Journal of Environmental Management 155 (2015) 97–105

Contents lists available at ScienceDirect

Journal of Environmental Management

journal homepage: www.elsevier.com/locate/jenvman

Predictors, spatial distribution, and occurrence of woody invasive plants in subtropical urban ecosystems

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ARTICLE INFO

Article history:
Received 17 November 2014
Received in revised form
3 February 2015
Accepted 5 March 2015
Available online 13 March 2015

Keywords:
Spatial analysis
Urban forest structure
Forest inventory and analysis
Socio-ecological systems
Predictive models

ABSTRACT

We examined the spatial distribution, occurrence, and socioecological predictors of woody invasive plants (WIP) in two subtropical, coastal urban ecosystems: San Juan, Puerto Rico and Miami-Dade, United States. These two cities have similar climates and ecosystems typical of subtropical regions but differ in socioeconomics, topography, and urbanization processes. Using permanent plot data, available forest inventory protocols and statistical analyses of geographic and socioeconomic spatial predictors, we found that landscape level distribution and occurrence of WIPs was not clustered. We also characterized WIP composition and occurrence using logistic models, and found they were strongly related to the proportional area of residential land uses. However, the magnitude and trend of increase depended on median household income and grass cover. In San Juan, WIP occurrence was higher in areas of high residential cover when incomes were low or grass cover was low, whereas the opposite was true in Miami-Dade. Although Miami-Dade had greater invasive shrub cover and numbers of WIP species, San Juan had far greater invasive tree density, basal area and crown cover. This study provides an approach for incorporating field and available census data in geospatial distribution models of WIPs in cities throughout the globe. Findings indicate that identifying spatial predictors of WIPs depends on site-specific factors and the ecological scale of the predictor. Thus, mapping protocols and policies to eradicate urban WIPs should target indicators of a relevant scale specific to the area of interest for their improved and proactive management.

1. Introduction

Urban areas are currently home to over 50% of the world's population and rates of urbanization will only increase through 2050 (Roberts, 2011). These urban areas are ecosystems offering habitats with novel disturbance regimes and new germination and colonization sites for the establishment of non-native species (Allen et al., 2013; Kowarik, 2011). Non-native or alien plant species now constitute an important and substantial part of the vegetation composition of urban ecosystems throughout the globe (Alston and Richardson, 2006; Kendal et al., 2014; Lima et al., 2013; Richardson and Rejmánek, 2011; Zhao et al., 2010a). However, alien vegetation has in many instances also become invasive, posing detrimental impacts to adjacent natural ecosystems (Bradley et al., 2012; Larson et al., 2011). Indeed, alien invasive plants have had major deleterious economic and ecological effects on urban and peri-urban landscapes throughout the globe because of their proximity to natural, agricultural and forest ecosystems. While much of the global research has been devoted to invasive plants in forested and agricultural landscapes, a little studied area is that of understanding and identifying the management relevant socio-ecological predictors of woody invasive plants (WIPs) in urban ecosystems where most invasive plants originate.

Plant invasions in urban areas affect ecosystem service provision (Escobedo et al., 2010; Kendal et al., 2014; Zhao et al., 2010b) and

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http://dx.doi.org/10.1016/j.jenvman.2015.03.012
0301-4797/

increase ecological homogenization (Groffman et al., 2014). In natural areas, invasive plants have been shown to reduce biodiversity and alter biogeochemical processes (Richardson and Rejmánek, 2011), change forest structure, and alter natural disturbance regimes (Vicente et al., 2013; Vitousek et al., 1995). Species such as *Schinus terebinthifolius* Raddi and *Melaleuca quinquenervia* (Cav.) S.F. Blake, for example, have displaced native plants in subtropical urban and natural areas, altering ecosystem function, and leading to reductions in some populations of associated native animal species (Larson et al., 2011; OTA, 1993).

Urban ecosystems and their inhabitants are primary sources of, and dispersal agents for, invasive plant species (Mack et al., 2000; Reichard and White, 2001). Invasive plants originate in urban ecosystems through horticultural plantings; 85% of all invasive woody species in North America were intentionally planted in urban areas (Martin et al., 2008). Invasive plants are able to spread as the boundaries between urban and peri-urban areas in many geographic locales are increasingly intermixed, and areas with natural vegetation become urbanized (Gavier-Pizarro et al., 2010). For example, the number of housing units in subtropical Florida has increased 23% over the last decade (US Census Bureau, 2012), and ~30% of its flora is non-native (Bradley et al., 2012). The introduction of *S. terebinthifolius* as an ornamental plant in urban and peri-urban areas which then escaped, has negatively affected expansive areas of the Florida Everglades, United States (US). The occurrence of invasive trees and shrubs is closely related to ecological processes and anthropogenic activities (Mack et al., 2000; Gavier-Pizarro et al., 2010; Richardson and Rejmánek, 2011), in particular land use change (Reichard and White, 2001; Vitousek et al., 1995). Therefore, identifying the socio-ecological factors, or spatial predictors influencing invasive trees and shrubs occurrence, in urban areas is necessary for their effective management and control (Alston and Richardson, 2006; Larson et al., 2011; Richardson and Rejmánek, 2011; Vicente et al., 2013).

Across the globe, urban WIP distributions have been associated with a variety of socio-ecological factors. In Phoenix, US and Santiago, Chile, plant diversity was shown to be driven by socioeconomic factors (de la Maza et al., 2002; Hope et al., 2003). Invasive plant richness and occurrence was also found to be strongly related to housing variables in the northern US, such as the boundary between low-density residential areas and peri-urban areas and the housing density (Gavier-Pizarro et al., 2010). Anthropogenic disturbance was found to influence alien plant richness in a subtropical South African peri-urban area, while alien stem density was not (Alston and Richardson, 2006). Allen et al. (2013) also found that regional patterns of urban development in the northern US were linked with woody plant invasions. Similarly, invasive trees and palms in Florida, US, were found primarily in residential land uses and natural areas as opposed to private and public non-residential land uses (Zhao et al., 2010a).

Studies have also shown how socio-ecological factors play a role in determining the spatial distribution of invasive species in urban forests. Urban and peri-urban chemical and physical soil properties and maintenance activities have been found to affect the composition, structure and function of urban vegetation in subtropical cities (Dobbs et al., 2011; Hagan et al., 2012). Climatic events, such as hurricanes have been reported to influence WIP occurrence, and spread (Zhao et al., 2010a). Vicente et al. (2013) for example used a multi-scale approach and 24 environmental predictors and geospatial data to develop a distribution model for prioritizing invasives management. Previous research on predicting urban WIPs has, however, been limited, as most studies have focused on temperate, herbaceous plants (Richardson and Rejmánek, 2011) in smaller sized study areas (Levine, 2008; Martin et al., 2008).

Overall, we found few landscape scale studies in the global literature that identified the socio-ecological predictors that could be used to predict subtropical, urban woody invasive tree and shrub occurrence. This is partially a result of the complexity of field data collection in urban areas, which is difficult and costly due to access, safety and logistical limitations. Given this gap in our understanding, the aim of our study was to analyze WIP distributions at the landscape scale and identify socio-ecological indicators that could spatially predict their occurrence. To better understand these management relevant factors, we chose two contrasting coastal urban ecosystems as our study sites: San Juan, Puerto Rico and Miami-Dade, Florida. These two study areas have similar climates and populations, are located between coastal and conservation areas, and encompass land uses and ecosystems typical of the Caribbean region and other subtropical areas in Asia, Australia, and elsewhere. However, they differ in socioeconomic patterns and topography, as Miami-Dade was relatively recently urbanized, whereas San Juan has a longer history of urbanization. We propose that these two cities could be used to develop an approach for use in other coastal cities in the subtropics, tropics, and elsewhere.

Specifically, our research objectives were to: (1) compare and contrast the spatial distribution, composition, and occurrence of WIPs in these two coastal cities, and (2) Identify regional commonalities and differences with respect to the socio-ecological predictors of urban WIP occurrence in similar climates, but with differing urban development histories. Landscape and regional scale knowledge about how the spatial distribution, abundance, and occurrence of WIPs in cities throughout the globe are related to site legacy, land use change, and site characteristics could be used to predict their occurrence, improve management and monitoring protocols, and better understand biodiversity dynamics in these novel ecosystems throughout the globe (Larson et al., 2011; Levine et al., 2003; Kendal et al., 2014; Kowarik, 2011; Richardson and Rejmánek, 2011).

2. Methods

2.1. Study areas

The Miami-Dade, Florida metropolitan area (MMA) covers 1273 km^2 and is located at 25° N and 80° W on the US mainland in southeast Florida, immediately adjacent to Everglades National Park (Fig. 1). Miami-Dade has humid subtropical and tropical climate with average maximum and minimum temperature of 28 °C and 20 °C, respectively. The mean annual precipitation is 1470 mm (Winsberg, 2003), with distinct wet and dry seasons. Miami-Dade, established in the late 1800s, is relatively recently urbanized, with most urbanization occurring after 1960. Substantial agriculture is common in the study area, where a variety of fruit and vegetable crops are grown. The MMA also has a wide range of ecological communities, including many wetland communities, though most of this area is classified as south Florida flatwoods, with interspersed hammock communities (USDA SCS, 1989). Soils are generally poorly-drained, shallow, non-hydric, upland soils with sandy marine sediments throughout the profile (USDA SCS, 1989).

The San Juan Metropolitan Area (SJMA) is located on the northeastern coast of the island of Puerto Rico at 18° N, 66° W (Fig. 1), and covers an area of 217 km^2. It has tropical marine climate with average minimum and maximum temperatures of 24 and 27 °C, and 1500–2300 mm of precipitation annually (Lugo et al., 2011), which is well-distributed throughout the year. Founded in 1521, SJMA is the second oldest European-established city in the western hemisphere. Its population peaked in the 1960's but has remained relatively constant since that time. Peri-urban areas encompass rangeland and agricultural areas, supporting a variety of

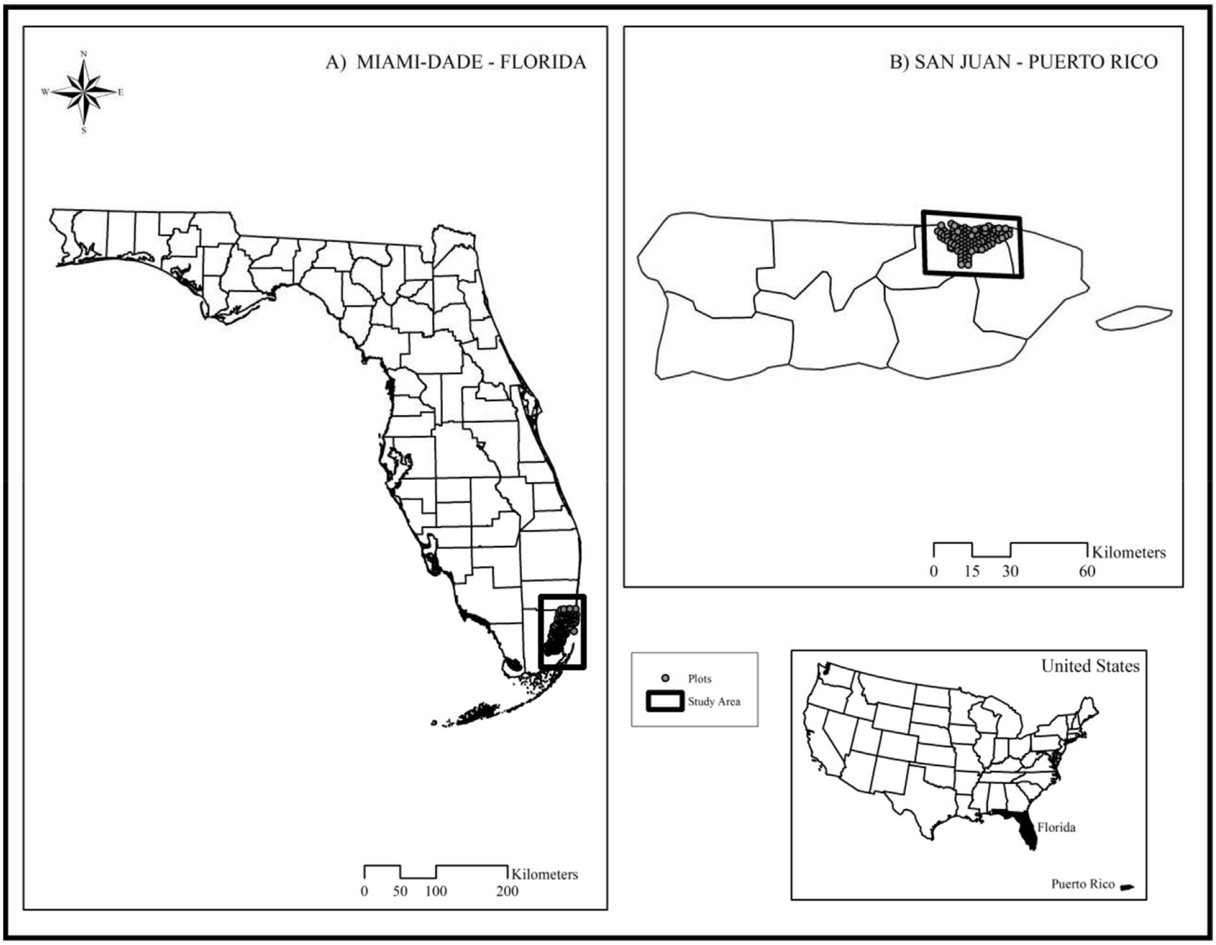


Fig. 1. The Miami-Dade Metropolitan area (MMA) and San Juan, Puerto Rico Metropolitan area (SJMA) study areas. Gray-filled circles represent plot locations. Plots were located randomly in MMA, whereas plot locations followed the systematic grid methodology of the USDA Forest Service's FIA program in SJMA.

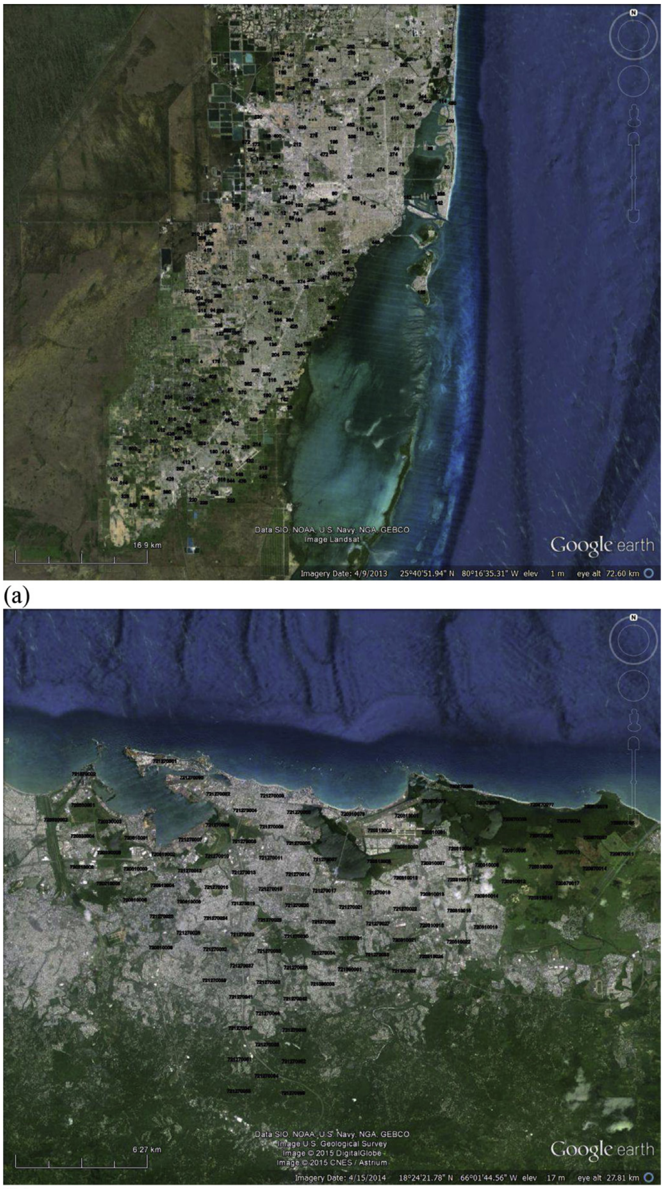
fruit and vegetable crops. The SJMA's three major physiographic areas encompass limestone hills, sloping coastal plain, and extensive igneous lands. Soils are mostly well-drained and deep, though the area surrounding Bahia de San Juan is poorly-drained and soils become shallower with altitude (USDA SCS, 1978). Ecosystems in the San Juan area include moist forests, lowland evergreen hemisclerophyllous shrubland and coconut palm forests, as well as evergreen and semi-deciduous forests and mangroves (Areces-Mallea et al., 1999).

Whereas most of the urbanization in MMA occurred after 1960, San Juan is a much older city, with a longer history of urbanization and change. In 2010, both MMA and SJMA had a population of 2.5 million; however, the density in MMA was 532 persons per km^2, while the density in SJMA was 3192 persons per km^2 (US Census Bureau, http://www.census.gov/newsroom/releases/archives/2010_census/cb11-cn120.html, accessed January 12, 2015). These two cities also differ socio-economically; Miami-Dade County's 2010 median household income was $40,219 whereas that of the metropolitan area of San Juan-Caguas-Guaynabo was $20,897 (US Census Bureau, http://factfinder2.census.gov/faces/tableservices/jsf/pages/productview.xhtml, accessed February 21, 2012). The highest elevation in MMA is 12 m, while San Juan is near Sierra de Luquillo at the El Yunque National Forest, with elevation >1000 m. Conversely, these cities are very similar in terms of climate and population. Overall, both urban areas encompass residential, commercial, and agricultural areas as well as natural areas protected from development, and both have diversity typical of coastal subtropical ecosystems (Lima et al., 2013; Zhao et al., 2010a).

2.2. Data collection

During January through May 2008, 229 0.04 ha circular plots were established via a random geographic point generator within the urbanized portion of Miami-Dade County (Fig. 2a) following USDA Forest Service urban tree and shrub inventory protocols (Brandeis et al., 2014). Plot center was recorded and data collected for each tree and palm with a minimum stem diameter of 2.5 cm at breast height (DBH), measured at 1.4 m above ground level. Tree and palm measurements included: species identification, number of stems, DBH, total height, height to crown base, crown widths and other site and land tenure variables. Crown light exposure (CLE) was measured following methods in Schomaker et al. (2007). Tree, palm, and shrub cover, as well as estimates of surface cover categories (e.g. maintained grass, herbaceous, pervious, impervious, buildings, and water) were measured at the plot level using USDA Forest Service definitions and methods (Brandeis et al., 2014). Species were named based on the USDA PLANTS database (http://plants.usda.gov/). During November 2008–February 2009, plots were re-visited to obtain more detailed information on shrubs. Woody shrubs and palm individuals greater than 30 cm in height and with no measurable DBH were identified to species, and their height and area was recorded.

Of the 229 plots, 73 did not contain trees or shrubs. Plots were located across a variety of land uses including residential,



(a)

(b)

Fig. 2. The Miami-Dade Metropolitan (MMA; a) and the San Juan Metropolitan (SJMA; b) study areas by plot number and location using Google Earth®.

commercial, industrial, transportation, institutional (e.g. schools, parks, recreational areas), and natural areas. Where plots encompassed more than one land use (n = 27), proportions of each land use present were noted, and plot-level variables were recorded for each land use. A small number of MMA plots (n = 4) fell in densely forested areas (i.e. remnant forests); in the interest of efficiency, trees were measured on 0.01 ha quarter subplots (the northeast quarter of the 0.04 ha plot), and data were weighted according to area sampled in subsequent analyses (Zhao et al., 2010a).

During June through October 2010, 92, 0.07 ha circular plots were measured in SJMA (Fig. 2b) using the USDA Forest Service Forest Inventory and Analysis sampling hexagons (Bechtold and Patterson, 2005; Brandeis et al., 2007). The base grid was intensified, decomposing it into smaller hexagons and reducing the sampling grid size from approximately one sampling point per 2400 ha to one per 200 ha. Field methods for 83 of the 92 plots were the same as that of MMA, utilizing 0.07 ha plots (Brandeis et al., 2014); because of different inventory objectives, a subset of standard FIA subplot clusters (0.07 ha total) were installed in 9 plots that met the Caribbean FIA criteria for forested land (see USDA Forest Service, 2011 for details). Plot size differences between SJMA and MMA were specifically accounted for in statistical analyses with appropriate weighting schemes. Small patches of tree-covered land that did not meet FIA minimum forest area requirements were considered urbanized and categorized as vacant land uses. Similar to MMA, 3 plots fell in densely forested areas, and trees were measured on 0.027 ha quarter or 0.033 half-plots (northern half of the 0.07 ha plot). Thirty-two of the 92 sampled plots in the SJMA did not contain trees or shrubs.

To address our second research objective, we used available socio-ecological spatial predictors to statistically analyze their use as predictors of WIP occurrence. National Land Cover Database land covers (www.mrlc.gov/nlcd01_data.php, accessed December 12, 2009) and FIA land use definitions (USDA Forest Service, 2011) were used to classify land use types for each site at the plot scale. Census block scale socioeconomic data including occupancy status, tenure, median annual income, housing age, population and housing density were obtained from the US Census Bureau (factfinder2.census.gov/faces/nav/jsf/pages/index.xhtml, accessed December 12, 2009).

2.3. *Invasive species classification*

Following FIA definitions and protocols we used tree, shrub, and palm growth form categories in our analyses. Specifically, any woody plant or palm with a DBH of at least 2.5 cm was considered a “tree” or “palm” while one with no measurable DBH but at least 30 cm in height was considered a “shrub”. Although this simplified diameter and height based tree-shrub definition limits analyses according to functional traits, it is a definition that is regularly used for the national forest inventory protocols, and thus is important for consistency in applied forest, urban ecosystem, and invasive species management and research (Dobbs et al., 2011; Kowarik, 2011; Richardson and Rejmánek, 2011; Zhao et al., 2010b). Various protocols also exist for categorizing invasiveness, including the use of invasive tree and shrub lists (Richardson and Rejmánek, 2011). But, we defined alien invasive species in MMA as those included in the Florida Exotic Pest Plant Council's (FLEPPC) Category I list (Florida Exotic Pest Plant Council, 2007), as well as those classified as Category II to encompass both established and imminent invasives (Fox et al., 2003). In SJMA, we utilized a local invasive plant list developed by the Puerto Rico Department of Natural Resources, which uses the same criteria as that of the FLEPPC (E. Gonzalez, Pers. Communication, Puerto Rico Departmento de Recursos Naturales y Ambientales, 2009).

2.4. *Data analyses*

The abundance of WIPs was estimated using invasive tree density by calculating the number of trees per hectare as represented by the occurrence of each invasive tree stem in each plot and its basal area (m^2 ha^{-1}). Additionally, to further characterize invasive shrub and tree abundance, we estimated the average percent cover of invasive species from field samples. We calculated the total crown cover by plot assuming that each tree or shrub had a circular canopy and that no crowns overlapped.

Prior to model estimation, we considered several multi-scale, socio-ecological spatial variables as potential predictors of WIP occurrence. At the landscape scale we investigated geographic relationships with UTM easting and northing, while at the census-block scale we considered socioeconomic variables such as median household income, median value for specified owneroccupied housing units, total human population, and number of housing units. At the plot-scale we investigated median year when structure was built, and percent cover of residential land use, buildings, and grass. Each predictor variable was standardized prior to model fitting. The relationship among potential predictors was also explored for each study areas via Pearson's correlation analysis. Because high levels of correlation between covariates makes interpretation of the estimated parameters challenging, only predictors with low correlations ($r < 0.25$) were included as model inputs in subsequent analyses.

Because observed numbers of WIPs were too low for individual species occurrence or abundance models, logistic regression models were fit to invasive tree and shrub presence at the plot level for each study area. We used a backward elimination procedure to select model effects via the SAS procedure PROC LOGISTIC (SAS/STAT® 9.3). This approach determines logistic regression model estimates via maximum likelihood, to identify a logistic model that retains predictors that minimize the Akaike Information Criterion (AIC). Hierarchical structure was maintained so that underlying main effects were retained whenever their interaction was included in the model. As predictor variables were eliminated, we also calculated the small sample, bias-corrected AIC (AICC), via the SAS procedure PROC GLIMMIX. The lowest AICC model was reported for each study site. Additionally, we report models with an AICC within 2 points of the lowest AICC model, as there is also substantial support for these alternative models (Burnham and Anderson, 2002; p. 70). Finally, to facilitate comparisons between SJMA and MMA, we also estimated a "comparative model", estimated with effects included in either site-specific model.

To evaluate model fit, we also computed the concordance index, C, which estimates the area under the Receiver Operating Characteristic (ROC) curve. A value of 0.7–0.8 indicates acceptable discrimination and values closer to 1 are preferred (Hosmer and Lemeshow, 2000). To test for lack of fit, we further calculated the Hosmer–Lemeshow and Pearson χ^2 goodness-of-fit tests.

The presence of spatial autocorrelation, or clustering, was assessed by considering a correlation structure for the logistic model selected from the stepwise selection process, resulting in a Generalized Linear Mixed Model (GLMM). The exponential, spherical, and Matérn covariance functions were evaluated using UTM easting and northing coordinates of the plot centroids to identify spatial location. For each spatial covariance structure, a test of the null hypothesis of no residual autocorrelation was performed for each model.

3. Results

3.1. Distribution, composition, and abundance of invasive trees and shrubs

On average, in plots where trees or shrubs were present, 23% in MMA and 37% in SJMA had WIPs. The MMA had less occurrence of invasive trees in terms of the number of plots with invasive trees (16% versus 24% in SJMA), whereas SJMA had about the same shrub occurrence as MMA (20% versus 21%). Spatial analyses show that invasive tree abundance in MMA, as measured by cover, increased towards coastal areas with some isolated, abundant areas inland (Fig. 2a). In the SJMA, invasive tree abundance and cover was concentrated farther inland and in areas east of the city center (Fig. 2b). We observed no obvious spatial trend in shrub occurrence in MMA, whereas invasive shrub presence in SJMA was patchier.

The MMA had greater invasive WIP diversity than did SJMA in terms of the number of species. Overall, 26 invasive tree and shrub species were recorded in MMA, whereas 11 were recorded in SJMA. In MMA, *M. quinquenervia* had the greatest abundance in terms of average number of stems per hectare of all observed invasive tree

Table 1
Summary statistics for invasive trees in occupied sites in the Miami-Dade, Florida and San Juan, PR study areas.

Species	Occurrence		Basal area per ha	Number of trees per ha	Crown cover %
	# Plots	# Trees	± SE	±SE	±SE
Miami-Dade (229 plots)					
Melaleuca quinquenervia	1	113	67.1	11169.2	301.1
Melia azedarach	1	17	3	420.1	23.1
Eugenia uniflora	4	21	0.6 ± 0.3	129.7 ± 42.3	3 ± 2.8
Ligustrum lucidum	1	4	0.5	98.8	4.5
Bischofia javanica	4	9	6.1 ± 3.4	79.3 ± 24.8	17.1 ± 6.2
Schinus terebinthifolius	8	18	2.6 ± 1.3	77.9 ± 18.6	28.5 ± 23.8
Ptychosperma elegans	9	20	0.8 ± 0.2	56.7 ± 9.1	5.2 ± 3.3
Ricinus communis	1	2	0.2	49.4	0.9
Casuarina equisetifolia	3	4	10.4 ± 9.4	33 ± 7.1	59.2 ± 13.4
Manilkara zapota	4	5	3.1 ± 1.1	30.9 ± 5.5	8.7 ± 2.9
Terminalina catappa	2	2	2.7 ± 2.1	24.7 ± 0	36.1 ± 25.8
Albizia lebbeck	3	3	4.7 ± 2.4	24.7 ± 0	19.7 ± 8.8
Bauhinia variegate	1	1	5.3	24.7	18
Nandina domestica	1	1	0.3	24.7	10.1
Phoenix reclinata	1	1	1.4	24.7	8
Psidium cattleyanum	1	1	0.1	24.7	3
Livistona chinensis	2	2	1.5 ± 0.9	24.7 ± 0	1.6 ± 0.7
Total Miami-Dade	36	224	4.2 ± 1.5	302.2 ± 108.4	22.8 ± 23.5
San Juan (92 plots)					
Spathodea campanulata	9	251	39.4 ± 20.9	1878.2 ± 173.3	125.6 ± 28.3
Senna siamea	2	12	24.4 ± 18.9	1111.1 ± 378	133.5 ± 11.6
Syzygium jambos	3	13	9.8 ± 5.8	802.5 ± 165.1	48.3 ± 2.4
Albizia lebbeck	9	33	9.1 ± 6.2	139.9 ± 53.1	34.1 ± 19.7
Terminalia catappa	3	10	6.8 ± 4	106.2 ± 27.1	37.7 ± 8.7
Casuarina equisetifolia	1	32	4.5	474.1	77
Delonix regia	4	28	2.6 ± 1.5	103.7 ± 10.5	27.6 ± 8
Thespesia populnea	1	6	1.6	88.9	9.6
Psidium guajava	3	5	0.3 ± 0.1	24.7 ± 3.8	4.5 ± 6.4
Total San Juan	22	35	15.8 ± 0	690.4 ± 0	62.1 ± 0

Table 2
Summary statistics for invasive shrubs in occupied plots in the Miami-Dade, Florida and San Juan, PR study areas.

Species	Occurrence: Number of plots	% Shrub cover % ±SE
Miami-Dade (229 plots)		
Washingtonia robusta	1	70
Ptychosperma elegans	2	3.5 ± 2
Imperata cylindrical	1	3.3
Ligustrum lucidum	1	2.5
Livistona chinensis	2	2.4 ± 2.1
Callisia fragrans	1	2.2
Eugenia uniflora	18	2.2 ± 0.5
Phoenix reclinata	7	2.1 ± 0.8
Epipremnum pinnatum	1	2
Schinus terebinthifolius	9	1.2 ± 0.6
Murraya exotica	4	1.2 ± 0.9
Bischofia javanica	3	0.6 ± 0.5
Rhoeo discolor	18	0.5 ± 0.1
Ardisia elliptica	1	0.3
Albizia lebbeck	1	0.3
Terminalia catappa	1	0.2
Schefflera actinophylla	1	0.2
Colocasia esculenta	2	0.1 ± 0.1
Total Miami-Dade	47	3.7 ± 10.1
San Juan (92 plots)		
Urena spp.	1	3.5
Albizia lebbeck	5	3 ± 1.4
Spathodea campanulata	9	1.3 ± 0.7
Terminalia catappa	2	0.8
Syzygium jambos	2	0.6 ± 0.4
Psidium guajava	3	0.4 ± 0.3
Adenanthera pavonina	1	0.2
Total San Juan	18	1.9 ± 2.2

species as well as the greatest average basal area (m^2/ha) across sampled locations where it occurred (Table 1). However, we observed only one plot with *M. quinquenervia*, which was extremely dense. About half of the invasive tree and shrub species observed in MMA were each observed in just one plot over the study area, whereas only about one-quarter of the invasive species in SJMA were observed in just one plot.

In SJMA, *Spathodea campanulata* P. Beauv. had the greatest abundance of all observed invasive tree species (Table 1), and was found in 10% of all sample plot locations. Although *Syzygium jambos* (L.) Alston and *Senna siamea* (Lam.) Irwin & Barneby had high densities, the average density of *S. campanulata* was almost twice that of the next most dense invasive tree species. It also had a large average basal area ($m^2\ ha^{-1}$), three times that of *Albizia lebbeck* (L.) Benth, which was the only other invasive tree with a higher occurrence (10% of all sample plot locations). Though MMA had a greater number of invasive trees, the SJMA had far greater invasive tree density, basal area and crown cover; indicating far greater stem numbers, stem area coverage, and canopy coverage (Table 1).

Nineteen invasive shrub species were observed in MMA, 9 of which could attain tree-size (Table 2). *Washingtonia robusta* H. Wendl had 20 times as much cover as the next most abundant invasive shrub; however, it occurred in just one plot. In SJMA, seven species of invasive shrub were observed, five of which were also found as tree-sized individuals. Most of SJMA's invasive shrub cover occurred in *Urena* spp., *A. lebbeck*, and *S. campanulata*. Overall, MMA had twice the cover of invasive shrubs as SJMA (Table 2).

3.2. Predictive models of invasive woody plant occurrence

Our analysis identified four variables that were potential predictors of WIP occurrence. In MMA, the highest correlation was with building presence ($r = 0.21$), whereas in SJMA, the highest correlations were with UTM northing ($r = -0.47$), a proxy for proximity to coastline, total housing units ($r = 0.34$), and total population ($r = 0.33$). However, some model predictors were highly significantly correlated with other predictors in both study areas. The total human population was highly correlated with total housing units ($r > 0.83$), median income was highly correlated with median house value ($r > 0.76$), and percent residential cover was highly correlated with building presence ($r > 0.58$). In SJMA, UTM easting and northing were highly correlated with housing units and year built, respectively ($r > 0.41$), whereas they were moderately, but still significantly correlated with residential cover in MMA ($r > 0.27$).

Although socioeconomic predictors had lower correlations to WIP occurrence than did geographic-based predictors (i.e. UTMs), the scope of inference of UTM easting and northing limits any regional analyses to our specific urban study sites. Therefore, to facilitate MMA and SJMA comparisons, only socioeconomic and plot-level surface cover predictors were included in subsequent two-factor interaction and logistic model analyses. These included: percent residential cover and percent grass cover as well as census block-level median annual income and median year of housing structures. For each study area, we failed to reject the null hypothesis of spatial independence, indicating that models without spatial autocorrelation were sufficient.

The group of selected predictors in the lowest AICC model differed between study areas. In both MMA and SJMA, the lowest AICC models indicated that the probability of WIP occurrence increased as percentage of residential land use increased; however, the lowest AICC model for MMA also included interactive effects between percent residential land use and both median income and percent grass cover (Table 3). There were two other, less parsimonious models which had AICCs within two points in MMA; adding the interaction of percentage grass cover with median income (AICC +0.4), and also adding median year of housing structures (AICC +1.5). For SJMA, there were also two other models which had substantial support: adding percentage grass cover (AICC +1.2), and further adding the interaction of grass cover and proportion residential land use (AICC +1.8). The lowest AICC MMA logistic model indicated an acceptable level of predictiveness ($C = 0.74$), whereas that of SJMA was inadequate ($C = 0.63$).

In MMA, the probability of WIP occurrence moderately decreased with increasing median annual income and increasing grass cover when residential land use percentage was low, whereas the probability increased with increasing income and increasing grass cover when residential land use percentage was high (Fig. 3a and c). The similarly formulated SJMA "comparative" model (with the same effects as the lowest AICC model for MMA model) had less

Table 3
Logistic regression model estimates of Woody Invasive Plant occurrence prediction for the Miami-Dade, Florida (lowest AICC model) and San Juan, Puerto Rico (comparative model).

Parameter	DF	Miami-Dade			San Juan		
		Estimate	Std error	$Pr > \chi^2$	Estimate	Std error	$Pr > \chi^2$
Intercept	1	−1.07	0.175	<0.0001	−0.741	0.234	0.002
% residential land use cover	1	0.817	0.177	<0.0001	0.505	0.232	0.030
% grass cover	1	0.088	0.185	0.633	−0.234	0.253	0.356
% residential × % grass cover	1	0.412	0.188	0.028	−0.301	0.257	0.242
median household income	1	0.168	0.181	0.351	−0.109	0.237	0.644
% residential × % median income	1	0.363	0.187	0.052	−0.166	0.234	0.479

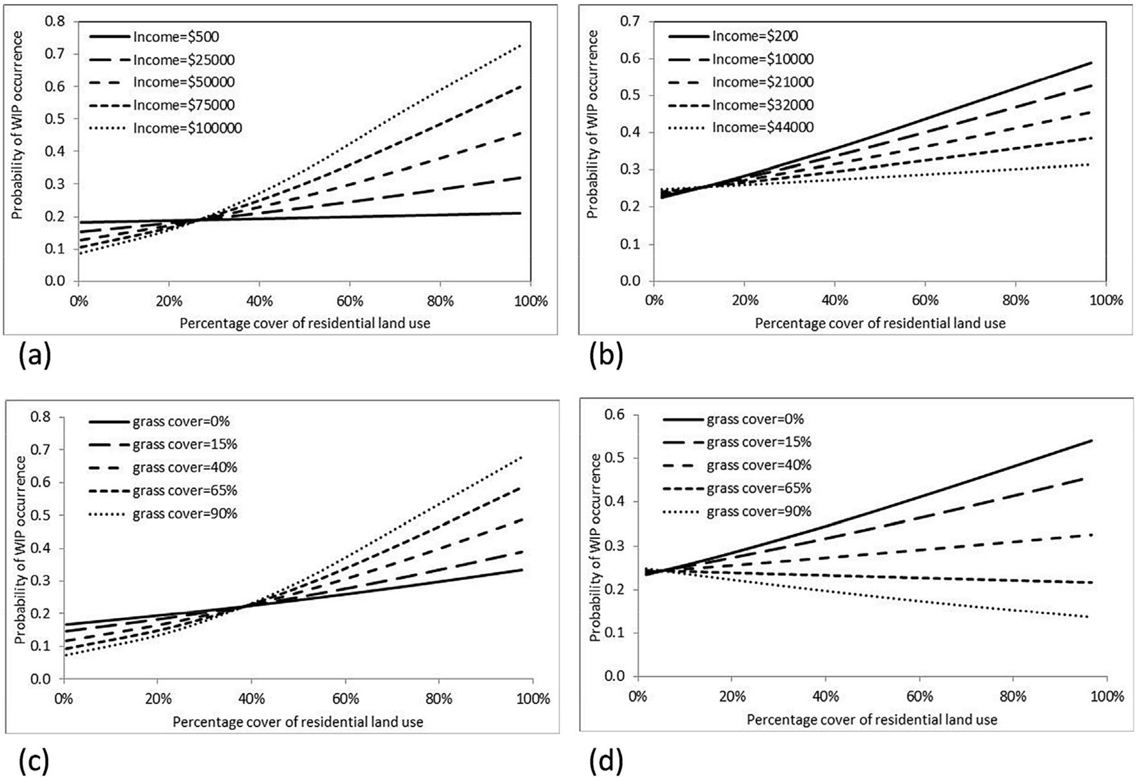


Fig. 3. Marginal mean values of predicted Woody Invasive Plant occurrence by amount of residential cover and five levels of median income for Miami-Dade Metropolitan area (MMA; a) and San Juan Metropolitan area (SJMA; b), and by amount of residential cover for five levels of percent grass cover for MMA (c) and SJMA (d). Note: All other variables in the model are at their mean values.

support (AICC +5.0); however, its predictiveness was much better (C = 0.70). In contrast to MMA, the probability of WIP occurrence in the SJMA "comparative model" stayed constant with increasing median annual income and increasing grass cover when residential land use percentage was low, and the probability decreased with increasing income and increasing grass cover when residential land use percentage was high (Table 3; Fig. 3b and d).

4. Discussion

Our initial correlation analysis identified variables such as building presence, proximity to coastline, total housing units and total population as significant predictors of WIP occurrence. The additional logistic model identified residential land cover as a significant and more consistent predictor of WIPs. Additionally, land use and proxies for maintenance activities (e.g. grass cover and median income) were also related to WIP presence, especially in the MMA study area. Thus, planting selection and the level of urban maintenance activities by different socioeconomic groups are influencing the presence of WIPs in this study area and likely other urban areas in the subtropics and tropics. In particular, the interactive effect of residential land use cover and median income affected the occurrence of WIPs, though their effects differed by city. Whereas WIP occurrence was greater as residential cover and income increased in both study cities, increases were greater for higher income areas in MMA, but lower for higher income areas in SJMA (Fig. 3). Additionally, for SJMA, the probability of occurrence decreased as grass cover and residential cover increased. This indicates that WIPs were less likely to occur in residential areas with increased home maintenance activities. When grass cover was low (i.e. less maintenance), WIP occurrence increased as residential cover increased, but this effect was opposite when grass cover was high, indicating more maintenance. In MMA, the effect was somewhat different; WIP occurrence increased with higher grass and residential cover.

While a more intense sampling grid could have led to more certainty and a more robust logistic regression, this modeling approach can provide a defensible and comparative method for determining and contrasting the most stable predictors for both MMA and SJMA. Studies, including ours, have shown that alien and invasive plants are affected by socio-ecological factors at the landscape and regional scale (Allen et al., 2013; de la Maza et al., 2002). For example, urban sites with invasive plants in Denmark decreased with increasing tax rates but increased with urbanization (Thiele et al., 2009). However, our results differ from those of Gulezian and Nyberg (2010); they found that presence of WIPs was not significantly correlated with any socioeconomic indicator, but there was a significant relationship between invasive plant abundance and measures of impervious surface and vacant land use at the landscape scale. Similarly, observed invasive species richness in Denmark was positively correlated with plant diversity, disturbance, and proximity to roadways (Thiele et al., 2009).

Although the effects of soil properties on WIP occurrence were not specifically tested, Hagan et al. (2012) and Alston and Richardson (2006) documented that soil quality can be tied to land uses and legacy effects and hence, can have an effect on WIPs at the landscape scale. However, although we predicted WIP occurrence across space, explaining their occurrence and subsequent distribution across time, especially for shrubs, is particularly difficult since ownership, budgets, maintenance, and planting preferences will quickly change over time for any given urban site (Reichard and White, 2001). For example, Dobbs et al. (2011) documented that urban forest composition, structure and subsequent functions were influenced by not only land use and legacy effects but by level of vegetation maintenance as well.

In SJMA, predicted invasive occurrence was greater inland; however, tests for spatial autocorrelation using GLMMs show that when predictors for socioeconomic and plot-level covers were accounted for, data describing WIP presence in each study area were spatially independent as indicated by a lack of spatial clustering. Although Gulezian and Nyberg (2010) and Zhao et al. (2010a) did not statistically test for spatial trends, these studies did not report finding any pattern in spatial distribution of WIPs. Correspondingly, Alston and Richardson (2006) found that distance from putative source populations in urban areas influenced alien richness but not stem density in peri-urban areas. Similar to this study, Zhao et al. (2010a) found more invasive trees in residential land uses and natural areas.

Although this study's data could not support species-specific analyses, we did find that the composition of invasive species differed between the two cities. While MMA had more WIP species, SJMA had much greater cover of WIPs. This is likely due to their differing histories of development. In the MMA *S. terebinthifolius* and *M. quinquenervia*, were found in high densities. This is of great concern, since these species can attain densities as high as 31,000 stems per ha, and can cause displacement of native plants, loss of wildlife habitat, and alter fire and water regimes (Mazzotti et al., 1997). These trees were mostly found in western and southern inland areas, where incomes are lower, and urbanization is more recent, and there is less residential cover due to the proximity of natural areas, thus indicating a potential for possible spread (Alston and Richardson, 2006; Zhao et al., 2010a). This observation is contrary to our logistic model prediction of occurrence, and is likely due to the rarity of samples. However, this is of particular interest, as these areas are in close proximity to natural areas and there is the potential for possible spread (Zhao et al., 2010b). *Eugenia uniflora* L, the most common invasive shrub in MMA, also has the potential to detrimentally affect these same natural areas (FLEPPC, 2007).

In SJMA, the invasive species *S. jambos* was found in very high densities. This species is of interest as it is shade tolerant and has become established in dense, monospecific forest stands at higher elevations, particularly in riparian areas and abandoned coffee plantations (Brandeis et al., 2009). This tree tended to occur in patches and was most common in disturbed areas, in vacant land uses. This tree is very common in the SJMA and both *S. jambos* and *S. siamea* occurred exclusively in forest land uses, making them likely threats to natural forest composition (Brandeis et al., 2007), especially as farmlands are abandoned due to migration from outlying areas into San Juan's city center.

In SJMA, by far the most common WIP was *S. campanulata*. The average density of *S. campanulata* in our study was more than thirteen times greater than that of *A. lebbeck*, but its average basal area was approximately four times as great as that of *A. lebbeck*. Thus, *S. campanulata* individuals are on average much smaller in diameter than *A. lebbeck* individuals and their shade intolerance might restrict their ability to regenerate in mature stands (Francis, 2000) and lead to high mortality (Lima et al., 2013). While *A. lebbeck* did not occur in forested areas, it is a species of concern to the SJMA as most were found in vacant and residential (44% in each) land uses. *Albizia* spp. have been reported to dominate in heavily disturbed soils (Chinea, 2002), and this was corroborated in the SJMA.

5. Conclusion

The distribution, composition, and predictors controlling WIP occurrence differed between our two study cities. While climate, soils, and other biotic factors play a role in determining the success of WIPs, legacy effects from urbanization and socio-ecological factors played an important role in our predictive models of WIP occurrence. While our study did have sampling limitations due to access to plots, safety, and difficulty of measurements in highly urbanized areas, our models did identify several strong socio-ecological predictors of WIP occurrence. Our approach based on these two urban areas can also be used by other cities in the subtropics an elsewhere to identify available geographic, socioeconomic, and socio-ecological predictors for use in geospatial distribution models and indices to manage occurrence, patterns, and even risk of urban invasive WIPs. Such information is necessary for their monitoring and proactive management. Identifying socio-ecological indicators influencing invasive plant distribution and abundance can also be used to develop effective landscape scale management and monitoring protocols and to predict occurrence before adjacent natural ecosystems and agricultural areas are negatively affected. Land use and other socioeconomic indicators for example can be used as consistent predictors of WIP occurrence in other cities.

Urbanization in both developed and developing counties will only continue to increase through 2050. Thus, knowledge about how the distribution, occurrence and abundance of woody invasive plants at the landscape and watershed scale are related to site legacy, land use change, and site characteristics could be used to develop management targets, ecological restoration objectives, and to better understand the biodiversity dynamics of these novel ecosystems. Most cities throughout the world, particularly those in the tropics and subtropics, currently lack the scientific understanding to link the spatial distribution of invasive woody plants to such driving factors. Thus, our findings can be used by local and regional decision makers in urban and urbanizing areas to aid in developing management objectives, land use planning policies, designing buffers around invaded sites, and education activities promoting appropriate tree, shrub, and palm selection.

Acknowledgments

This research was funded by a grant from the USDA Tropical and Subtropical Agricultural Research Program (TSTAR-C FY2008). The authors would like to thank Joy Klein and Henry Mayer in Florida, and Robin Morgan, Terry Hoffman, Olga Ramos, Eileen Helmer, Jeffrey Glogiewicz and Edgardo Gonzalez in Puerto Rico for field logistics and data assistance, and Donald Hagan for his extremely helpful comments on an earlier draft of this manuscript.

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