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Distribution and Abundance of Big-Leaf Mahogany (*Swietenia macrophylla*) on the Yucatan Peninsula, Mexico

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Abstract

Big-leaf mahogany (*Swietenia macrophylla* King) is an economically important timber species in the Neotropics. For over three centuries, it has been selectively extracted from tropical forests, threatening its populations. We investigate the actual and potential distribution of big-leaf mahogany and assess its abundance on the Yucatan Peninsula based on the National Forest and Soils Inventory database. Furthermore, we evaluate environmental factors associated with its distribution, abundance, and tree size. The actual and potential distribution models show the presence of mahogany in a wide geographic area covering the southern and eastern portions of the Yucatan Peninsula. Abundance of mahogany in the landscape varies and in general is low. The spatial potential distribution model was best explained by the environmental variables of vegetation cover (medium- and high-stature semievergreen tropical forest) and elevation (upland areas). Results also indicate that mahogany remains relatively abundant and contain larger size classes in localities where the species has been harvested and managed for decades under community forest management. Furthermore, statistical analyses show greater tree density of mahogany mostly associated with low-stature semievergreen tropical forest having deep soils (gleysols and vertisols), while larger tree size (diameter at breast height) was associated with medium-stature semievergreen tropical forests in upland areas with moderately deep or shallow soils (mostly rendzinas or leptosols). Despite deforestation, land-use change and forestry activities on the Yucatan Peninsula, particularly in the past 20 years, the distribution and abundance of mahogany do not appear to be as drastically reduced as described in other neotropical regions.

Keywords

big-leaf mahogany, national forest and soils inventory, MaxEnt, Yucatan Peninsula, community forestry

Introduction

Swietenia macrophylla King (Meliaceae), commonly known as big-leaf mahogany, is a species that grows as an emergent tree in moist and dry tropical forests of the Neotropics in a wide variety of climatic and edaphic conditions (Grogan, Barreto, & Veríssimo, 2002; Mayhew & Newton, 1998; Pennington & Styles, 1981). It is a large tree, reaching a height of up to 40 m and a diameter of up to 2.0 m (Gillies et al., 1999; Lamb, 1966). Globally, the species is distributed in Latin America from Mexico in the north to Brazil and Bolivia in the south, spanning 8,000 km (Figueroa, 1994; Navarro, Wilson, Gilles, & Hernández, 2003). According to Lamb (1966), mahogany reaches its optimal development in dry tropical forest

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habitat with an annual precipitation of between 1,000 and 2,000 mm and an average temperature of 24 °C, but it can also grow in humid and subtropical environments (Gullison, Panfil, Strouse, & Hubbell, 1996; Snook, 1993). In Mexico, its altitudinal range is from sea level to 750 m, although in other countries, it has been reported at higher altitudes, up to 1,400 m (Gullison et al., 1996).

Big-leaf mahogany is a timber species with great economic importance in the Neotropics due to the aesthetic characteristics and working properties of its wood. Throughout its range, natural populations of this species have been selectively logged during the past 300 years (Lamb, 1966; Mejía, Buitrón, Peña, & Grogan, 2008; Snook, 1998; Weaver & Sabido, 1997). Because of its long history of logging and conversion of tropical forests to ranching and farming, mahogany is commercially extinct in some areas of its natural distribution (Navarro et al., 2003; Newton, 2008; Patiño-Valera, 1997; Verwer, Peña-Claros, van der Staak, Ohlson-Kiehn, & Sterck, 2008). The species is now listed as vulnerable to extinction (International Union for Conservation of Nature, 2010; Mayhew & Newton, 1998; Navarro et al., 2003; Newton, 2008), and since 2003, it has been included in Appendix II of CITES (Grogan & Barreto, 2005). Its original range in Mesoamerica has also decreased dramatically for the reasons mentioned earlier. It is estimated that at the end of the 20th century, only 36% of the original area of this species was preserved (Grogan et al., 2010; Navarro et al., 2003). In the case of Mexico, 76% of its tropical forests with mahogany have been lost (Calvo & Rivera, 2000). However, some authors consider that these estimates are somewhat speculative (Kometter et al., 2004).

According to Mexico's National Forest and Soils Inventory 2004–2009 (INFyS), big-leaf mahogany is distributed within six states in the southeast of the country (Comisión Nacional Forestal [CONAFOR], 2009). On the Yucatan Peninsula, mahogany grows within one of the largest continuous masses of tropical forest in the Neotropics after the Amazon (Rodstrom, Olivieri, & Tangley, 1999; Whigham, Lynch, & Dickinson, 1999), adding to their importance for biodiversity conservation (Comisión Nacional de Áreas Naturales Protegidas, 2011; Nations, Primack, & Bray, 1999). In this region of Mexico, mahogany mainly grows in low elevation, flat terrain, and in a variety of soils (Negreros-Castillo et al., 2014; Synnott, 2009). Abundance and tree size of mahogany trees in the forest varies according to soils, topography, and history of disturbances (Brown, Jennings, & Clements, 2003; Grogan et al., 2002; Gullison et al., 1996; Naranjo et al., 2009; Snook, 1996, 1998, 2003; Synnott 2009; Vester & Navarro-Martínez, 2005). On the Yucatan Peninsula, it is frequent to find mahogany forming groups of between two and eight individuals larger than 10 cm diameter at breast height (DBH) per hectare, which has been attributed to the presence of episodic disturbances from hurricanes and fires that have favored its regeneration (Gullison et al., 1996; Snook, 1993, 1996, 1998). In contrast, *S. macrophylla* also persists in areas that lack large-scale disturbances as in Pará, Brazil (Grogan, 2001). Mahogany on the Yucatan Peninsula develops well on moderately deep calcareous soils or soils of alluvial origin (Cabrera Cano, Sousa Sánchez, & Tellez Valdás, 1992; Negreros-Castilo & Mize, 2013), where it coexists with more than 100 species of trees, being the more abundant *Manilkara zapota* (L.) P. Royen (sapodilla), *Brosimum alicastrum* SW. (ramon), and *Bursera simaruba* (L.) Sarg. (red chacah) (Snook, 2003). Some authors (Mayhew & Newton, 1998; Miranda, 1978) argue that big-leaf mahogany prefers deep and well-drained soils (which are rare in the Yucatan peninsula). In addition, it is noted that mahogany survival and growth is associated with secondary vegetation caused by forest disturbance (Gerhardt, 1996; Macario-Mendoza, 2003; Negreros-Castillo et al., 2014; Snook, 1993, 1996, 1998, 2003), although its development in specific forest types on the Yucatan Peninsula has not been described.

Forestry on the Yucatan Peninsula is mainly based on the extraction and transformation of big-leaf mahogany timber, which enjoys a stable and secure market (Ellis et al., 2015). Although other tropical timber species are harvested, mahogany is central to sustainable forest management in the region, and it has been used as a focal species for silviculture and forestry regulation (Ellis et al., 2015; Snook, 2005). However, centuries of mahogany extraction have also led to the degradation of many stands, of declining numbers of individuals with harvestable size, and reduced stocks of residual trees have been reported in the region (Argüelles-Suárez, 1999). Because of both its economic and ecological importance at global and regional levels, mahogany has become the center of an international debate around its management and conservation (Gullison, Rice, & Blundell, 2000; Lugo, 2005; Snook, 1996, 1998, 2003). On the Yucatan Peninsula, many forest communities depend on mahogany harvests to obtain suitable profits from their forest management operations (Ellis, Kainer, Sierra, Negreros-Castillo, & DiGiano, 2014). Community forest management in the region has also been shown to maintain forest cover (Ellis & Porter-Bolland, 2008). The REDD + program in Mexico has been especially interested in community forest management as a *plus* strategy for enhancing carbon stocks as well as reducing emissions from deforestation while providing economic benefits to marginalized rural communities (Ellis, Rodriguez-Ward, Romero-Montero, & Hernandez-Gómez, 2014).

Because of mahogany's role in sustainable forest management and conservation in Mexico, there has been a recent rise in interest on the ecology and distribution of the species. Surprisingly, despite the historical, cultural, and economic significance of big-leaf mahogany on the Yucatan Peninsula, research on its actual and potential distribution and abundance has been scarce. Knowledge on the presence and abundance of mahogany in the region is fundamental to its effective silviculture and conservation in the region. In this study, we model actual and potential distribution of *S. macrophylla* on the Yucatan peninsula based on the most part on INFyS presence data and using MaxEnt software for ecological niche modeling, which considers environmental conditions where the species has been recorded. In addition, we map the abundance (tree density and basal area) of mahogany by spatially interpolating INFyS data using GS + software and evaluate abundance and tree size in selected localities of importance for community forestry in the region. Finally, we statistically evaluate vegetation cover and soil characteristics associated with mahogany abundance (tree density and basal area) and size (DBH). MaxEnt has been widely used to assess the distribution and ecological niche of a wide variety of plant and animal species (Merow, Smith, & Silander, 2013; Saatchi, Buermann, ter Steege, Mori, & Smith, 2008), supporting decision-making for biodiversity conservation (Anderson, Lew, & Townsend, 2003; Brotons, Thuiller, Araujo, & Hirzel, 2004; Guisan & Thuiller, 2005; Guisan & Zimmermann, 2000; Guisan et al., 2007; Naoki, Gómez, López, Meneses, & Vargas, 2006). However, it has been little used to evaluate the distribution of species under forest management, even though the information generated can be useful in developing conservation policy for institutions such as CITES, as is the case of mahogany.

Methods

Study Area

The Yucatan Peninsula is located in southeast Mexico and is conformed of a karst plateau that emerged from the ocean during three different geological periods (Bautista, Palacio-Aponte, Ortiz-Pérez, Batllori-Sampedro, & Castillo-González, 2005; Lugo & Garcia, 1999). It includes the states of Campeche, Quintana Roo, and Yucatán (Figure 1), and from the point of view of some authors, it includes the northern portion of Belize and the Petén region of Guatemala (Carnevalli, Ramírez, & González, 2003; Durán, Trejo, & Ibarra, 1998) occupying a surface area of approximately 181,200 km^2 (Espadas-Manrique, Durán, & Argáez, 2003). Elevation ranges from sea level to 350 m with rolling hills concentrated toward the central and southern portion of the Yucatan Peninsula. The climate is generally warm and humid toward the south and drier in the northern region of the peninsula. Precipitation generally varies between 800 and 1,200 mm with higher

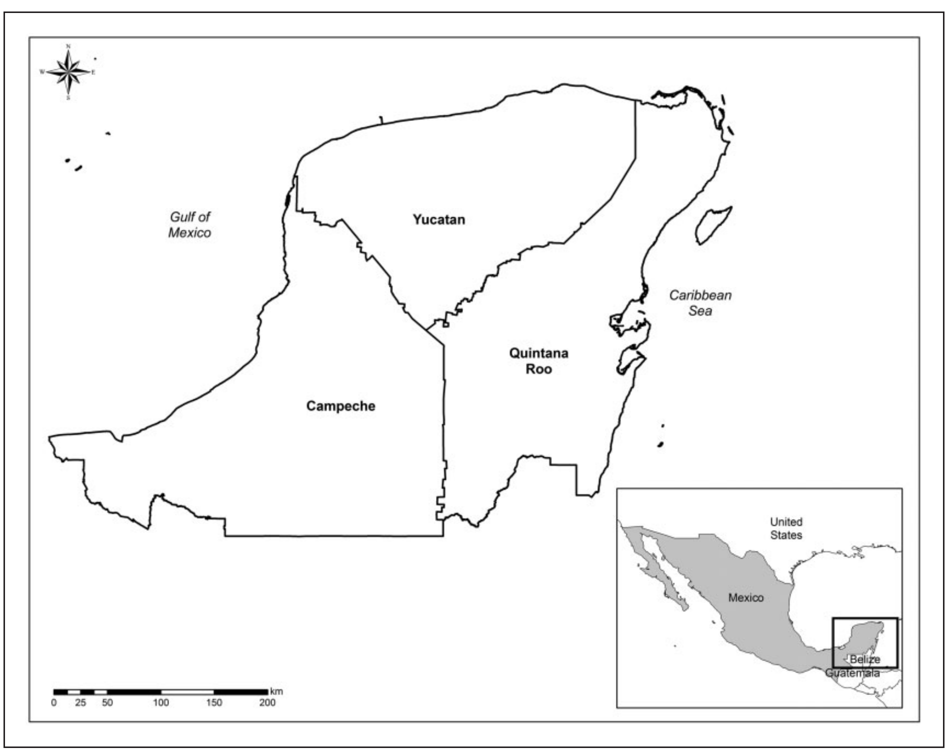

Figure 1. Yucatan Peninsula and study area comprising of the states of Yucatan, Campeche, and Quintana Roo, Mexico.

rainfall toward the southern and eastern portions of the peninsula (Lugo & Garcia, 1999; Orellana-Lanza et al., 1999). Soils are mainly derived from limestone and consist mostly of rendzinas (leptosols and phaeozems according to the World Reference Base for Soil Resources) in upland regions and gleysols and vertisols in lowlands. In upland areas, soils are shallow to moderately deep, rocky, relatively poor in organic matter, and well drained, while in the lowlands, they are moderately deep to deep, often rich in organic matter and with poor drainage (Bautista et al., 2011, Vester & Navarro, 2007). Vegetation types are associated with geomorphology, soils, and climate, and the predominant vegetation type is dry tropical forest (Durán & Olmsted, 1999; Flores, Durán, & Ortiz, 2010; Miranda, 1978). Forest vegetation on the Yucatan Peninsula is subcategorized as low-, medium-, and high-stature semievergreen and semideciduous tropical forest (Miranda & Hernández, 1963). Medium- and high-stature semievergreen and semideciduous forests tend to be located in upland areas, while low-stature semievergreen and semideciduous forests are usually located at lower elevations and in depressions that are often seasonally inundated. The Yucatan Peninsula is subject to frequent disturbances such as hurricanes and fires (Navarro-Martínez, Durán-García, & Méndez-González, 2016; Snook, 1996, 2003; Whigham, Olmsted, Cabrera, & Hartman, 1991). Natural forests in the region have adapted and developed a high resiliency to these impacts, including anthropogenic disturbances, for more than 3,000 years (Snook, 1993, 1996, 1998, 2003; Turner, 1978).

Data Used for Study

To determine actual distribution and model potential distribution and abundance of *S. macrophylla*, we compiled presence data originating from the INFyS (2004–2009) database. The INFyS database has been developed and used to support national policy and programs for sustainable forestry development using quality information, containing up-to-date and accurate information on the size, location, and condition of forest resources in Mexico (CONAFOR, 2009). This inventory contains species level data on height, DBH, basal area, and environmental conditions of vegetation cover and soils. It comprises 248 conglomerates systematically stratified throughout the Yucatan Peninsula, containing 566 records of mahogany trees: 298 in Campeche and 268 in Quintana Roo but none from Yucatan. INFyS conglomerates on the Yucatan Peninsula are composed of four rectangular (40×10 m) sample plots of 400 m^2 each. All four plots are located within a circular area with a radius of 56.42 m; one plot in the center and the rest distributed as an inverted *Y* with 36.42 m between the centers of each plot. We also used the coordinates associated with two herbarium samples from El Colegio de la Frontera Sur and the Centro de Investigación Científica de Yucatán. In total, 568 records of big-leaf mahogany presence were collected and employed to map the actual distribution of mahogany on the Yucatan Peninsula.

Modeling Potential Distribution

We use ecological niche modeling to determine the potential distribution of *S. macrophylla* utilizing MaxEnt software version 3.3.3 (Phillips, Anderson, & Schapire, 2006; Phillips, Didók, & Schapire, 2004). MaxEnt is based on a statistical approximation called maximum entropy, which formulates predictions using incomplete information, in this case, data on the presence of the species, to estimate its potential distribution (Phillips et al., 2006; Phillips & Didik, 2008). The ability to use presence only data overcomes the difficulty of having to obtain absence data, which often is not reliable (Ward, Hastie, Barry, Elith, & Leathwick, 2008). To integrate records of species presence into the model, all coordinates were converted to geographical projection and WGS84 datum. MaxEnt used a random sample of 393 presence records of our total sample.

Climatic variables used in the MaxEnt model were obtained from the Global Climate Data (WorldClim) database available at (http://www.worldclim.org/; Hijmans, Cameron, Parra, Jones, & Jarvis, 2005). These bioclimatic variables have an approximate resolution of 1 km^2 and are shown in Table 1. In addition, land use and land cover data form the National Forestry Commission (Scale 1: 250,000; CONAFOR, 2009) and digital elevation model from INEGI (30×30 m) were integrated into the model. All spatial variables used for the model were processed, and results visualized and mapped using ArcGIS version 9.2. MaxEnt provides an AUC value to validate the model and measure model performance in discriminating between sites where species are present and sites where species are absent (Elith et al., 2006). An AUC greater than 0.5 means the model performed adequately (Hernández-Gómez, 2014).

Mapping Abundance (Tree Density and Basal Area)

We used 560 records of the INFyS data corresponding to 248 conglomerates to determine the abundance (tree density and basal area) of big-leaf mahogany on the Yucatan Peninsula. Mean density of trees greater than 7.5 cm DBH were estimated based on the number of individuals present in the plots of each INFyS conglomerate and extrapolating to the number of individuals per hectare. Abundance of mahogany was also determined by calculating the mean basal area per hectare with the conglomerate basal area data provided by INFyS. Using geostatistical tools and the mean values for tree density

Table 1. WorldClim Bioclimatic and Other Variables Used in Maxent Ecological Niche Model to Derive Potential Distribution of *Swietenia macrophylla*.

Variable	Description	Source
usveg07	Land use and vegetation	INFyS. 2007
alt	Altitude	INEGI. 1998
biol 2	Average monthly average maximum and minimum temperature	Bioclim. 1950–2000
biol 14	Precipitation of the driest month	Bioclim. 1950–2000
biol 13	Precipitation of wettest month	Bioclim. 1950–2000
biol 15	Seasonality of precipitation	Bioclim. 1950–2000
biol 19	Precipitation of the coldest quarter	Bioclim. 1950–2000
biol 3	Index of variability of temperature	Bioclim. 1950–2000
biol 9	Average temperature of the driest month	Bioclim. 1950–2000
biol 17	Precipitation of driest quarter	Bioclim. 1950–2000
edafo	Edaphology	Bioclim. 1950–2000
biol 11	Average temperature of the coldest quarter	Bioclim. 1950–2000
biol 6	Minimum temperature of the coldest month	Bioclim. 1950–2000
biol7	Annual temperature range	Bioclim. 1950–2000
biol 1	Average annual temperature	Bioclim. 1950–2000
biol 18	Precipitation of warmest quarter	Bioclim. 1950–2000
biol 5	Maximum temperature of the warmest month	Bioclim. 1950–2000
biol 16	Precipitation of wettest quarter	Bioclim. 1950–2000
biol 8	Average temperature of the month with the highest precipitation	Bioclim. 1950–2000
biol 12	Annual precipitation	Bioclim. 1950–2000
biol 10	Average temperature of the warmest quarter	Bioclim. 1950–2000
biol 4	Seasonality of temperature	Bioclim. 1950–2000

and basal area calculated from the INFyS spatially referenced conglomerates, we then mapped the distribution of abundance of mahogany on the Yucatán Peninsula by applying kriging and inverse distance weighting with GS + software (Robertson, 2000) used for spatial surface interpolation. In addition, we evaluated tree density and size (DBH) distribution of *S. macrophylla* for selected INFyS conglomerates located within important community forest management areas or localities in the states of Quintana Roo and Campeche.

Statistical Analysis

Based on INFyS (2004–2009) data, we evaluate the relationship between mahogany abundance (tree density and basal area per hectare) and size (mean DBH per conglomerate) with vegetation cover type, percent tree cover and soil characteristics (soil depth and type and humus layer depth and type) recorded for each conglomerate. Due to the resulting Poisson distribution of our response variables of tree density, basal area, and DBH, we use log-linear regression to evaluate explanatory variables explaining greater abundance and size of mahogany on the Yucatan Peninsula. Table 2 describes the response and explanatory variables used for the log-linear regressions employed for the analysis.

Results

Actual and Potential Distribution of S. macrophylla on the Yucatan Peninsula

The actual and potential distributions of mahogany are shown in Figure 2. The actual distribution of mahogany presence conforms well with the potential distribution model, except for areas in the northern part of the Yucatan Peninsula where the species is now locally extinct due to harvesting and land-use change. The potential distribution of *S. macrophylla* obtained from the MaxEnt model predicted the greatest probability of occurrence in the southern and southeastern regions of the Yucatan Peninsula (mainly within the states of Campeche and Quintana Roo), indicating a wide and continuous area of habitats where the species has suitable conditions (Figure 2). Within mahogany actual and potential distribution, the best conditions for its

Table 2. Response and Explanatory Variables Used for Log-Linear Regressions of *Swietenia macrophylla* Abundance (Tree Density and Basal Area) and Tree Size (DBH) in Relation to Vegetation and Soil Characteristics on the Yucatan Peninula (Source: INFyS 2004–2009, $n = 246$).

Variable	Type or categories	Descriptive statistics
Response	Quantitative	*M* (*SD*)
Tree density (# ind/ha)		14 (14.5)
Tree Size (Mean DBH/parcel)		22.8 (12.3)
Basal area (BA/ha)		0.66 (0.78)
Explanatory		
Humus layer depth (cm)		2.4 (1.9)
Soil depth (cm)		43.3 (27.2)
	Categorical	Frequency (%)
Vegetation type	High-stature semiperennial	7 (2.8)
	Medium-stature semiperennial	210 (85.3)
	Low-stature semiperennial	22 (8.9)
	Medium-stature semideciduous	5 (2.0)
	Low-stature semideciduous	2 (0.8)
Percent tree cover	0–10%	2 (0.8)
	11–25%	11 (4.5)
	26–50%	17 (6.9)
	51–75%	60 (24.3)
	76–100%	156 (63.4)
Humus layer type	Fibric	121 (49.2)
	Hemic	106 (43.1)
	Sapric	5 (2.0)
	Other (or not recorded)	14 (5.7)
Soil type	Other (Luvisol and Histosol)	4 (1.6)
	E+Gv+I/3/L (Rendzina-Gleysol)	42 (17.1)
	E+I/2/L (Rendzina-Litosol)	125 (50.8)
	E+Vp+I/3/L (Rendzina-Vertisol)	5 (2.0)
	Gv+Vp/3 (Gleysol-Vertisol)	8 (3.2)
	Gv/3 (Gleysol)	41 (16.7)
	Vp+E+I/3 (Vertisol-Rendzina)	10 (4.1)
	Vp+Gv/3 (Vertisol-Gleysol)	11 (4.5)

development are found in the largest community forestry *ejidos* in Quintana Roo, notably Petcacab and Noh Bec in the center of the state and Tres Garantías and Caobas in the southern part of the state. Also, in Campeche, the best chance for the establishment of mahogany was found in the Calakmul region in the central and southeastern part of the state. The potential distribution model of mahogany generated by MaxEnt performed adequately with an AUC value of 0.88, similar to the model developed by Hernández-Gómez (2014) for the same species which had an AUC value of 0.95. The variable which had the greatest model contribution in defining potential distribution with MaxEnt was vegetation cover (27%; Table 3), specifically high- and medium-stature semievergreen forest, corresponding with results by Hernández-Gómez (2014). Another important explanatory variable was elevation (16.5%), relating to topographical and edaphic conditions in the region. Climatic variables presented lower contributions, and of these variables, precipitation during driest (biol 14) and wettest (biol 13) months and seasonality of rainfall (biol 15) showed the most important contributions to the model with 9.9%, 9.1%, and 7.7%, respectively. Mean temperature of the driest month (biol 19) and the range of annual temperature (biol 17) had high importance values, 13% and 9.7%, respectively, although their contributions to the model were not significant (Table 3).

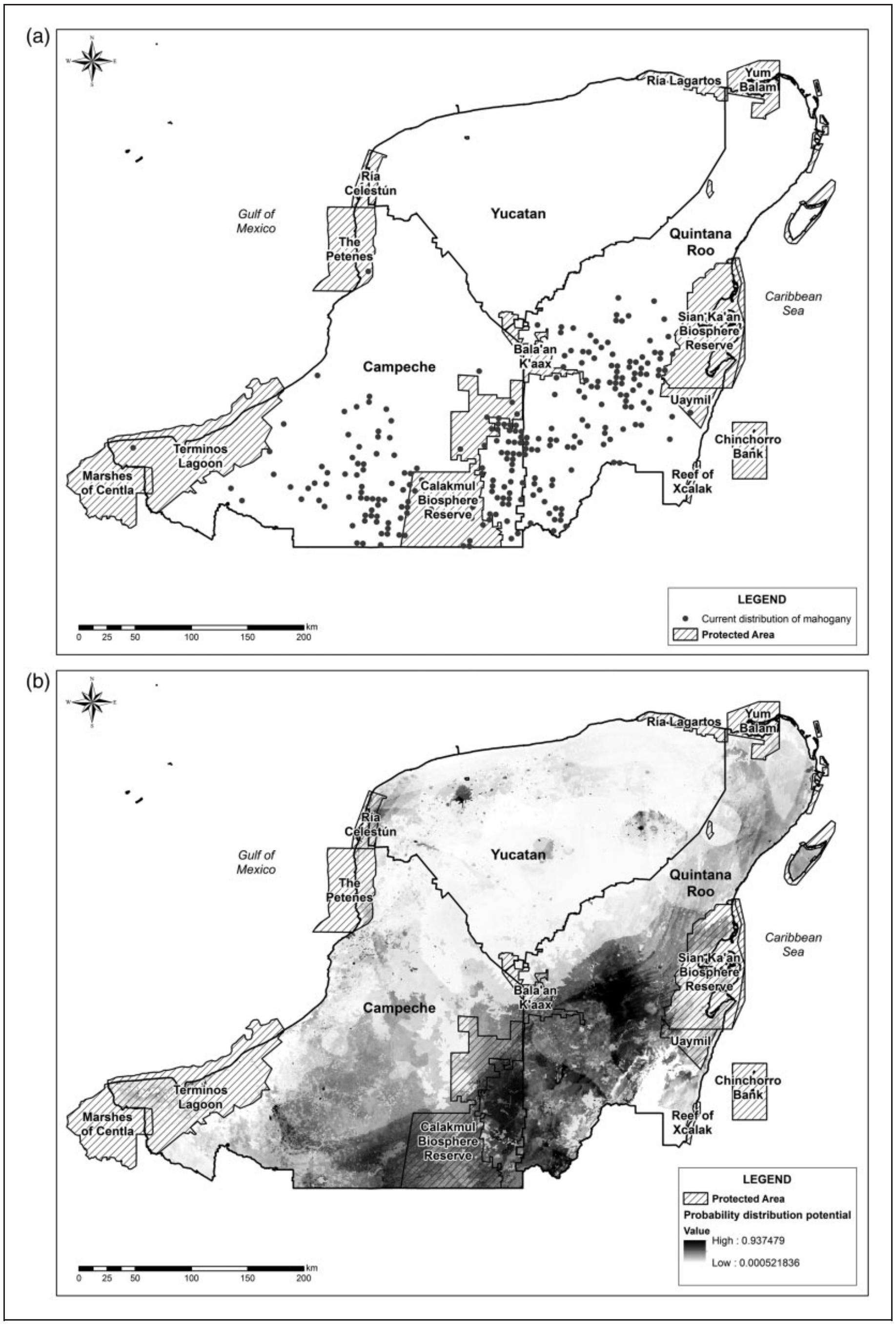

Figure 2. Actual (a) and potential distribution (b) of Swietenia macrophylla in the Yucatan Peninsula modeled with MaxEnt. AUC = 0.884. Circles in (a) corresponds to INFyS conglomerates or plots with big-leaf mahogany.

Abundance of S. macrophylla on the Yucatan Peninsula

Based on INFyS data of conglomerates on the Yucatan Peninsula, abundance of mahogany trees with DBH $\geq$ 7.5 cm varied from 0 to 106 individuals per hectare. The majority of conglomerates with mahogany presence contained a tree density of six individuals per hectare and were mainly located within the state of Campeche (Figure 3(a)). In general, abundance of mahogany represented as tree density per hectare was similar for sampled conglomerates within the state of Campeche (6–106 ind/ha, mean 13.9 ind/ha) compared with Quintana Roo (6–81 ind/ha, mean 14.1 ind/ha). With respect to abundance represented by basal area, results show the same distribution patterns as described for tree density. Basal area of trees greater than 7.5 cm DBH varied from 0.03 to 3.0 m^2/ha (Figure 3(b)). Greater basal areas were found within

Table 3. Contribution (%) and Permutation Importance of Variables Used in the MaxEnt Potential Distribution Model (see Table 1) for *Swietenia macrophylla* on the Yucatan Peninsula.

Variable	Percent contribution	Permutation importance
usveg07	27	18.9
alt	16.5	24.2
biol 2	9.9	9
biol 14	9.9	2.8
biol 13	9.1	4.5
biol 15	7.7	1.2
biol 19	5.3	0.4
biol 3	5	3.5
biol 9	4.9	13
biol 17	2.3	1.2
edafo	0.8	1.9
biol 11	0.7	3
biol 6	0.4	6.4
biol 7	0.3	9.7
biol 1	0.2	0.4
biol 18	0.1	0
biol 5	0	0
biol 16	0	0
biol 8	0	0
biol 12	0	0
biol 10	0	0
biol 4	0	0

conglomerates in Campeche compared with Quintana Roo.

Table 4 shows the abundance of trees by size class (DBH) in selected sites under community forest management in the states of Quintana Roo and Campeche. The abundance of large trees (DBH $\geq$ 30 cm) varied from 0 to 12.5 individuals per hectare, and the highest abundance values were located at the Guadalupe Victoria locality in the state of Quintana Roo, resembling results by Vester and Navarro (2007) from the same area. Nonetheless, most conglomerate sites (79.3%) only had 0 to 1 trees greater than 30 cm DBH per hectare. In Quintana Roo, the abundance of larger trees was greatest in areas that coincide with the most important localities with community forest management such as Petcacab, Noh Bec, Laguna Om, Xhazil, and Tres Garantías (Table 4). In Campeche, only the localities of El Mirador and Nuevo Becal contained mahogany trees with commercial diameter classes, having an average of 6.3 individuals (with DBH $\geq$30 cm) per hectare (Table 4). With respect to smaller size classes (DBH 7.5–30 cm) in these community forestry localities, tree density also varied greatly ranging from 3.1 (Tres Garantías, Quintana Roo) to 28.1 (El Ramonal, Quintana Roo; Table 4). These results are like those reported by Vester and Navarro (2007) in central Quintana Roo, showing higher densities in comparison to other regions of Mexico and the Neotropics. For example, Grogan et al. (2008) found densities between 0.014 and 1.18 trees ($\geq$20 cm DBH) per hectare in the Brazilian Amazon.

Abundance of S. macrophylla in Relation to Vegetation and Soil Characteristics

Based on the INFyS data, we found that 85% of all sampled conglomerates on the Yucatan Peninsula with presence of mahogany corresponded to areas with medium-stature semievergreen forests, including both mature and secondary forest resulting from natural or anthropogenic disturbances. In addition, 9% of conglomerates with mahogany were in low-stature semievergreen forest which are present in topographical depressions and often seasonally flooded (Figure 4(a)). Moreover, INFyS data indicate that *S. macrophylla* presence is more frequent in conglomerates with rendzina soils (leptosols-lithosols, 50.8% and leptosols-gleysols, 17.1%), followed by gleysols (16.6%) and vertisols (4.1%; Figure 4(b)). Rendzina or leptosols in the region, known locally as Tzequel Lu'um or Pus Lu'um by the Mayans, are dark, young, clayey soils that can be shallow (<25 cm) to moderately deep (30–60 cm) with rocky outcrops, calcium carbonate residues, and high mineral content; these soils tend to be well drained and have abundant organic matter (Bautista, Maldonado, & Zinck, 2012).

Log-linear regression results testing the independent variable of tree density produced a statistically significant model ($\chi^2 = 245.3$, $p < .0001$; Table 5). Tree density was associated with both low- and medium-stature semievergreen forest ($p < .0001$ and $p = .007$, respectively), 26% to 50% ($p < .0001$) and over 50% tree cover ($p = .002$), gleysols ($p < .0001$), and vertisols ($p = .003$), greater soil depth ($p < .0001$), and thinner humus layers ($p < .0001$). In general, greater densities were found in forests characteristic of depressions or lowland areas that are often seasonally flooded. However, rendzina-lithosols soils (leptosols; $p = .02$) present in uplands and under medium-stature semievergreen tropical forest were also associated with greater densities of mahogany on the Yucatan Peninsula. Log-linear regression results testing the independent variable of tree size also produced a significantly suitable model ($\chi^2 = 266.2$, $p < .0001$; Table 6), showing greater mean DBH of mahogany in conglomerates having thicker humus layers ($p < .0001$) but shallower soils ($p < .0001$), opposite of the results obtained with tree density. Hemic ($p < .0001$) and sapric ($p = .002$)

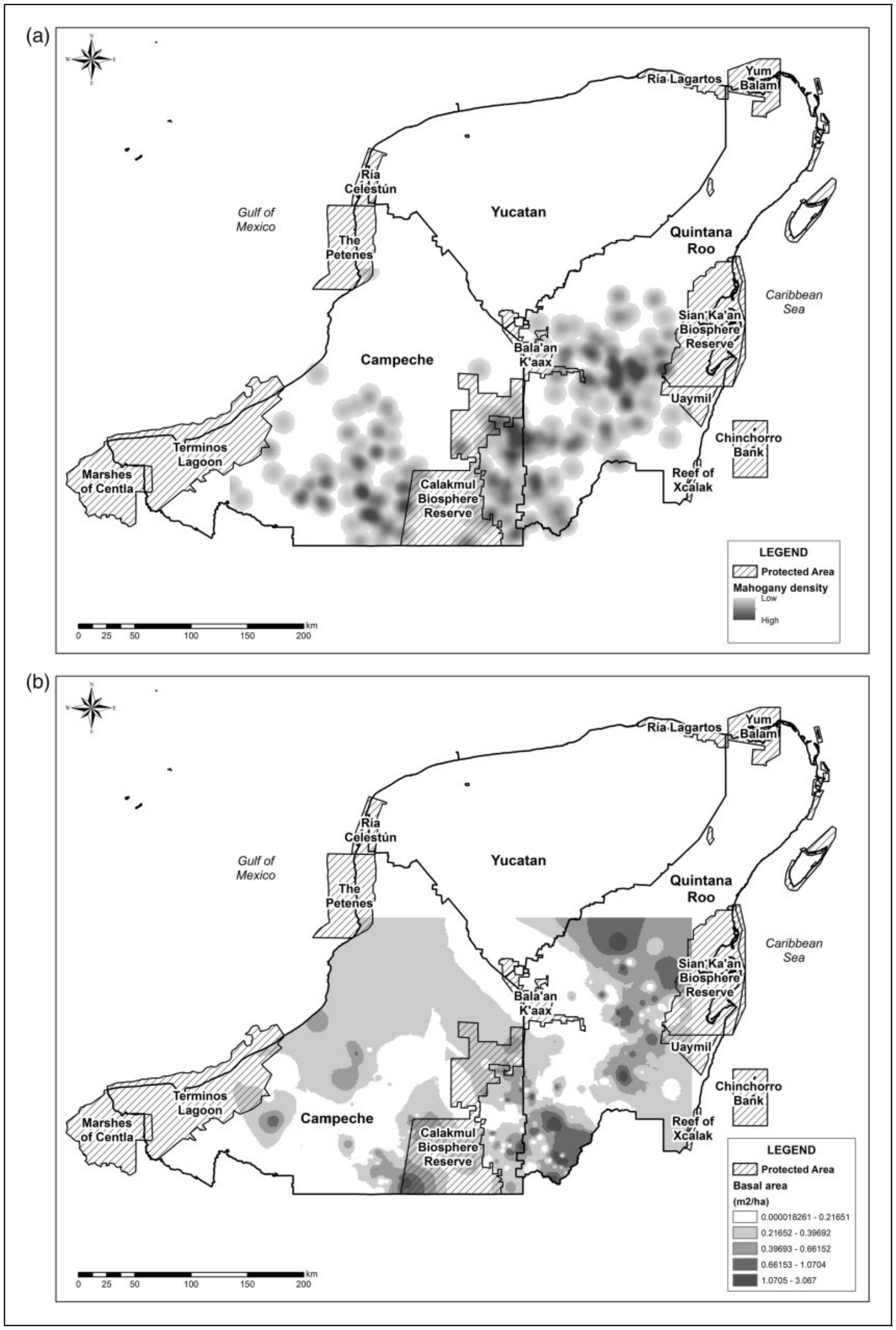

Figure 3. Map of tree density (a) and basal area per hectare (b) of *Swietenia macrophylla* (DBH $\geq$ 7.5 cm) on the Yucatan Peninsula.

organic matter in the humus layer and 26% to 50% tree cover ($p < .0001$) were also related with greater tree size, and only redzina-lithosols (leptosols) soils were significantly related to greater tree size ($p = .02$). The log-linear regression result testing the independent variable of basal area did not yield a significantly suitable model ($\chi^2 = 21.9$, $p = .35$).

Discussion

Distribution of S. macrophylla

The actual and potential distribution models of mahogany on the Yucatan Peninsula conformed very well to each other, showing similar distribution patterns. It is

Table 4. Tree Density and Basal Area Per Hectare of *Swietenia macrophylla* for Selected Forest Management Sites on the Yucatan Peninsula (States of Campeche and Quintana Roo).

Campeche

DBH class	El Bajo	El Cedral	El Mirador	Aguada Grande	El Tablón	Buena Vista	Nuevo Becal
10–20	68.8	34.4	18.8	15.6	21.9	31.3	12.5
20–30	0	9.4	12.5	15.6	9.4	0	12.5
30–40	6.3	0	6.3	0	3.1	0	0
40–50	0	0	0	3.1	0	0	0
>50	0	0	6.3	0	0	0	6.3
Total	75.0	43.8	43.8	34.4	34.4	31.3	31.3

Quintana Roo

DBH class	Gpe. Victoria	Ramonal	Petcacab	Noh-Bec	Xhazil Sur	Laguna Om	Tres Garantías
10–20	18.8	56.3	7.8	6.3	6.3	4.7	6.3
20–30	31.3	0	6.8	2.1	2.1	3.1	0.0
30–40	12.5	0	2.6	2.1	1.0	3.1	2.1
40–50	0	0	2.6	8.3	3.1	0.8	0.0
>50	0	0	2.1	2.1	0	0.8	2.1
Total	62.5	56.3	21.9	20.8	12.5	12.5	10.4

important to note that the potential distribution of mahogany in the region coincides with the Mesoamerican Biological Corridor, a strategic region for biodiversity conservation. According to modeling results, mahogany on the Yucatan Peninsula reaches its northern limits of natural distribution in central Quintana Roo. Although both models show there are a few areas where the species can potentially grow in northern Quintana Roo and Yucatan, most populations in these areas are considered locally *extinct* (Argüelles-Suárez, 1999; Patiño-Valera, 1997) due to deforestation for agricultural, livestock, and tourism development (Ellis et al. 2015). The distribution models of mahogany on the Yucatan Peninsula agree with those developed by Argüelles-Suárez (1999) who also reports a small protected population in the Ría Celestún Reserve located in northwest Yucatan Peninsula. However, the potential distribution result obtained from this study was more restricted than that obtained by Argüelles-Suárez (1999). A recent study suggests that by 2030, there will be a loss of 60% of the current habitat of mahogany in the Yucatan Peninsula, particularly in the state of Quintana Roo (Garza-López et al., 2016). However, our study shows that mahogany is distributed within large community forestry *ejidos* which are more prone to conserve this valuable timber resource and forest habitat (Ellis & Porter, 2008).

Abundance of S. macrophylla

Abundance models show that in general, mahogany populations were larger in Campeche, compared with Quintana Roo, showing higher total tree densities and basal areas within sampled conglomerates. Possible reasons may be that in Campeche, the harvesting of timber has not been as important an economic activity as in the state of Quintana Roo (Ponce, 1991). In the state of Campeche, the most abundant and conserved populations are in the Calakmul and La Montaña regions in the southeast, perhaps because of the protection status of around 800,000 ha of tropical forest and conservation measures in and around the Calakmul Biosphere Reserve established in 1989 (Diario Oficial de la Federación, 1989). Another reason may be the topography and higher elevations in the Calakmul region which has a wetter climate than the rest of the Peninsula (Garza-López et al., 2016).

Greater densities and abundance of mahogany were found at major localities where community forest management has been historically practiced in the states of Quintana Roo and Campeche. Moreover, our results show that mahogany populations in Quintana Roo have not been drastically reduced within major community forest management regions that had greater abundance (tree density and basal area) of larger mahogany trees (with DBH $\geq$ 30 cm) compared with sites in Campeche. These specific regions are contained within a conservation priority area denominated as Forest Management Zones of Quintana Roo (Arriaga, 2000) where forest cover has been maintained (Bray, Ellis, Armijo-Canto, & Beck, 2004; Chiappy & Gama, 2004; Ellis & Porter, 2008), and the harvesting and commercialization of mahogany is an important economic activity (Bray et al., 2003; Ellis, Kainer, et al., 2014; Ellis et al., 2015).

This study demonstrates that despite deforestation, land-use change and forestry activities in the Yucatan Peninsula, particularly in the past 20 years, the distribution and abundance of mahogany do not appear to be as drastically reduced as described in other neotropical regions. Kometter et al. (2004) found that the original distribution of mahogany in Peru and Bolivia decreased by 4% and 8%, respectively, resulting in a reduction of 50% and 90% of commercial sized trees, respectively. In addition, Grogan et al. (2010) estimate that of the original distribution of mahogany (278 million ha) in a region between Venezuela and Bolivia, 58 million ha were lost by 2001.

Biophysical Variables Related to S. macrophylla Distribution and Abundance

Vegetation cover and elevation were important variables explaining 27% and 16.5%, respectively, of the potential

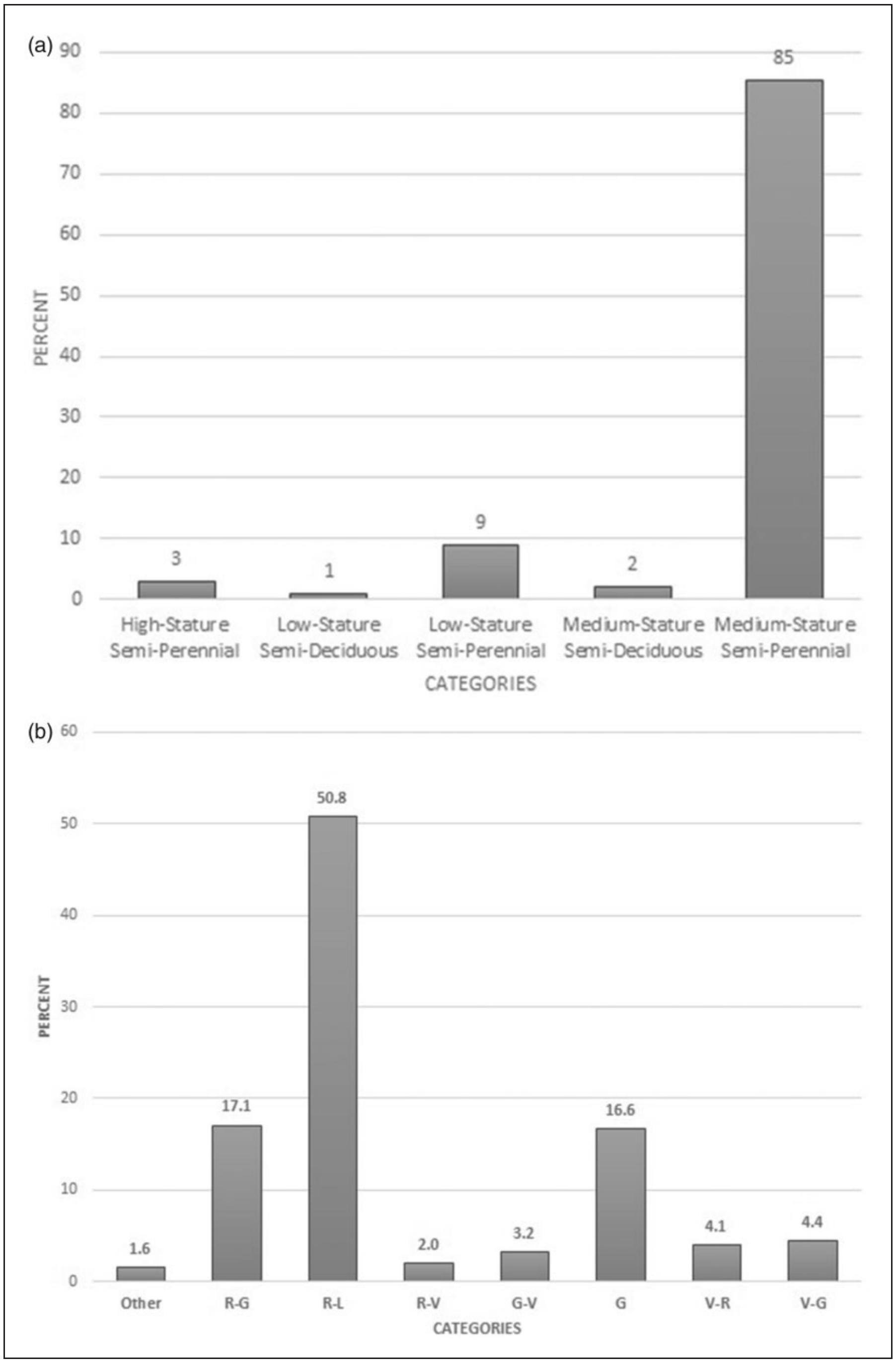

Figure 4. Frequency (%) of INFyS (2004–2009) conglomerates (four sample plots of 400 m^2 each) with presence of *Swietenia macrophylla* ($n = 248$) in relation to forest vegetation (a) and soil (b) types (Other = Luvisol and Histosol, R-G = Rendzina-Gleysol, R-L = Rendzina-Litosol, R-V = Rendzina-Vertisol, G-V = Gleysol-Vertisol, G = Gleysol, V-R = Vetisol-Rendzina, V-G = Vertisol-Gleysol) on the Yucatan Peninsula.

distribution model. Evidently, the vegetation cover of both mature and secondary low- and medium-stature semievergreen tropical forest in the region is important to the presence and distribution of mahogany on the Yucatan peninsula, as also reported by other authors (Cabrera Cano et al., 1992; Hernández-Gómez, 2014; Lamb, 1966; Macario-Mendoza, 2003; Mayhew & Newton, 1998; Vester & Navarro-Martínez, 2005). This result is far from trivial considering deforestation processes for agricultural, livestock, and urban development continue to threaten the region (Ellis, Romero-Montero, & Hernández-Gómez, 2017). Moreover, it indicates the

Table 5. Results of Log-Linear Regressions for Association Between Tree Density (# ind/ha) of *Swietenia macrophylla* and Vegetation and Soil Characteristics on the Yucatan Peninsula.

Model variable	Value	*SE*	Wald Chi-Square	$p > \chi^2$
Intercept	0.794	0.355	4.996	.025
Humus layer depth	−0.051	0.011	20.601	<.0001
Soil depth	0.004	0.001	23.002	<.0001
High-stature subperennial forest	0.000	0.000		
Low-stature subdeciduous forest	0.223	0.375	0.353	.552
Low-stature subperennial forest	0.509	0.138	13.488	.000
Medium-stature subdeciduous forest	0.517	0.191	7.371	.007
Medium-stature subperennial forest	0.505	0.132	14.569	.000
0—10% tree cover	0.000	0.000		
11–25% tree cover	0.707	0.299	5.582	.018
26–50% tree cover	1.204	0.293	16.876	<.0001
51–75% tree cover	0.914	0.290	9.937	.002
76–100% tree cover	0.952	0.289	10.809	.001
Fibric humus layer	0.000	0.000		
Hemic humus layer	0.069	0.039	3.104	.078
Other humus layer	−0.199	0.090	4.883	.027
Sapric humus layer	−0.787	0.169	21.709	<.0001
Other soils (Luvisol and Histosol)	0.000	0.000		
E+Gv+I/3/L (Rendzina-Gleysol)	0.381	0.162	5.532	.019
E+I/2/L (Rendzina-Lithosol or Leptosol)	0.223	0.158	1.976	.160
E+Vp+I/3/L (Rendzina-Vertisol)	−0.191	0.256	0.556	.456
Gv+Vp/3 (Gleysol-Vertisol)	0.612	0.181	11.455	.001
Gv/3 (Gleysol)	0.563	0.160	12.300	.000
Vp+E+I/3 (Vertisol-Rendzina)	0.364	0.180	4.117	.042
Vp+Gv/3 (Vertisol-Gleysol)	0.513	0.176	8.531	.003

Model: −2 Log Likelihood = 269.06, $df = 20$, R^2 (Nagelkerke) = 0.7.
$p < .0001$.

need to conserve and restore these specific forest types for mahogany conservation and management.

Medium-stature semievergreen tropical forest in the landscape, where mahogany had larger size classes, typically coincides with upland areas and leptosol soils with good drainage conditions, compared with lower stature and denser semievergreen forest located in lowland areas on gleysol soils with poor drainage, where greater densities can be found (Ellis & Porter-Bolland, 2008; Vester & Navarro, 2007). As mentioned, our potential distribution result shows elevation as a strong explanatory variable, indicating greater mahogany presence in upland areas inland from the lower coastal areas. Juárez (1988) and Negreros-Castillo and Mize (2013) report that mahogany prefers to grow inland and in flat areas with dark and deep soils characterized locally as *box luum* (leptosol; Bautista et al., 2005), as opposed to hilly and undulating areas where soil conditions differ. Our results also confirm the preference of rendzina (leptosol-lithosol and leptosol-gleysol) soil types, sharing the same characteristics of *box luum* soils described earlier. However, we also find an important presence of mahogany in moderately deep leptosol soils present in hilly undulating terrain characteristic of central and southern parts of the peninsula.

Implications for Conservation

Mahogany on the Yucatan Peninsula is a tree species of economic importance in addition to being of high conservation value. Results obtained from this study demonstrate that the conservation of semievergreen and semideciduous forest habitat in the region is necessary for populations of the species to remain. We find that greater tree density and abundance of the species both coincide with protected areas (Calakmul Biosphere Reserve) and community forestry ejidos in Quintana Roo and Campeche, indicating the need to integrate both as a strategy to conserve mahogany. Greater densities of larger size classes of mahogany in areas with community forest management add to the importance of

Table 6. Results of Log-Linear Regression for Association Between Tree Size (DBH) of *Swietenia macrophylla* and Vegetation and Soil Characteristics on the Yucatan Peninsula.

Model variable	Value	*SE*	Wald Chi-Square	$p > \chi^2$
Intercept	2.504	0.235	113.191	<.0001
Humus layer depth	0.055	0.008	52.811	<.0001
Soil depth	−0.002	0.001	14.305	.000
High-stature subperennial forest	0.000	0.000		
Low-stature subdeciduous forest	−0.324	0.250	1.677	.195
Low-stature subperennial forest	−0.138	0.104	1.788	.181
Medium-stature subdeciduous forest	−0.013	0.134	0.010	.921
Medium-stature subperennial forest	0.080	0.093	0.734	.391
0–10% tree cover	0.000	0.000		
11–25% tree cover	0.435	0.183	5.631	.018
26–50% tree cover	0.246	0.181	1.844	.174
51–75% tree cover	0.240	0.176	1.870	.171
76–100% tree cover	0.275	0.175	2.461	.117
Fibric humus layer	0.000	0.000		
Hemic humus layer	0.090	0.031	8.419	.004
Other humus layer	0.379	0.062	37.334	<.0001
Sapric humus layer	0.284	0.092	9.596	.002
Other soils (Luvisol and Histosol)	0.000	0.000		
E+Gv+I/3/L (Rendzina-Gleysol)	0.073	0.130	0.315	.575
E+I/2/L (Rendzina-Lithosol or Leptosol)	0.305	0.127	5.817	.016
E+Vp+I/3/L (Rendzina-Vertisol)	0.194	0.175	1.234	.267
Gv+Vp/3 (Gleysol-Vertisol)	0.213	0.150	2.037	.154
Gv/3 (Gleysol)	0.079	0.130	0.370	.543
Vp+E+I/3 (Vertisol-Rendzina)	−0.176	0.149	1.388	.239
Vp+Gv/3 (Vertisol-Gleysol)	0.147	0.142	1.076	.300

Model: −2 log likelihood = 251.08, $df = 20$, R^2 (Nagelkerke) = 0.6.
$p < .0001$.

forestry ejidos for the conservation of the species. However, conservation of the species in community forest areas on the Yucatan Peninsula will also depend on ensuring and promoting sustainable forest management. Currently, United Nations Development Programme and REDD+(Reduction of Emissions from Deforestation and Degradation) projects on the Yucatan Peninsula are adopting community forest management as a conservation and rural development strategy, focusing on reducing community forestry's impacts on biodiversity and carbon emissions through improved forest management, reduced impact logging, promoting sustainable forestry certification such as that from the Forest Stewardship Council, and strengthening ejido governance and timber markets.

Conservation of tropical forests on the Yucatan peninsula should be a priority conservation strategy to maintain mahogany populations and sustainable community forest management in the region. Moreover, these forests provide valuable ecosystem services such as carbon sequestration and storage to mitigate climate change. To arrive at more complete knowledge and robust recommendations for adequate management practices of the species and associated habitats, mapping and monitoring the distribution of mahogany in the Yucatan peninsula should be continued with further research, including demographic analysis of mahogany populations.

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