, comprehensive occurrence data for the invasive plants, and to match sampling time with land cover and percent tree canopy cover data. Presence data corresponded to all the plots where the focal species were present between 2015 and 2019 (Table 1), whereas absence data corresponded to 10,000 plots where the corresponding species has been absent since 2002, when the FIA program started collecting data on invasive species in the region. The absence plots were selected within the distributional range of the corresponding invasive plant, which was defined by delineating the area occupied by each plant using minimum boundary geometry (convex hull). We included in the analyses those plots that were classified as “forestland” by the FIA program, which includes those areas with at least 10% canopy cover by trees of any size, have a continuous length of at least 110.6 m, and a width of at

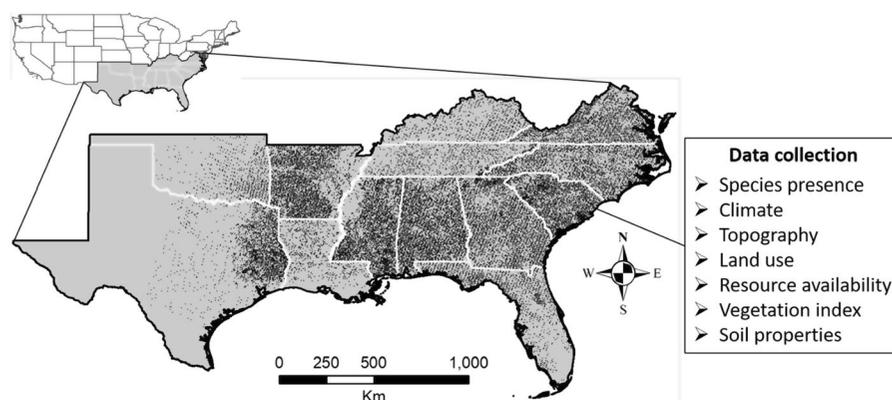


Fig. 1 Study region and data collection. Continuous lines delimitate U.S. states. The shaded area corresponds to the Southern Region of the Forest Service (Region 8). The black dots indicate the location of the Forest Inventory and Analysis (FIA) plots used in this study

Table 2 Overview of predictor variables

	Source	Original resolution
Climate		
Precipitation of the driest quarter	WorldClim database	30 arc sec (~ 1 km ²)
Minimum temp. of coldest month	"	"
Maximum temp. of warmest month	"	"
Topography		
Elevation	US Geological Survey database	100 m × 100 m
Slope	"	"
Land cover/land use		
Land cover	National Land Cover Database (NLCD 2016)	30 m × 30 m
Dist. to nearest developed area	"	"
Dist. to nearest pasture/crop area	"	"
Vegetation		
Percent tree canopy cover	"	"
NDVI	NASA's Landsat 8	"
Soil properties		
Percent of sand	Soil Survey Geographic (SSURGO) database	Shapefile*
Percent of silt	"	"
Percent of clay	"	"
Effective cation exchange capacity	"	"
Organic matter	"	"
Available water capacity	"	"
pH	"	"
Depth to soil restrictive layer	"	"

*Soil attributes in the SSURGO database are mapped at varying scales, depending on the variable type and the local soil conditions

least 36.6 m. The FIA plots are 0.4 ha and consist of four circular 7.3-m radius subplots, where invasive species are surveyed (USFS 2018).

Environmental variables

We compiled a broad range of geospatially-explicit environmental variables related to climate, topography, land use, tree canopy, vegetation index, and soil that are likely to influence spatial dynamics of the selected invasive taxa across the USFS Southern Region landscape (Table 2). All environmental variables were resampled, when needed, to a grid of 30-m resolution using the bilinear resample technique, which calculates the value of each pixel by averaging (weighted for distance) the values of the four nearest pixels (ESRI 2018). This resampling method has been broadly

implemented in ecological studies (Arif and Akbar 2005; Chapman et al. 2005; Lázaro-Lobo et al. 2020).

We obtained digital elevation data from the US Geological Survey database (USGS 2020) and calculated slope gradient using ArcGIS 10.5.1 (ESRI 2018). Biologically relevant bioclimatic variables that could potentially affect the establishment and spread of invasive species throughout southern US were downloaded from the WorldClim database (Fick and Hijmans 2017; Booth et al. 2014). Precipitation of the driest quarter may be too low for a plant to become established, whereas minimum temperature of coldest month and maximum temperature of warmest month may be too low and high, respectively, for the species survival (Ficetola et al. 2007; Lázaro-Lobo et al. 2020).

We obtained land cover data from the National Land Cover Database 2016 (NLCD 2016; Multi-

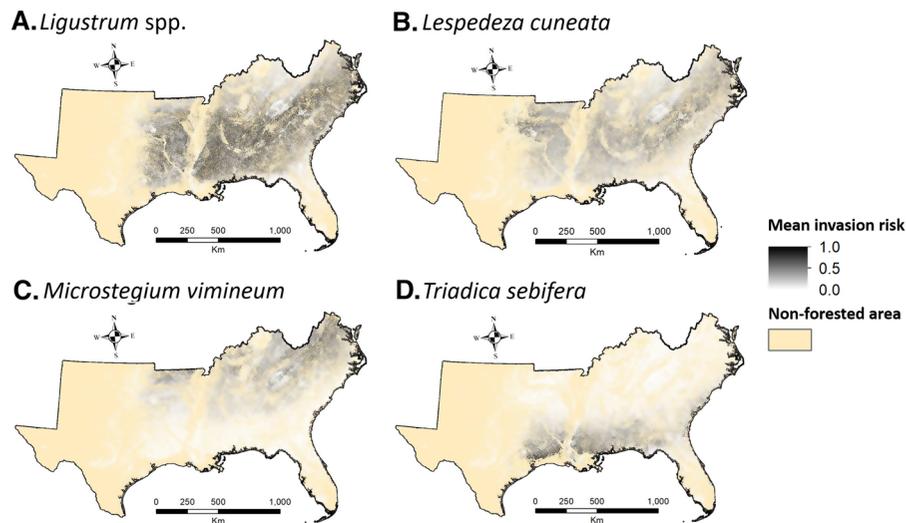


Fig. 2 Invasion risk maps for: (A) *Ligustrum* spp., (B) *Lespedeza cuneata*, (C) *Microstegium vimineum*, and (D) *Triadica sebifera*. The maps were generated using a combination of three modeling techniques: generalized additive model, maximum entropy, and generalized boosted model. Darker colors indicate

higher risk of invasion, while whiter colors illustrate the opposite. Forested areas are based on NLCD 2016 (Multi-Resolution Land Characteristics Consortium, 2019) and include deciduous, evergreen, and mixed forests, as well as woody wetlands

Resolution Land Characteristics Consortium 2019), then, calculated Euclidean distance from the center of FIA plots to the nearest developed and pasture/crop raster cell using ArcGIS 10.5.1 as surrogates of human land use influence. Developed areas refer to those areas with some constructed materials (NLCD categories 21, 22, 23, and 24), whereas pastures/crops correspond to those areas where plants are planted for livestock grazing or crop production (NLCD categories 81 and 82; Multi-Resolution Land Characteristics Consortium 2019). We also used NLCD (2016) to obtain percent tree canopy cover data, which was generated using multi-spectral Landsat imagery and other available ground information (Homer et al. 2015). The normalized difference vegetation index (NDVI) was obtained from NASA's Landsat 8 and included the average values from May to August between 2015 and 2017. Both tree canopy cover and NDVI described the presence of live green vegetation canopies. Lastly, we used the US Department of Agriculture, Soil Survey Geographic (SSURGO) database (Soil Survey Staff 2020) to generate raster layers with data from multiple soil properties related to nutrient and water holding capacity. Soil properties included percent of sand, silt and clay, effective cation exchange capacity (CEC), organic matter, available water capacity (AWC), pH, and depth to soil

restrictive layer. Such soil properties were extracted in the top 50-cm of soil (fertile layer), except for depth to soil restrictive layer.

We tested collinearity among environmental variables with Pearson's correlations, and retained those variables that were not highly correlated to each other (Pearson's $r < 0.5$; *sensu* Dormann et al. 2013) to predict the distribution of each invasive species in the study area. If two variables were correlated to each other, we excluded the variable that was less important in explaining species distributions in our study area, based on previous research and expert knowledge. In this sense, we excluded maximum temperature of warmest month, elevation, and slope from the SDMs because they were correlated with minimum temperature of coldest month. Similarly, we dropped NDVI because it was correlated with tree canopy cover. We also dropped percent of clay and silt, effective CEC, and AWC because they were correlated with percent of sand.

SDM development and validation

We used three of the most popular species distribution modeling algorithms (i.e., generalized additive model (GAM; Hastie and Tibshirani 1990); maximum entropy (MaxEnt; Phillips et al. 2006); and

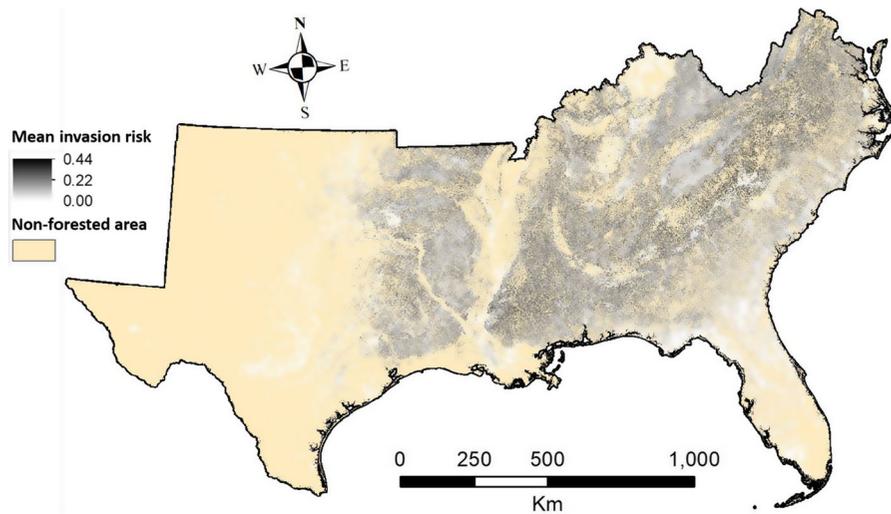


Fig. 3 Average susceptibility to invasion across all the species for each pixel occupied by forested areas. Darker colors indicate higher risk of invasion, while whiter colors illustrate the opposite. Forested areas are based on NLCD 2016 (Multi-

Resolution Land Characteristics Consortium, 2019) and include deciduous, evergreen, and mixed forests, as well as woody wetlands

generalized boosted model, also known as boosted regression trees (GBM; Friedman et al. 2000), and a weighted ensemble model to estimate the potential distribution of each evaluated invasive species in southern forests. The ensemble model was produced to find agreements in areas estimated as suitable by individual models, reduce the uncertainty associated to individual models, and thereby reduce the prediction error (Araujo and New 2007). All SDMs were generated in the program R (R Core Team 2019). We calibrated each of the three individual models using the same set of occurrence (presence and absence) points and environmental predictor variables for each species. Once calibrated, each of the three individual models was projected across the whole study area to generate three independent prediction maps of invasion risk (susceptibility to invasion) at 30-m resolution with pixel values ranging 0 (low susceptibility to invasion) to 1 (high susceptibility to invasion).

We used a 5-fold cross-validation procedure to evaluate the predictive power of each model. This method separates the presence and absence points into equal-sized groups (folds) and every iteration leaves out one different fold, using, therefore, all of the data for validation (Phillips 2017; Lázaro-Lobo et al. 2020). Thus, we generated five subsets of predicted values (i.e. test values) that were then compared to the observed presence and absence values to evaluate

model performance (model's goodness of fit) using the metric area under the curve (AUC) of the Receiver Operator Characteristic (ROC) plot (Franklin 2009). While the AUC is the most popular metric used to evaluate the performance of a SDM, we calculated two additional metrics as a robustness check: the area under the precision-recall curve (AUC-PR; Sofaer et al. 2019); and the true skill statistic (TSS; Allouche et al. 2006). We calculated these metrics (AUC, AUC-PR, and TSS) for each of the five-folds and then averaged these metric score values to obtain the mean performance score associated to the model. AUC and AUC-PR values range from 0 to 1. Higher AUC and AUC-PR values indicate better performance of the model (Peterson et al. 2011). However, the TSS ranges from -1 to 1 , with values of 0 or less representing that the model is no different than random, whereas a value of 1 indicates 100% agreement of the model with the data (Allouche et al. 2006; Lázaro-Lobo et al. 2020).

Lastly, we generated a final model ensemble for each species by averaging the output of the individual modeling techniques (GAM, MaxEnt, and GBM), weighted by their model performance scores (AUC values; Araújo and New 2007; Guisan et al. 2017; Ramirez-Reyes et al. 2021). Thus, an individual model with a higher performance had a higher weighted contribution in the development of the final model ensemble. This ensemble modeling approach resulted

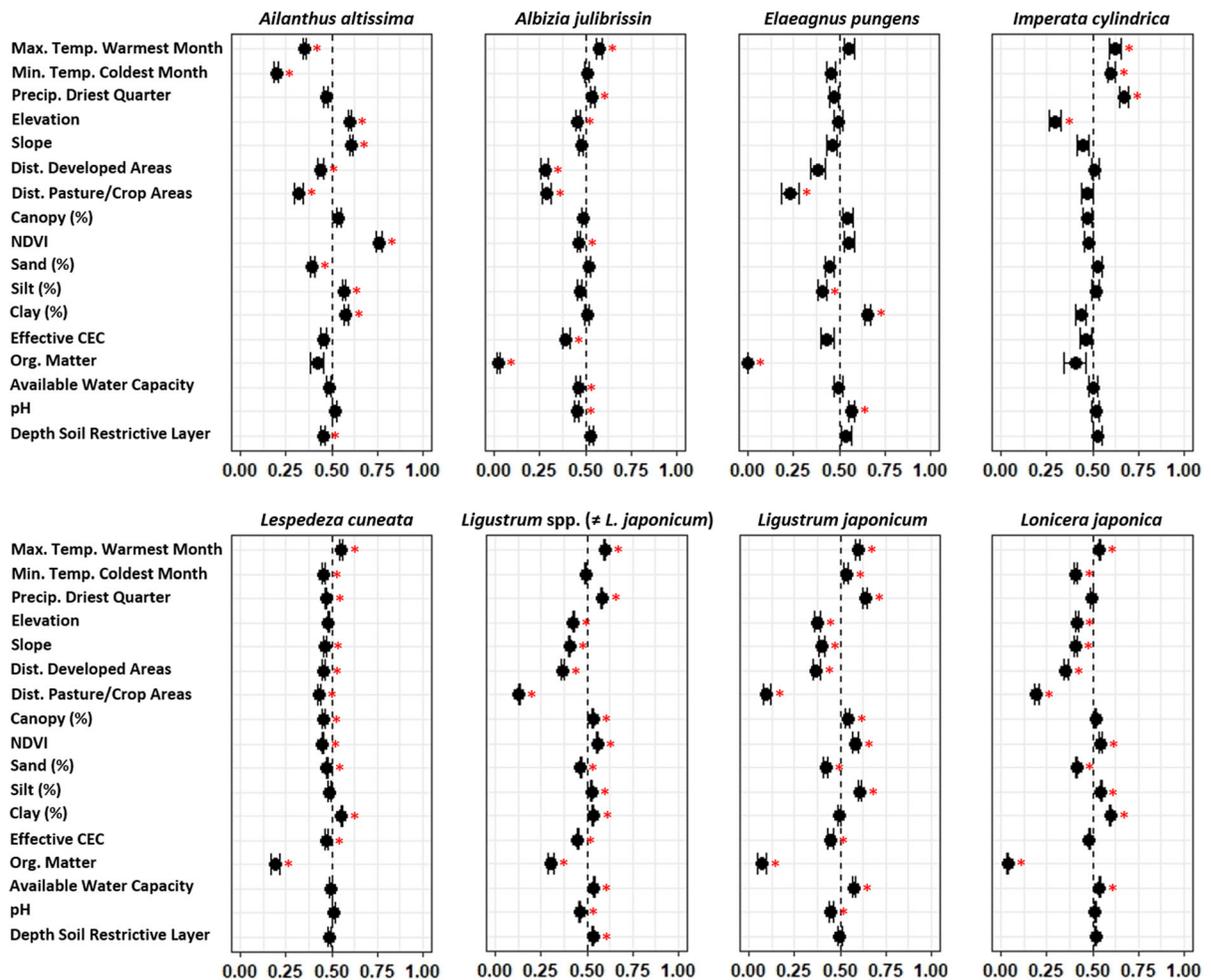


Fig. 4 Relative contribution of environmental predictor variables to explain invasive species distributions (based on presence-absence data). Dots represent the parameter estimates and bars indicate standard errors. The higher the distance of the dots to the vertical dashed line, the more influence the variable has on the corresponding invasive species distribution. Values higher and lower than 0.5 indicate positive and negative

relationships between environmental variables and invasive species, respectively. Statistically significant relationships were evaluated considering the multiple-comparison (Bonferroni) correction (corrected $\alpha = 0.003$) and are indicated with a red asterisk to the right of the corresponding parameter estimate (dot). Statistical results are also shown in Supplementary Table 2

in SDM outputs with 30-m resolution pixels, which pixel values ranged from 0 (low susceptibility to invasion) to 1 (high susceptibility to invasion).

Evaluating invasion risk

We required a binary suitable/non-suitable map for each species to measure the percent of forested land cover within the study area that was predicted to be at risk of invasion. Since the output format generated by the final ensemble model consisted of grid cells with values ranging continuously from 0 (low susceptibility

to invasion) to 1 (high susceptibility to invasion), we used the maximum sensitivity plus specificity threshold to differentiate between suitable and unsuitable grid cells. Sensitivity measures the percentage of correctly classified presences, while specificity measures the percentage of correctly classified absences (West et al. 2016). This approach is highly efficient and has been widely used in SDM studies (e.g., Jorge et al. 2013; Liu et al. 2013; Kebede 2014). Values for this metric ranged from 0.28 to 0.55 among species. Then, we calculated the ratio of percent forested area having pixel values higher than the

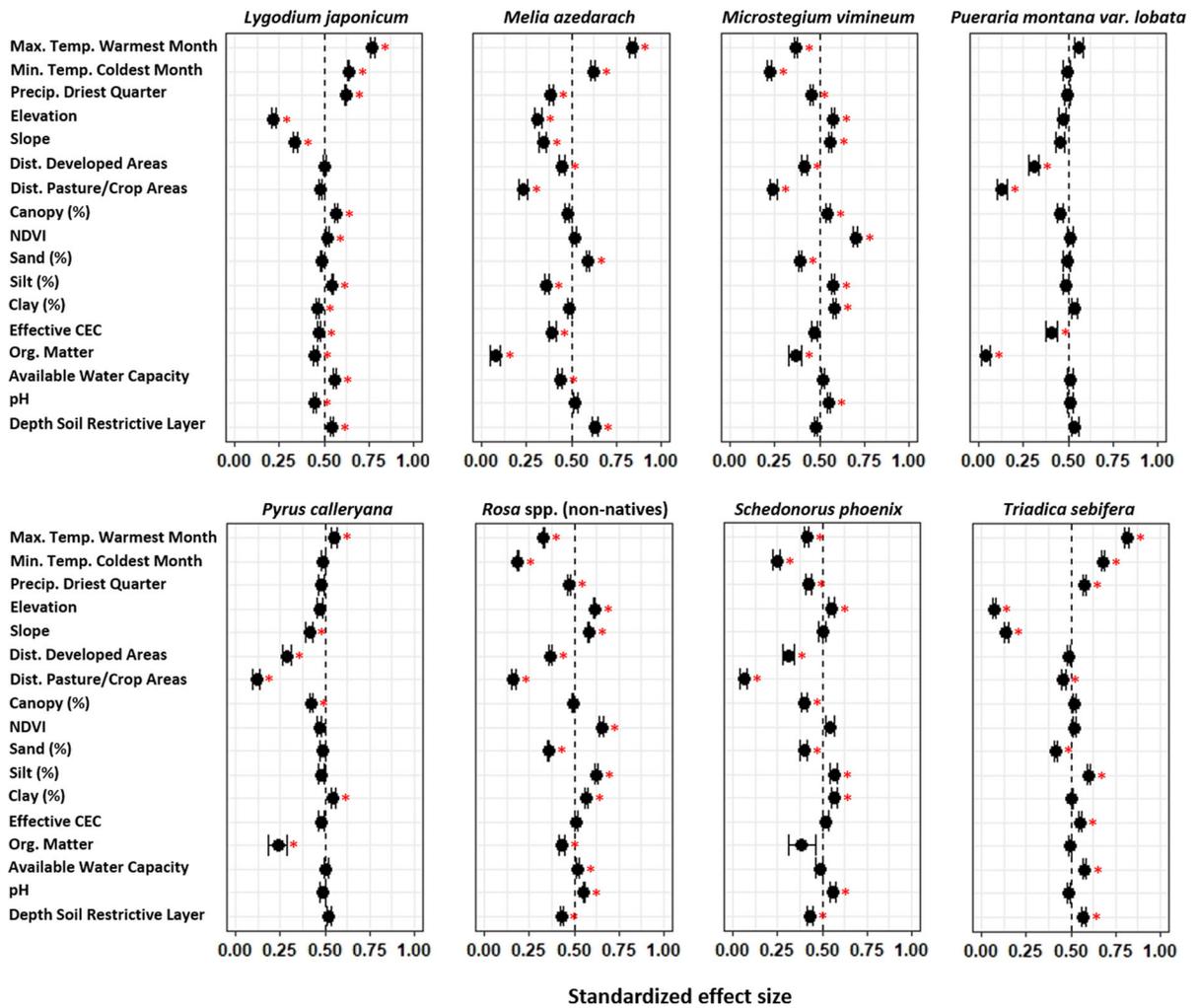


Fig. 4 continued

maximum sensitivity plus specificity threshold for a given species to the total forested area, and multiplied the result by 100 to obtain the percentage of forested area predicted to be susceptible to invasion by that species. Lastly, we calculated the mean susceptibility to invasion across the evaluated species for each cell in the resulting risk maps. This allowed us to delineate areas at high risk of invasion (hotspots) in southern US forests.

Relative influence of environmental predictor variables

Each model algorithm uses a different method to evaluate the contribution of predictor variables to

develop the models. GAM uses approximate significance of smooth terms in *p*-values, MaxEnt indicates percent contribution of environmental predictors, and GBM shows the relative influence of variables. We compared the results obtained from each model to assess the relative importance of the environmental variables on invasive species distributions. In addition, we conducted generalized linear models (GLMs) with binomial distribution of residuals (Zuur et al. 2009) to evaluate the effect size of each environmental variable. We conducted individual GLMs for each environmental variable due to the high degree of collinearity among the evaluated variables. Thus, GLMs provided insights into the effect size of variables not included in SDMs (GAM, MaxEnt, and

GBM) and added more information about the effect size of those already included in SDMs. Since the environmental variables were measured with different units, we standardized their values using the function “scale” of the program R before conducting this analysis, to make the interpretation of their effect sizes more comparable. We used a multiple-comparison (Bonferroni) correction to lower the critical p -value and accommodate the high number of statistical tests being performed simultaneously (Cabin and Mitchell 2000). This reduced the likelihood of having a significant result by pure chance (Type I error) when making multiple statistical tests. Lastly, we back-transformed the parameter estimates and standard errors to the original scale using the appropriate inverse link function for binomial distribution.

Results

SDM model outputs and model performance evaluation

The invasive taxa with the greatest potential to establish across southern US forests were *Ligustrum* spp. (exotic privets) and *Lonicera japonica* (Japanese honeysuckle). For these two species, 37–39% of the forested area across our study region was estimated to be susceptible to invasion. These species were followed by *Rosa* spp. (exotic roses), *Imperata cylindrica* (cogongrass), and *Lygodium japonicum* (Japanese climbing fern) (18–23%) (see Table 1 for nomenclature for the 16 exotic taxa). By contrast, *Albizia julibrissin* (silktree), *Elaeagnus pungens* (thorny olive), and *Pueraria montana* var. *lobata* (kudzu) were predicted to occupy < 1% of the forested area. Lastly, our models indicate that 1–10 % of the area occupied by southern US forests is suitable for the remaining 8 invasive taxa (Table 1).

We also found that each evaluated species is likely to occupy different areas of the southern US (Fig. 2; Supplementary Fig. 1). For example, our models show that the predicted distributions of *Lygodium japonicum* and *Triadica sebifera* (Chinese tallow) are restricted to coastal areas of the Gulf and East Coasts of the study region, whereas *Ailanthus altissima* (tree of heaven), *Microstegium vimineum* (Nepalese browntop), *Rosa* spp., and *Schedonorus phoenix* (tall fescue) will likely occupy interior areas of the study region.

However, other species such as *Ligustrum* spp., *Lonicera japonica*, and *Pyrus calleryana* (Callery pear) have the potential to establish throughout southern US forests. Furthermore, the average susceptibility to invasion across all the species for each pixel occupied by forested areas is indicated in Fig. 3.

We obtained relatively high values of model performance metrics (especially for AUC values; Supplementary Table 1), which indicates that the models had a high predictive power, and, thus, had the ability to discriminate between presences and absences of our focal invasive species. However, the GBM modeling approach performed better than GAM and MaxEnt for all of the evaluated species, and, thus, had a higher weighted contribution for the final model ensembles (Supplementary Table 1).

Relative influence of the environmental variables

The results obtained from GAM, MaxEnt, GBM, and GLM models were generally similar to each other with respect to the influence of environmental predictor variables on invasive species distributions (Fig. 4; Supplementary Tables 2 and 3). Climatic variables had a high number of significant relationships with the evaluated invasive taxa (Fig. 4; Supplementary Tables 2 and 3). Maximum temperature of the warmest month was positively related with ten species and negatively associated with four species (out of 16 taxa evaluated). Minimum temperature of the coldest month had five positive and six negative relationships with the invasive species in our list, whereas precipitation of the driest quarter was positively related with six and negatively associated with five of these species.

Topographic variables (elevation and slope) were negatively correlated with climatic variables, and, thus, most significant relationships with topographic variables were the opposite of those with climatic variables. This was only seen for GLMs, because topographic variables were excluded from SDMs (GAM, MaxEnt, GBM) due to collinearity. Elevation and slope gradients affected the presence of the 16 focal invasive species taxa similarly, with most of the species having a significant negative relationship with these topographic variables (Supplementary Table 2). However, *Ailanthus altissima*, *Microstegium vimineum*, and *Rosa* spp. resulted in positive relationships.

Elevation was also positively associated with *Schedonorus phoenix*.

Land use variables significantly explained invasion susceptibility for most of our species across the study area (Fig. 4; Supplementary Tables 2 and 3). Distance to developed areas and pastures and croplands generally resulted in a significant negative relationship with the focal species' presence. However, distance to pastures and croplands were always more negatively related with species presence than was distance to developed areas. We did not find any significant positive relationship between such land use variables and invasive species presence. Tree canopy and NDVI did not have the highest influence on invasive species presence (Fig. 4); however, these variables had a significant positive relationship with *Ligustrum* spp., *Lygodium japonicum*, and *Microstegium vimineum*, and a negative significant relationship with *Lespedeza cuneata* (sericea lespedeza). Tree canopy values were also negatively related with *Pyrus calleryana* and *Schedonorus phoenix*, whereas NDVI also had a negative relationship with *Albizia julibrissin*, and a positive association with *Ailanthus altissima*, *Rosa* spp., and *Lonicera japonica*.

Among the soil variables examined, organic matter exhibited the highest correlation with invasive species presence (Fig. 4). This variable was strongly negatively related with most of the evaluated 16 focal invasive species. We did not find any positive relationship (significant or not) between organic matter and invasive species presence. The rest of the soil variables analyzed also had a high number of significant relationships with invasive species occurrence (Supplementary Tables 2 and 3); however, they had a lower contribution to explain invasive species distributions than climatic and land-use variables. We found that higher soil sand composition was significantly correlated with decreasing presence of many invasive species, except for *Melia azedarach* (Chinaberrytree), which was positively influenced by sand content in the soil. Silt and clay content gave the expected results, based on correlations with sand content. These variables were generally positively associated with invasive species presence, except for *Elaeagnus pungens* and *Melia azedarach*, which had negative significant relationships with silt, and *Lygodium japonicum*, which was negatively related with clay. Effective CEC was significantly negatively related with *Albizia julibrissin*, *Lespedeza cuneata*,

Ligustrum spp., *Lygodium japonicum*, *Melia azedarach*, and *Pueraria montana* var. *lobata*; however, it had a positive relationship with *Triadica sebifera*. Available water capacity was positively related with 6 species and negatively associated with two species. On the contrary, pH had an equal number of positive and negative significant relationships with invasive species (4 for each type of relationship). Depth to soil restrictive layer also had a similar number of positive and negative significant relationships with invasive species (4 positive and 3 negative).

Discussion

Relative influence of the environmental variables

The resulting models supported our initial hypothesis that susceptibility to invasion in forested areas is affected by a combination of landscape and local factors (Fig. 4). Climate variables were among the predictors that most contributed to invasion susceptibility of the study area, especially in those species whose distribution was restricted to specific parts of the USFS's Southern Region. However, climatic variables seem to play a secondary role for those species with broad acclimation capacity and distributions throughout large swaths of the region, such as *Ligustrum* spp., *Lonicera japonica*, and *Pyrus calleryana*. Thus, minimum temperature of coldest month, maximum temperature of warmest month, and precipitation of driest quarter are most likely to restrict the distribution of species with less capacity to endure extreme climatic conditions within the study area (Pattison et al. 2008; Zimmermann et al. 2009; Wang and Grant 2012). However, future climatic conditions could allow invaders to expand into new ranges, as has been demonstrated by previous research conducted within the study region with three of our focal invasive taxa (*Pueraria montana* var. *lobata*; *Ligustrum* spp., and *Imperata cylindrica* (Bradley et al. 2010). Furthermore, variables related to temperature generally had a higher influence on invasive species occurrence than precipitation, which could be explained by the absence of an important hydric deficit (drought) period throughout the region (Lázaro-Lobo et al. 2020). This result is consistent with previous research conducted in our study area, where multiple invasive species

were evaluated considering all the land cover types (Lázaro-Lobo et al. 2020).

Topographic variables also had a great effect on the distribution of the evaluated invasive species. Previous work suggested that elevation and slope gradient can affect the establishment of exotic species (Rouget and Richardson 2003; Pauchard and Alaback 2004; Lemke et al. 2011; Yang et al. 2021). However, in our study, the effect of topographic variables on species distributions could be intensified by their negative correlation with climatic variables. Most of the parts of southern US have a relatively low topographic relief, except for the Appalachian Mountain chain, which also have the lowest temperatures within the study area. Therefore, areas with higher elevation and slope overlap with areas with lowest temperatures, which could confound the effect of topographic variables on species distributions. For example, *Ailanthus altissima*, *Microstegium vimineum*, *Rosa* spp., and *Schedonorus phoenix* were predicted to occupy interior mountainous areas of the study region and were positively associated with elevation and negatively related with minimum temperature of coldest month and maximum temperature of warmest month.

Human land use in the surrounding area was also one of the most relevant predictor variables to explain invasive species distributions, even with our focus restricted to forested areas. Pastures, croplands, and developed areas nested within forest boundaries provide suitable habitat for many invasive species, which are or have been often planted for soil stabilization, ornamental purposes, and cattle forage (Booth et al. 2003; Säumel and Kowarik 2010; Brown and Sawyer 2012). These land cover types can serve an important role by sourcing plant propagules that can be dispersed to neighboring and/or surrounding forested areas (Booth et al. 2003; Lázaro-Lobo and Ervin 2019). Human land use increases landscape fragmentation, which increases susceptibility to biological invasions (Anderson et al. 2013; Iannone et al. 2015; Guo et al. 2018; Riitters et al. 2018). However, in our study, distance to pastures/crops were more important in explaining invasion susceptibility than distance to other developed areas. This suggests that forested areas close to pastures and croplands are more prone to be invaded than those closer to other developed areas, which were mainly represented by roadsides. This could be due to a higher area occupied

by pastures and crops, which could support higher population densities of invasive species than linear infrastructures. This result agrees with previous research conducted in forests of the study area, which states that the landscape context associated with a road, including land use, is more important than the existence of a nearby road (Riitters et al. 2018). However, a study conducted in all land cover types of the study area suggested that distance to developed areas were more important than distance to pastures/croplands to model species distributions (Lázaro-Lobo et al. 2020) as driver of introduction and dispersal.

Tree canopy cover and the presence of live green vegetation in the study plots had a secondary role to explain forest invasion susceptibility. Some species had a significant relationship with those variables; however, the effect size (or strength) of such relationship was lower than with other environmental factors (Fig. 4). This could be due to the restriction of our study to forested areas, which lowered the variance of tree canopy cover among the study sites. Generally, biological invasions are favored by increases in resource availability (e.g., light, space, and nutrients; Davis et al. 2000). Thus, forest disturbances that increase canopy openness and, therefore, resource availability, would favor the establishment of invasive species. Previous research suggests that high values of native tree biomass and evolutionary diversity increase biotic resistance to invasions (Iannone et al. 2016). The species evaluated in this study were differentially affected by tree canopy and therefore, light availability, which suggests that some species, such as *Lespedeza cuneata*, *Pyrus calleryana*, and *Schedonorus phoenix* (high-light), prefer open or edge habitats, while others occur in forest interiors, such as *Lygodium japonicum* and *Microstegium vimineum* (shade tolerant).

Finally, among soil variables, organic matter played a major role to explain invasive species distributions (Fig. 4). Soil organic matter results from the accumulation of materials produced by living organisms that are in various stages of decomposition (Gurevitch et al. 2002). Organic matter facilitate root and fungal hyphae penetration, supplies essential nutrients and increase the availability of others, attracts and retains ions, and increases water holding capacity (Gurevitch et al. 2002). Thus, we expected that organic matter content would facilitate the establishment of invasive species. However, study

plots with high values of soil organic matter had a lower presence of most of the evaluated invasive species. This could be due to a large accumulation of organic matter, derived from litter and woody debris, as expected in interior forestlands and in areas where native species were abundant, which could be explained by an increased resilience due to biotic resistance (Iannone et al. 2016; Lázaro-Lobo and Ervin 2020). The remaining soil variables had a low-moderate effect size to explain invasion susceptibility. Our results suggest that invasive species presence generally decreases with high values of percent of sand in the soil. In sandy soils, the limiting factor is often nitrogen, which is necessary for plant functioning and growth (Gurevitch et al. 2002). Thus, nutrient deficiency could impede the establishment of invasive exotic species in forested areas. On the contrary, invasive species presence was generally favored by high values of percent of silt and clay in the soil. Clayey soils have a great ability to retain water and minerals, whereas silty soils have intermediate properties between sandy and clayey soils (Gurevitch et al. 2002), which could favor the establishment of plant species. As expected, water availability was usually positively related to invasive species presence. We expected that cation exchange capacity (CEC) would increase the presence of invasive species because there would be more nutrients available for plant growth. However, CEC generally had a negative relationship with invasive species presence. Lastly, pH and depth to soil restrictive layer had mixed results, which indicates that the susceptibility to invasion of study plots with different values of such variables is species specific.

Species-level patterns

Our results indicate that southern US forests are especially susceptible to be invaded by *Ligustrum* spp. and *Lonicera japonica*, consistent with previous literature (Table 1; Oswalt and Oswalt, 2011). We found that large areas throughout southern US are suitable for the establishment of both of these invasive taxa, which are already widely widespread in southern US forests and whose distribution is expected to increase by ~ 35% over the next 40 years (Miller et al. 2013). Regarding the rest of invasive taxa with high probability of occupying a relatively large portion of the region's forests, *Rosa* spp., which

includes over 21 non-native rose species, was indicated to have potential to expand its distribution in the northern part of the region. Our models show that *Lygodium japonicum* will likely occupy coastal areas, especially in the Gulf Coast, and that both northern and southern areas of the region's forests are susceptible to *Imperata cylindrica* invasion.

In contrast, our results suggest that southern US forests can act as a barrier for the spread of the invasive species *Albizia julibrissin*, *Elaeagnus pungens*, and *Pueraria montana* var. *lobata* (Table 1). Previous research indicated that *A. julibrissin* stands should generally be found scattered throughout the USFS Southern Region, especially along highways (Miller et al. 2013). Similarly, the vine *Pueraria montana* var. *lobata* is mostly present along forest edges and disturbed forests because it is shade intolerant (Carter and Teramura 1988; Miller et al. 2013). However, the thorny shrub *E. pungens* is in its early "lag" phase of forest invasion with scattered individuals, which indicates that its potential to invade forests could significantly increase during the next decades (Miller et al. 2013). The lag time that often exists between introduction of an exotic species and the actual observation of negative impacts of invasion could be due to ecological (e.g., lag phase of an exponential growth curve), evolutionary (e.g., adaptation to a new environment), and/or sociological (e.g., public awareness) factors (Crooks 2005; Müller-Schärer and Steinger 2004).

Land managers and policy makers should pay special attention to forested areas at high risk of invasion to protect the abundance and diversity of native and desirable forest communities. Specifically, monitoring programs that evaluate the presence and abundance of our focal invasive species and others should be started (or continued) in areas at high risk of invasion provided in this study. This would allow managers to detect and control invasive plants before they spread across the landscape, which would reduce both management effort and long-term impacts associated to plant invasions. Moreover, managers can use our results to evaluate how different ecosystem characteristics affect invasive plant distributions in forested areas. This would allow them to act on those characteristics with management potential, such as canopy cover and land use, to reduce landscape susceptibility to invasion.

Conclusions

The results of this study demonstrate that environmental variables differentially affect invasive species distributions in forested areas across large spatial extents. We found that surrounding land use and soil organic matter content were especially important to explain invasive species distributions within forested areas in general. However, nearby pastures, croplands, and developed areas (e.g., roadsides) are important sources of invasive plant propagules. Among these, distance to pastures and croplands had a higher importance to explain invasion susceptibility than distance to developed areas. Soil organic matter was negatively correlated with invasive species presence, which could be due to higher accumulation of organic matter in areas where native species were abundant, and, thus, more resistant to biological invasions. Invasive species presence also was favored by high light availability and soil capacity to retain nutrients and water, but these were less influential than the above factors. Other soil properties, such as pH and soil depth, showed species specific patterns among the 16 focal taxa (Table 1). At the larger spatial scale, climate extremes seemed to function primarily in restricting some of the focal species to parts of the region, such as the coastal distribution exhibited by several species in the south.

Furthermore, our species distribution modeling allows for the delineation of forested areas in southern US likely to be invaded by major invasive plant taxa. Our results indicate that southern US forests are especially susceptible to be invaded by *Ligustrum* spp. and *Lonicera japonica* (37–39% of the forested area), and by *Rosa* spp., *Imperata cylindrica*, and *Lygodium japonicum* (18–23%). On the other hand, forests can act as a barrier for the spread of the invasive species *Albizia julibrissin*, *Elaeagnus pungens*, and *Pueraria montana* var. *lobata*. The resulting invasion risk maps should be incorporated in conservation and restoration strategies to prevent and control the establishment of invasive plant taxa.

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Data availability All the relevant data for the article can be found in Tables, Figures, and Supplementary Tables and Figures.

Declarations

Conflict of interest Not applicable.

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