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Geographic distribution and spatial attributes of African tulip tree forests in north-central Puerto Rico: Implications for social-ecological resilience[1,2]

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ABSTRACT

Agricultural abandonment resulted in the expansion of forests dominated by invasive tree species that were introduced throughout Puerto Rico. These novel forests are increasingly common worldwide but little is known about the drivers and consequences of their expansion. This study describes the geographic distribution and spatial attributes of novel forests dominated by the African tulip tree, *Spathodea campanuata* Beauv., in north-central Puerto Rico. I used aerial photography to map *Spathodea* forests, determined their distribution by geological substrate, soil type and previous history, and estimated the area and perimeter to area ratio (P/A) of each patch. The 443 mapped *Spathodea* forests covered 0.7% of the region, ranged from 0.03 to 9.1 ha (mean=0.5, S.E.=0.03) in area, and from 0.03 to 0.3 m/m^2 (mean=0.09, S.E.=0.0002) in P/A. *Spathodea* forests were more frequent on lands previously used for sugarcane, which are typically on fertile Mollisols on alluvial substrate. Half the *Spathodea* forests were over 30 years old and those on former sun coffee farms on volcanic extrusive substrate had larger area and

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lower P/A. Novel *Spathodea* forests rehabilitate agricultural lands, increase spatial connectivity and create favorable conditions for agroforestry and species restoration interventions, representing an asset for social-ecological resilience to climate change and socio-economic development.

Key words: ecosystem services, introduced invasive species, land cover change, novel secondary forests, *Spathodea campanulata*, sugarcane and sun coffee, tropical islands

RESUMEN

Distribución geográfica y atributos espaciales de bosques de tulipán africano en el norte-central de Puerto Rico: Implicaciones para la resiliencia social-ecológica

El abandono agrícola ha favorecido el crecimiento de especies de árboles introducidos e invasores en Puerto Rico. Estos bosques noveles son frecuentes en paisajes agrícolas a través del mundo, pero poco se conoce acerca de los determinantes y consecuencias de su expansión. Este estudio describe la distribución geográfica y los atributos espaciales de bosques noveles dominados por el tulipán africano, *Spathodea campanuata* Beauv., en la región norte-central de Puerto Rico. Utilicé fotos aéreas del 1998 para cartografiar bosques de *Spathodea*, los cuales aparecen rojos en flor, y determiné su distribución a través de substratos geológicos, tipos de suelo e historias de uso, y el área y razón de perímetro a área (P/A) de cada bosque. Los 443 bosques de *Spathodea* cartografiados representaron un 0.7% de la región y fluctuaron de 0.03 a 9.1 ha (media=0.5, S.E.=0.03) en área y de 0.03 a 0.3 m/m^2 (media=0.09, S.E.=0.0002) en P/A. Los bosques de *Spathodea* resultaron más comunes en terrenos previamente usados para caña de azúcar, los cuales típicamente se encuentran en substratos aluviales fértiles. La mitad de los bosques de *Spathodea* poseen una edad mayor a los 30 años y aquellos en fincas abandonadas de café al sol en substrato volcánico extrusivo mostraron mayor área y menor P/A. Estos resultados muestran que los bosques noveles de *Spathodea* rehabilitan terrenos agrícolas abandonados, aumentan la conectividad espacial del paisaje y proveen lugares idóneos para producción agroforestal o restauración de especies, representando un activo para la resiliencia social-ecológica al cambio climático y para el desarrollo socio-económico puertorriqueño.

Palabras clave: bosques secundarios noveles, café de sol, cambio de cobertura de terreno, caña de azúcar, especies introducidas invasivas, islas tropicales, servicios ecológicos, *Spathodea campanulata*

INTRODUCTION

Anthropogenic modification of abiotic conditions coupled with species transport has resulted in ecosystems comprising novel combinations of species, also known as novel ecosystems, that thrive naturally and are adapted to the new conditions created by humans (Hobbs et al., 2006 and 2009; Lugo, 2009). The ecological conditions resulting from the expansion of novel ecosystems in post-agricultural landscapes will increasingly need to be considered for biodiversity conservation and ecosystem service management efforts aimed at improving social-ecological resilience to climate change and socio-economic pressures, especially in tropical islands (Ewell et al., 2013; Lugo, 2013; Hobbs et al., 2014). On the Caribbean island of Puerto Rico, agricultural abandonment coupled with species introductions have resulted in a landscape that is increasingly covered by novel forest ecosystems (Lugo and Helmer, 2004; Lugo 2009; Martinuzzi et al. 2013). Many, if not most, of these novel forests are dominated by the African tulip tree, *Spathodea campanulata* Beauv., which is the most abundant tree species in the forests of Puerto Rico since at least 1990 (Franco et al., 1997; Brandeis et al., 2007; Marcano et al., 2015). This introduced tree species readily invades deforested and abandoned lands in the moist regions of Puerto Rico, which are typically covered with introduced and invasive forage grasses (e.g., *Megathyrsus maximus* and *Sorghum halepense*) that hinder the establishment of native early-successional secondary forest tree species such as *Cecropia scheberiana* (Silander, 1979; Aide et al., 2000; Lugo, 2004). The novel forests dominated by *Spathodea* harbor many other tree species, floral and faunal assemblages that are mostly native, have similar structure compared to native forests and have an equal higher capacity for biomass, carbon and nutrient storage compared to other forests in Puerto Rico (Abelleira et al., 2010; Lugo et al., 2012a; Pérez et al., 2012). In addition, the high nutrient content of *Spathodea* leaves appears to combine with high litterfall and decomposition rates to speed up nutrient cycling to the forest floor and soils, potentially enhancing the establishment and growth of trees growing in the forest understory (Abelleira, 2011; Lugo et al., 2011; Lugo and Abelleira 2018). Their widespread distribution is evident when, from November to March, patches of novel *Spathodea* forests cover many landscapes of the moist regions of Puerto Rico with an intensely red-colored bloom superimposed on a green canopy matrix (Abelleira, 2010 and 2011).

The geographic distribution of novel forests has disproportionally expanded on tropical islands, such as Hawaii and Puerto Rico, and their distribution is likely to increase worldwide (Lugo, 2009; Ewel et al., 2013; Radeloff et al., 2015). Since they are a relatively new phenomenon, little is known about what factors make lands more prone to the successional processes that result in the establishment and expansion of novel forests. Sites with a given combination of geological substrate, soil type or previous land use history may have favored the growth of *Spathodea* forests in moist regions of Puerto Rico, and this can help predict where these forests will occur and expand to in the future. Knowing whether there is a set of conditions that makes abandoned farmlands more prone to transition into novel *Spathodea* forests, and whether a set of these conditions results in forests with a desired set of spatial attributes, helps define their potential to support interventions aimed at agroforestry production and ecological restoration. For example, *Spathodea* forest patches of relatively large area and low perimeter to area (P/A) ratio may support higher animal and plant species diversity and may be better suited for enrichment plantings of shade crops, such as cacao and coffee, and of native late-successional and shade-adapted threatened tree species whose geographic range has been reduced by deforestation (Wadsworth, 1950; Yamaura et al., 2008). This type of knowledge will help guide public policy and land management in Puerto Rico as the island strives to re-position agricultural production as top priority to support socio-economic development and improve social-ecological resilience to a higher frequency of extreme events, such as droughts and hurricanes, due to anthropogenic climate change.

This study describes the geographic distribution and spatial attributes of novel *Spathodea* forests across the geological substrates, soil types and land use histories found in moist north-central Puerto Rico. *Spathodea* is a light-demanding colonizer of abandoned agricultural fields and grows best on mesic fertile soils (Francis, 2000; Chinea and Helmer, 2003; Lugo, 2004). I expected a higher proportion of *Spathodea* forests to be found on alluvial floodplains and fertile Mollisols, and on lands whose previous histories consisted of intensive agriculture, such as sugarcane and grazing, which largely exclude remnant tree cover. Previous studies have shown that differences in landform and topographic heterogeneity related to various geological substrate types have an effect on the spatial attributes of secondary forests in Puerto Rico (Lugo, 2002; Helmer, 2004). Therefore, *Spathodea* forest patch area and P/A is unlikely to be homogeneous across the geological substrates found in the study region. I expected that *Spathodea* forests on alluvial substrate, which appear to be mostly riparian, would have higher P/A, and those on karst to be of smaller area due to the fine-grain spatial heterogeneity of karst substrate, which is composed of various landforms that include mesic depressions and xeric ridges where *Spathodea*'s growth is limited (Monroe, 1976; Brandeis, 2006). I also expected older *Spathodea* forests would be larger in area due to a longer time for growth into surrounding abandoned lands.

METHODS

Study Region

The study region lies within the subtropical moist forest life zone in north-central Puerto Rico and rises in elevation progressively from 0 m on the coastline to 300 m inland (18° N, 66-67° W; Figure 1; Holdridge, 1967; Ewel and Whitmore, 1973). The region is underlain by alluvial, karst, non-karst sedimentary, volcanic extrusive and intrusive geological substrates, or terranes (Bawiec et al., 2001), which are distributed roughly in that order ascending the elevational gradient. Topography at lower elevations consists of flat alluvial floodplain valleys intermittently dissected by haystack hills that merge into the northern karst belt (Monroe, 1976). As elevation rises inland, the karst belt meets volcanic terrain, which continues south to higher elevations in the central mountain range. The prevalent soil orders in the region are Inceptisols, Mollisols and Ultisols, interspersed with rock outcrop (Acevido, 1982; Beinroth et al., 2003). Although mass deforestation started with European arrivals, human influence upon vegetation on the northern coast dates back 5,000 years (Burney et al., 1994; Domínguez, 2000). Land and resource intensive agricultural crops, such as sugarcane, sun coffee and tobacco, coupled with grazing, progressively increased in area ever since European colonization (Silén, 1993). The region was extensively used for agriculture up to the 1950s when production declined due to industrialization, leading to rural-urban migration and large-scale reforestation (Rudel et al., 2000; Lugo and Helmer, 2004).

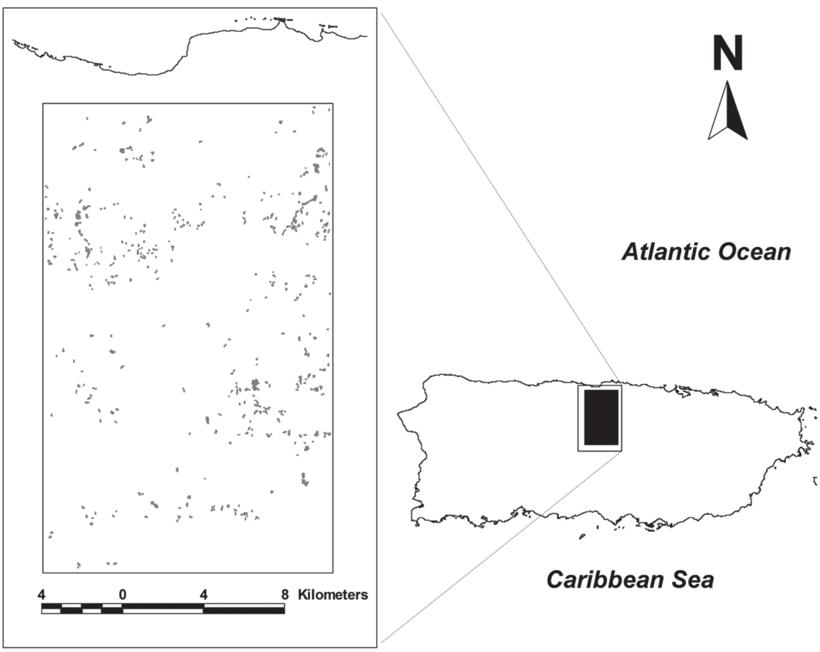

FIGURE 1. Detail showing forests dominated by *Spathodea campanulata* (left pane) mapped based on visual interpretation of aerial photography of 1998 for the delimited study region in north-central Puerto Rico.

Urbanization has halted this trend and led to some loss of agricultural lands and forest cover to urban development (López et al., 2001).

Mapping and Sampling

One-meter resolution digital aerial photography from 1998 (CRIM, 2004) was used to map *Spathodea* forest patches (Figures 1 and 2). Aerial photos were taken during the months of February and March, coinciding with low cloud cover and the peak of flowering for *Spathodea* in the region (Abelleira, 2011). Forest canopies that appeared orange to red were assumed to be dominated by flowering *Spathodea* trees and were mapped using Arc View 3.2 (ESRI, 1999). The criteria used for mapping were a closed and continuous red canopy with a minimum width of 30 m. Of the 443 mapped forest patches, 60 were visited to corroborate that they were indeed *Spathodea* forests.

Data Analysis

The *Spathodea* forest map was cross-tabulated with maps of geological substrate (Figures 1 and 3; Bawiec et al., 2001), soil series (Acevi-

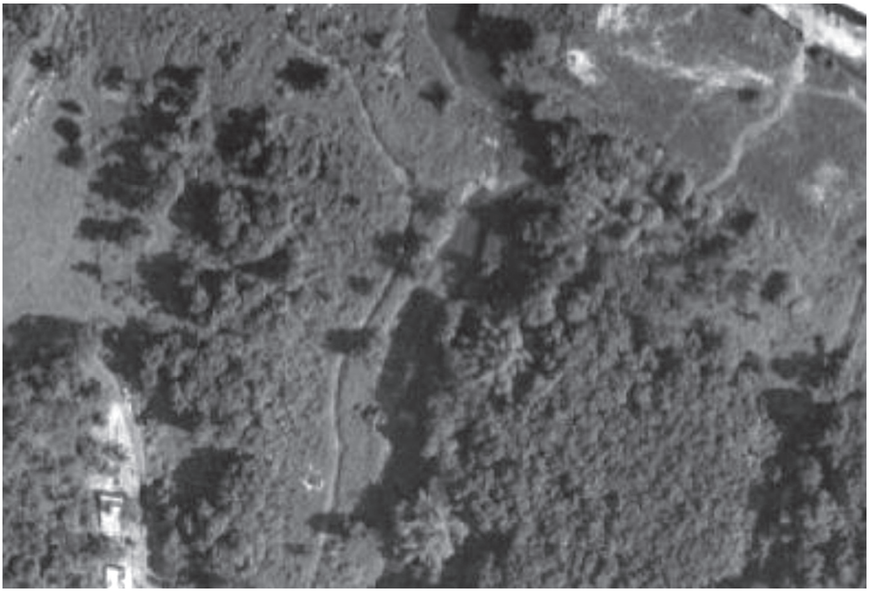

FIGURE 2. Aerial photography taken in 1998 over the Río Indio and Expressway 22 (top right) junction in Vega Baja, Puerto Rico. The river is bordered on both sides by *Spathodea* forest stands that have a reddish colored canopy due to flower bloom. The stand on the right side of the river corresponds to the Paso del Indio site (Abelleira, 2011). A karst haystack hill dominated by native forest is in the lower left corner.

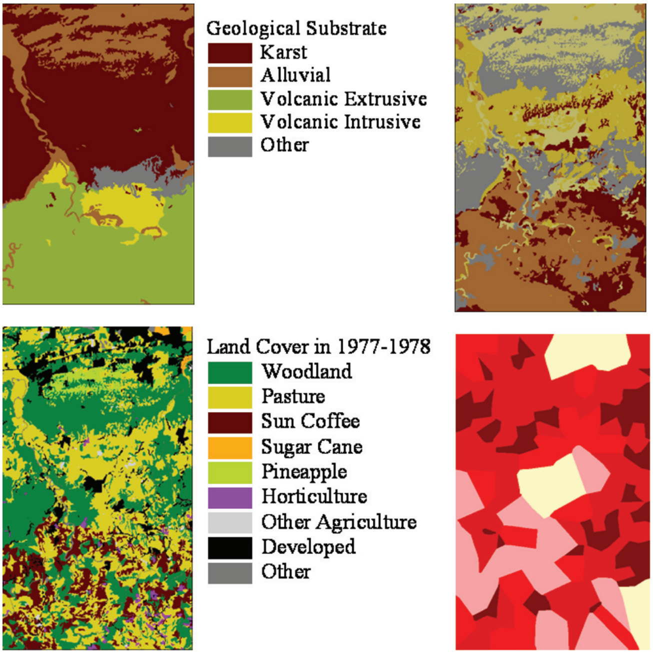

FIGURE 3. Maps of geological substrate (Bawiec et al., 2001), soil orders (Acevido, 1982, Beinroth et al., 2003; USGS, 2000), land cover in 1977-1978 (Ramos and Lugo, 1994) and *Spathodea* forest patch density in the study region. The agriculture class in the land cover map is segregated by the most common crops.

do, 1982; USGS, 2000) and land cover in 1977-1978 (Ramos and Lugo, 1994) using Idrisi 32 (Eastman, 2001). When more than one class underlain a forest patch, the patch was assigned to the predominant class in area within the patch. The 72 series in the soils map were re-classified into 11 soil orders (Figure 3; Beinroth et al., 2003). The 1977-1978 land cover map was classified into woodland, pasture, agricultural and urban areas. Woodland included lands with sparse woody vegetation such as shrubs and isolated trees. Previous land use corresponding to agriculture was further classified into horticultural crops (e.g., fruits, plantains and tubers), pineapple, sugarcane and sun coffee. I used the Spatial Analyst Tool and X-tools in Arc View 3.2 to establish where *Spathodea* forests were concentrated in the region and to estimate the area (ha) and perimeter to area ratio (P/A) of each *Spathodea* forest patch.

Contingency tables and Chi-Square (χ^2) tests were used to assess whether the distribution of *Spathodea* novel forest patches was skewed towards any class of the geological substrates, soil orders, soil series, previous land use histories and previous agricultural crops found in the study region. These analyses were conducted separately for each geographic variable and were based on the percentages of *Spathodea* forest patch area found in each class as dependent variable contrasted with the total area of each corresponding class in the study region as independent variable. The analysis was restricted to the top four classes ranked by the corresponding percentage of *Spathodea* forest area found per geographic variable class in the study region. I used analysis of variance (ANOVA) to determine if geological substrate, soil type, previous land use history and previous agricultural crop had any effects on *Spathodea* forest patch area and P/A in the same top four ranked classes using LSD-Fisher (F) tests and non-parametric ANOVA (Kruskal-Wallis; H) based on means of value ranks per class for non-normal data. Chi square and ANOVA tests corresponding to previous agricultural use excluded all other previous land uses. Shapiro-Wilks and F-max tests were used to test data normality and variance homogeneity, respectively. Infostat was used for all statistical analyses (Di Rienzo et al., 2014).

RESULTS

I mapped 443 red forest patches that covered 220 ha out of the 32,912 ha in the study region, which amounts to 0.7% of the landscape (Figure 1). Of the 60 mapped forest patches visited, 57 had canopies dominated by *Spathodea*, yielding a classification accuracy of 95%. Two of the misclassified patches were dominated by *Delonix regia*, an introduced species whose flower blooms in a similar red. The other misclassified patch was atop a karst ridge and was dominated by *Bursera simaruba*, a deciduous species with a yellow to orange leaf canopy for that part of the year. In other instances, the forest patches visited had been partly cut or more forest than mapped was found, but *Spathodea* always dominated the sites.

About half of all *Spathodea* forest patches were located on karst, which combined with alluvial and volcanic extrusive geological substrates corresponded to more than 80% of all patches (Table 1; Figures 1 and 3). About a third of *Spathodea* forest patches were found on Mollisols, which comprised 18% of the region, and combined with Inceptisols, rock outcrop and Ultisols corresponded to more than 80% of all forest patches. Likewise, there was a higher percentage of *Spathodea* forest patches on San Sebastián, Colinas and Toa soil series, which are all Mollisols. Nearly half of all *Spathodea* forest patches were on lands classified as woodland in 1977-1978, and the other half were on lands classified as pasture, agriculture and developed lands. Of all *Spathodea* forest patches on lands previously classified as agriculture, sun coffee

TABLE 1.—*Geographic distribution of* Spathodea campanulata *forest patches found in the top four-ranked classes of geological substrate, soil order and series, land use history and previous agricultural crop in the study region.* [The percentages reported are based on 443 patches found within the 32,912 ha region except for previous agricultural crop, which was based on 68 forest patches found within the 4,887 ha classified as agriculture in 1977-1978 (Ramos and Lugo, 1994). Values in bold denote significant differences ($p<0.05$; Chi-square test) in the percentages of forest patch area found in each variable class relative to the percentage area of each class in the study region.]

Class	Number of *Spathodea* Forest Patches (%)	Area of *Spathodea* Forest Patches (%)	Area of Class in the Study Region (%)
Geological Substrate			
Karst	49.7	41.9	42.0
Alluvial	19.0	21.0	17.7
Volcanic extrusive	15.8	18.6	31.0
Volcanic intrusive	9.5	8.5	5.5
Non-karst sedimentary	6.1	10.0	3.8
Soil Order			
Mollisols	34.1	31.4	18.1
Inceptisols	17.6	21.3	25.3
Rock outcrop	17.4	14.8	22.5
Ultisol	16.5	16.6	14.2
Others	14.4	15.8	19.9
Soil Series			
San Sebastián	12.9	9.1	4.4
Tanamá rock	11.7	9.3	12.0
Colinas	10.2	11.7	6.1
Toa	7.4	8.0	2.1
Others	57.8	61.8	73.1
Previous Land Use			
Woodland	48.5	46.7	37.0
Pasture	27.3	28.0	36.6
Agriculture	15.3	17.4	14.8
Developed	5.6	5.4	9.9
Others	3.2	2.4	1.7
Previous Agricultural Crop			
Sun coffee	66.2	**77.1**	71.9
Sugarcane	14.7	**9.0**	2.7
Pineapple	11.8	**3.2**	13.6
Horticulture	4.4	**2.6**	7.3
Others	2.9	**8.1**	4.5

was the most common previous agricultural crop followed by sugarcane and pineapple. Sugarcane comprised 3% of land area classified as agriculture in 1977-1978, yet the percentage of *Spathodea* forest patches and patch area on lands previously classified as sugarcane was 15% and 9%, respectively, suggesting a high affinity of these forests for abandoned sugarcane fields. Contingency table analysis showed the distribution of *Spathodea* forest patch area was not skewed toward any geological substrate (χ^2=5.64, df=3, p=0.1), soil order (χ^2=5.26, df=3, p=0.2), soil series (χ^2=4.92, df=3, p=0.2) or previous land use (χ^2=4.21, df=3, p=0.2). However, the distribution of *Spathodea* forest patch area on lands previously used for agriculture was skewed towards lands previously used for sugarcane and sun coffee crops (χ^2=11.81, df=3, p=0.008). The spatial distribution of *Spathodea* forests was concentrated in the northwest, northeast and east quadrants of the study region, and they were mostly absent in the mid-northern and central areas, which coincide with urban centers (Figures 1 and 3).

The area of most *Spathodea* forest patches (86%) ranged between 0.1 and 1 ha (Table 2, Figures 4 and 5; n=443, mean=0.5, range: 0.03 – 9.1, S.E. = 0.03) and P/A of all patches ranged between 0.03 and 0.3 m/m^2 (n=443, mean=0.09, S.E.=0.0002). The relationship of area and perimeter of *Spathodea* forest patches was best described by a power function that shows larger *Spathodea* patches have lower P/A than smaller patches, and that *Spathodea* forests have higher P/A than perfectly circular or square shaped patches of the same area (Figure 6). *Spathodea* forest patches on volcanic extrusive geological substrate were of larger area than those on other substrates (Table 2, Figure 4; H=10.34, n=412, df=3, p=0.02) and *Spathodea* patches on lands previously used for sun coffee were of larger area than those on lands previously used for other crops (Figure 5; F=7.91, n=62, df=3, p=0.0002). There was no effect of soil type or previous land use on *Spathodea* forest patch area (Table 2). *Spathodea* forest patches on volcanic extrusive substrate had lower P/A than those on other substrates (H=10.28, n=412, df=3, p=0.02), and patches on Toa soil series had higher P/A than those on other series (H=8.71, n=183, df=3, p=0.03). *Spathodea* forest patches on lands classified as woodland and agriculture in 1977-1978 had lower P/A than those on lands classified as pastures and urban areas (H=27.73, n=425, df=3, p<0.0001). Of the *Spathodea* forest patches on lands previously used for agriculture, those in sun coffee had lower P/A than those in other crops (Table 2, Figure 5, F=12.24, n=62, df=3, p<0.0001).

DISCUSSION

Novel *Spathodea* forests covered a small percentage of the study region in 1998, the date of the aerial photography samples used in this study. Active pastures at the time of sampling may have limited

TABLE 2.—*Spatial attributes of* Spathodea campanulata *forest patches found in the top four classes of geological substrate, soil order and series, land use history and previous agricultural crop in the study region*. [Mean patch area (MPA; ha) and perimeter to area ratio (P/A; m/m^2) reported per class are based on 443 patches found within the 32,912 ha region except for previous agricultural crop, which were based on 68 forest patches found within the 4,887 ha classified as agriculture in 1977-1978 (Ramos and Lugo, 1994). Numbers in parenthesis are standard errors and letters denote significant differences ($p<0.05$) in MPS and P/A of patches found across classes based on non-parametric rank-based analysis of variance (Kruskal-Wallis test) applied to data with non-normal distribution according to a Shapiro-Wilks test.]

Class	Mean Patch Area (ha)	Perimeter to Area Ratio (m/m^2)
Geological Substrate		
Karst	0.42 a (0.02)	0.091 a (0.002)
Alluvial	0.55 a (0.08)	0.100 a (0.005)
Volcanic extrusive	0.59 b (0.06)	0.080 b (0.003)
Volcanic intrusive	0.44 a (0.07)	0.093 a (0.004)
Soil Order		
Mollisols	0.46 (0.05)	0.097 (0.003)
Inceptisols	0.60 (0.12)	0.093 (0.004)
Rock outcrop	0.42 (0.03)	0.083 (0.003)
Ultisol	0.50 (0.06)	0.087 (0.003)
Soil Series		
San Sebastián	0.35 (0.03)	0.088 a (0.005)
Tanamá rock	0.40 (0.32)	0.084 a (0.013)
Colinas	0.57 (0.09)	0.089 a (0.004)
Toa	0.53 (0.15)	0.120 b (0.010)
Previous Land Use		
Woodland	0.48 (0.03)	0.083 a (0.002)
Pasture	0.51 (0.09)	0.100 b (0.003)
Agriculture	0.56 (0.08)	0.090 a (0.004)
Developed	0.48 (0.18)	0.122 b (0.013)
Previous Agricultural Crop		
Sun coffee	0.66 a (0.10)	0.078 a (0.004)
Sugarcane	0.34 b (0.12)	0.120 b (0.013)
Pineapple	0.15 b (0.03)	0.130 b (0.013)
Horticulture	0.34 ab (0.12)	0.097 ab (0.007)

Spathodea forest expansion, since active grazing hinders *Spathodea's* invasion (Rivera and Aide, 1998). Although *Spathodea* trees can flower when relatively small (~1 m; Francis, 2000; Abelleira and González, 2015), there were possibly many abandoned pastures being invaded by *Spathodea* at the time of sampling that were not mapped and accounted for in this study due to lack of a closed canopy. Land cover and socioeconomic trends in Puerto Rico reveal that areas of active agriculture

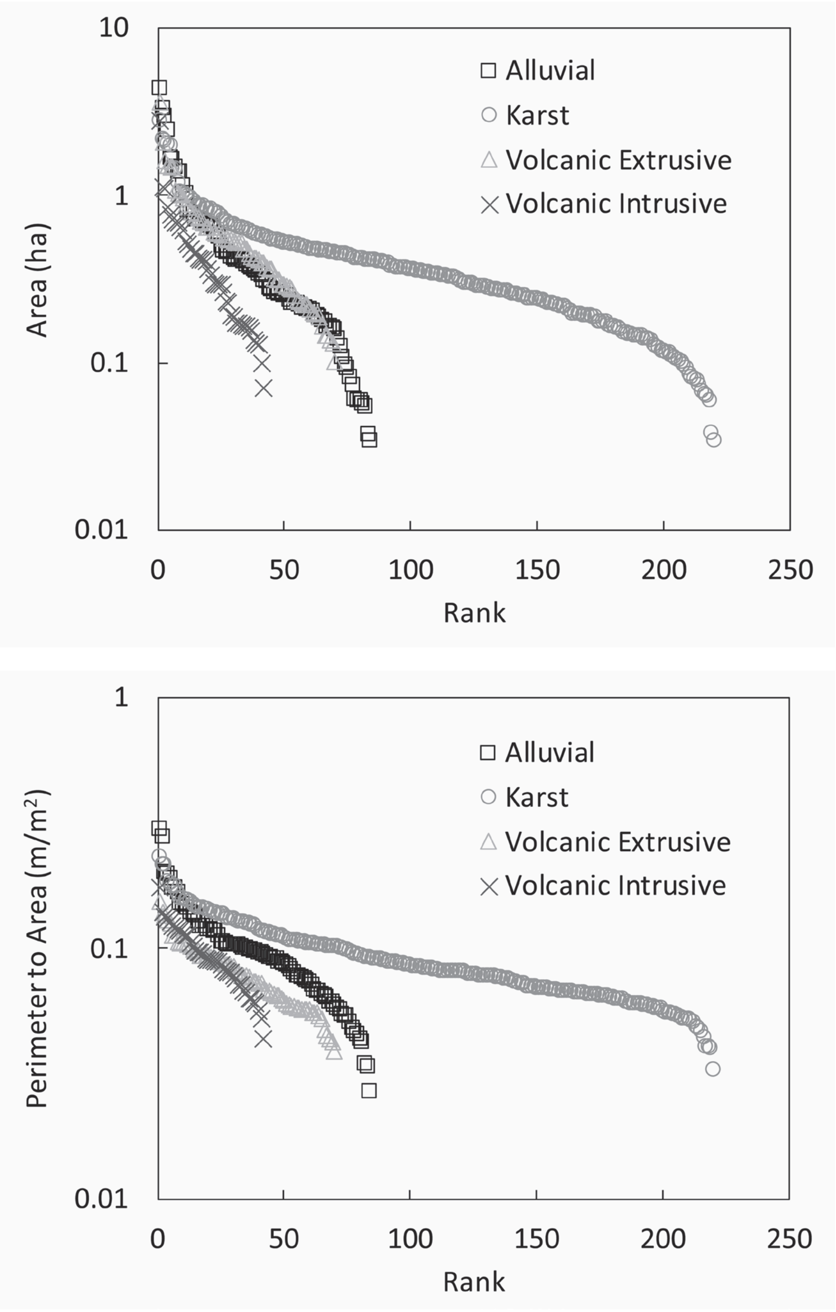

FIGURE 4. Ranked area and perimeter to area (P/A) ratio of *Spathodea* forest patches found for the four most extensive geological substrates in the study region.

and grazing have been abandoned since 1998; this may have further facilitated *Spathodea* forest expansion (Aide et al., 2000; Álvarez et al., 2013; Marcano et al., 2015). Indeed, assessments based on island-wide forest inventories and remote sensing suggest the area of *Spathodea* forests and other novel forest types increased over the last two decades, representing up to 15% of Puerto Rico's land cover around 2010 (Brandeis et al., 2007; Marcano et al., 2015). This estimate is based on a forested area of 60%, of which 25% is estimated to be novel (Álvarez et al., 2013; Martinuzzi et al., 2013).

Spathodea forests were more frequent on abandoned sugarcane fields and sun coffee farms (Table 1). As in abandoned pastures, favorable growth conditions for light-demanding *Spathodea* are found in abandoned sugarcane fields and sun coffee farms because they typically are devoid of remnant shade trees. The markedly skewed distribution of *Spathodea* forest area towards lands previously classified as sugarcane is indicative of more favorable growth conditions for *Spathodea* following the abandonment of this crop. The tendency of *Spathodea* forests for abandoned sugarcane fields can also be related to the fertile Mollisols found in lands previously used for sugarcane in the northern alluvial valleys of Puerto Rico (Acevido, 1982). Although the distribution of *Spathodea* forests was not significantly skewed towards any soil order (p=0.2), one third of all *Spathodea* forests patches were found on Mollisols (Table 1; Figures 1 and 3). Lands classified as Mollisols, which comprise the most fertile soils of Puerto Rico, were extensively cleared and intensively used for agriculture, mostly sugarcane, which resulted in soil compaction and nutrient depletion after centuries of use (Wadsworth, 1950; Vélez and Muñoz, 1991; Sotomayor and Martínez, 2006). The expansion of *Spathodea* forests in alluvial valleys has overcome this severe soil disturbance by improving soil structure, supporting soil biota, accumulating nutrients and creating favorable conditions for establishment and growth of native tree species that typically cannot invade abandoned pastures (Chinea and Helmer, 2003; Abelleira and Lugo, 2008; Lugo et al., 2012a). In doing so, novel *Spathodea* forests rehabilitate and protect some of the best agricultural lands of Puerto Rico, which are currently threatened by urban development (López et al., 2001; Helmer et al., 2008; Parés et al., 2008). The low concentration of *Spathodea* forests near urban centers can be due to urban sprawl limiting their expansion into nearby abandoned lands by deforestation and urban development. *Spathodea* forest patches found on developed lands may be covering abandoned lots, unpaved roads and housing.

The lack of significant affinity of *Spathodea* forests for any geological substrate, soil order or series is surprising and suggests there are few abiotic conditions in this region where *Spathodea* cannot grow

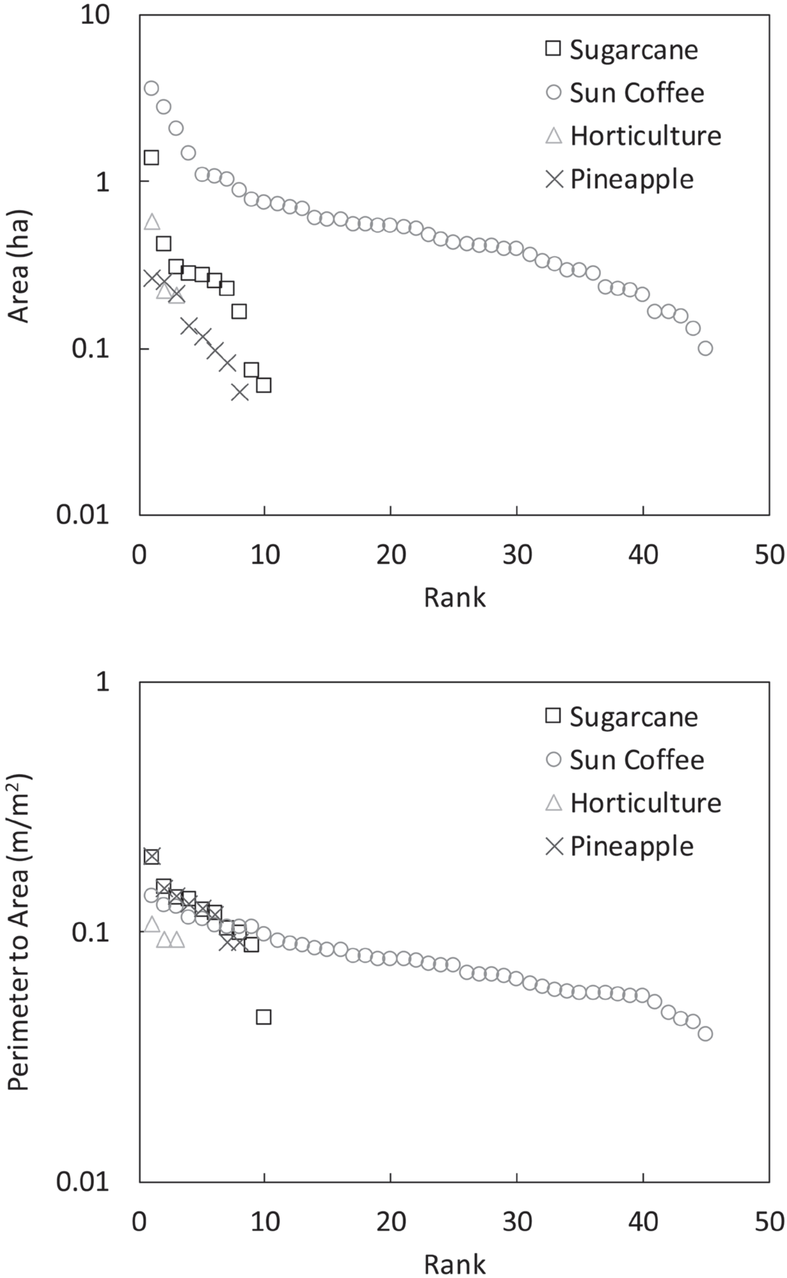

FIGURE 5. Ranked area and perimeter to area (P/A) ratio of *Spathodea* forest patches found for the four most extensive previous agricultural crops in the study region.

and thrive (Table 1). Nevertheless, there appears to be less affinity of *Spathodea* forests towards volcanic extrusive geological substrate in the region, and this may be due to active sun coffee farms and pastures in the mountains at the time of sampling. The distribution of *Spathodea* forests on rock outcrop as a soil order may be limited by remnant vegetation on topography not suitable for agriculture, and by poor growth conditions for *Spathodea* in xeric and infertile soils (Brandeis, 2006). Rock outcrop usually corresponds to haystack hills, or mogotes, on karst substrate and further classification into landforms may reveal a higher affinity of *Spathodea* forests for mesic depressions over xeric haystack hills (Monroe, 1976; Beinroth et al., 2003).

If the vegetation present on lands classified as woodland in 1977-1978 constitutes the same forest vegetation found in *Spathodea* forests mapped in 1998 aerial photography and has not been replaced since, roughly half of all *Spathodea* forests are more than 30 years old (Table 1). Land classified as woodland in 1977-1978 could have been cleared and later invaded by *Spathodea*, yet this situation is unlikely due to the presence of a closed canopy, which takes about 20 to 30 years to develop in the region (Aide et al., 2000; Lugo and Helmer, 2004). After 30 years of abandonment, *Spathodea* forests attain tree density and basal area similar to that of old-growth secondary forests of Puerto Rico (Abelleira et al., 2010). The older *Spathodea* forests mapped in this study likely comprise the structurally mature stands of this novel forest type in the region.

The *Spathodea* forests of north-central Puerto Rico occur in a fragmented and dynamic agricultural landscape and thus are much smaller in area than old-growth forests on protected lands but comparable to mature secondary forests (Table 2, Figures 4-6; Foster et al., 1999; Lugo, 2002; Helmer, 2004). For example, Thomlinson et al. (1996) found a mean patch area of 6.8 ha for mature secondary forests around El Yunque National Forest in northeastern Puerto Rico in 1988, with a range of about 0.5 to 50 ha and patches skewed towards smaller areas. Likewise, the P/A of *Spathodea* forests is comparable to secondary forests in northeastern Puerto Rico, which ranged from about 0.001 to 1.0 m/m^2 in 1995 (Lugo, 2002). The lower P/A of *Spathodea* forests of larger area is consistent with reductions in P/A and increments in area observed for secondary forests between 1977 and 1995 in northeastern Puerto Rico (Figure 6; Lugo, 2002).

As expected, *Spathodea* forests on alluvial substrate had higher P/A than those on other geological substrates, attributable to their small patch area and the location of many of these patches on riparian areas, amounting to gallery forests (Tables 1 and 2; Figures 1, 4 and 6). The higher P/A of *Spathodea* forests patches on alluvial substrate can be

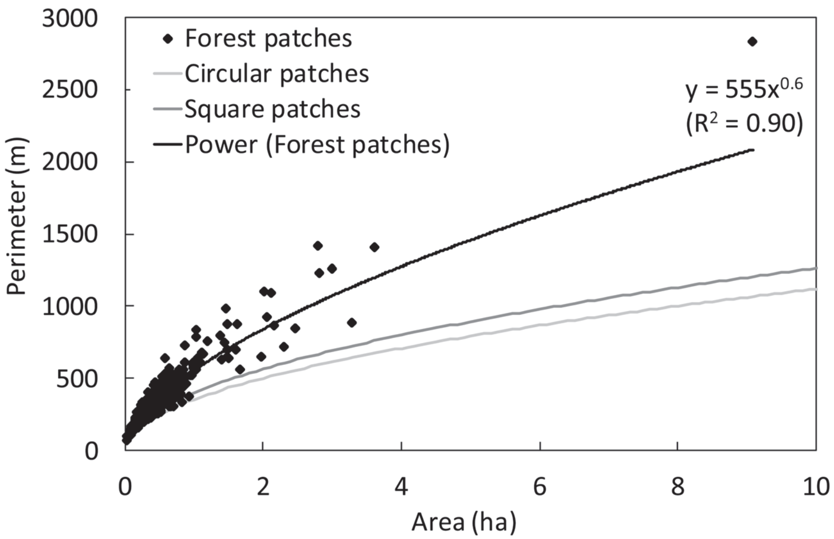

FIGURE 6. Perimeter to area (P/A; m/ha) relationship of novel *Spathodea campanulata* forest patches compared to that of perfectly circular and square patches. The power function next to the trendline provided the best fit (R^2) for the P/A relationship of *Spathodea* forest patches.

associated to the higher P/A of patches found on Toa soil series, which is abundant in the northern alluvial valleys (Acevido, 1982). Wide alluvial valleys could allow growth of riparian *Spathodea* forests into floodplains and flats away from rivers, potentially harboring forest patches of larger area and lower P/A. However, some alluvial valley areas in the region are still active in agriculture, and some valleys are narrow and surrounded by karst, which can limit the area and expansion of *Spathodea* forests. Consistent with this, some of the *Spathodea* forests on alluvial valleys mapped in this study have been deforested and converted to agricultural crops, mainly hay for cattle fodder. Urban developments that can limit or reduce *Spathodea* forest growth and expansion are also more frequent on alluvial valley floodplains and flats near the coast (López et al., 2001; Parés et al., 2008). Indeed, some of the *Spathodea* forest patches mapped in this study have been deforested and replaced by urban development.

Contrary to expectations, *Spathodea* forests on karst were not smaller but similar in area to those on other geological substrate types except volcanic extrusive (Table 2). The larger patch area and lower P/A of *Spathodea* forests on volcanic extrusive substrate can be due to the relatively continuous expanse of abandoned sun coffee farmland on mountain slopes, unlimited by urban developments. Rugged and highly heterogeneous topography combined with poor soil fertility may have initially limited farmland to smaller suitable areas in karst and volcanic intrusive geological substrates relative to volcanic extrusive substrates (Doerr and Hoy, 1957; González, 1995; Helmer, 2004).

It is possible that a longer time for growth into nearby areas resulted in the lower P/A of *Spathodea* forests on lands classified as woodland in 1977-1978, and that land use patterns near urban areas caused deforestation, fragmentation and higher P/A of nearby *Spathodea* forests (Table 2, Figure 6; Lugo, 2002; Helmer, 2004; Kennaway and Helmer, 2007). However, the hypothesis that "older" *Spathodea* forests, which would be represented by those classified as woodland in 1977-1978, would have larger patch area was not supported. The growth of *Spathodea* forest patches into the surrounding matrix depends on the availability of suitable abandoned farmland, which is inversely related to land accessibility and arability (Helmer et al., 2008). Agricultural re-activation of accessible abandoned farmland and urban development could be limiting older *Spathodea* forests from attaining larger patch area and lower P/A in the region.

The application of new remote sensing technologies and a wider geographical extent can help better understand island-wide patterns in *Spathodea* forest distribution. For example, prevailing easterly to north-easterly trade winds could result in a higher abundance of older and larger *Spathodea* forest patches in north-central Puerto Rico compared to lands located further east and west. Wind-dispersed *Spathodea* was introduced in about 1903 and was chiefly planted for shade and ornament near urban centers and roads (Britton, 1928). Its heavy use in metropolitan urban areas near San Juan may have facilitated its spread downwind to north-central Puerto Rico relative to lands further west or upwind to the east (Figure 1). Recent high-resolution aerial photography and Lidar images of tracts of the island may help to test this or similar hypotheses at an appropriate scale.

Implications for Social-Ecological Resilience

Most forests cleared for urban development in Puerto Rico are young (<15 years old) secondary forests in accessible arable lands (Helmer et al., 2008). Many *Spathodea* forests on fertile alluvial valleys and terraces fit this description, and some of these forests have been cleared for commercial urban developments such as gas stations, warehouses and fast food restaurants. If there is interest in conserving fertile alluvial soils for purposes other than urban development, more attention should be paid to the ecological roles fulfilled by novel *Spathodea* forests. For example, it may be desirable to conserve riparian gallery

Spathodea forests on alluvial valleys that could prevent soil erosion; remove excessive nutrients from river, floodwater and runoff inputs; reduce soil and nutrient exports to coastal waters; reduce flood levels through higher evapotranspiration rates relative to pastures; and perform other functions related to soil rehabilitation and biodiversity conservation (Brauman et al., 2007; Lugo, 2013).

Spathodea's introduced origin and its status as a highly invasive species may be part of the obstacle to constraining urban developments in flat alluvial lands and floodplains because high dominance by this species may be deemed undesirable (Labrada and Díaz, 2009). This conception overlooks the desirable ecological functions fulfilled by novel *Spathodea* forests, such as adaptations to thrive in and rehabilitate degraded soils, their role in ecological succession and their capacity to sustain ecological processes necessary for the support of ecosystem services (Davis et al., 2011; Hobbs et al., 2013; Lugo, 2013). It also overlooks the importance of conserving these sites for agriculture, forestry and related activities. The implications of the expansion of novel forests can vary due to context-specific tradeoffs between human interests in biodiversity conservation and ecosystem services, which may or may not be in conflict (Mascaro et al., 2012). In Puerto Rico, preventing novel *Spathodea* forests on agricultural lands from being cleared could provide concurrent ecosystem services such as soil rehabilitation, nutrient retention and carbon sequestration, and increases the amount of suitable habitat and spatial connectivity to support the dispersal and establishment of native flora and fauna. These services are still to be quantified and are lost indefinitely once these lands are converted to urban development.

Spathodea forests provide an important ecological service by increasing spatial connectivity between forest patches. Seed-dispersing vertebrate fauna thrive in *Spathodea* forests and act to increase tree species diversity on-site and possibly in adjacent forested lands that would otherwise be isolated by abandoned farmlands and pastures (Holl, 1999; Abelleira, 2010; Lugo et al., 2012b). Similarly, the abundance and diversity of pollinators in *Spathodea* forests could support pollination of tree species and agricultural crops within the forest and in surrounding areas, but this has not been studied. The flowers of *Spathodea* contain insecticidal chemical compounds, and it is important to know whether if this affects the abundance and diversity of insect pollinators (Trigo and Dos Santos, 2000; Abelleira, 2008). Chemical compounds from *Spathodea* tissue have uses in traditional medicine for the treatment of venereal diseases, malaria, bacterial and fungal infections (Ngouela et al., 1991; Pianaro et al., 2007; Dhanabalan et al., 2008). Potential applications and product development in Puerto Rico warrant more research. More broadly, the once barren landscape of north-central Puerto Rico now possesses a rich flora and fauna that is adapting to land abandonment by forging new ecological relations between introduced and native species. Understanding this process is necessary for sound forest management and conservation in the 21st century. Although most tree species invading these forests are native, the tree species composition of novel *Spathodea* forests may never come to resemble that of the native forests that once occupied this region because widespread deforestation extirpated many rare old-growth forest species, and because *Spathodea* and other introduced species will keep thriving in abandoned and degraded agricultural lands. However, *Spathodea* forests set the template for conservation and management interventions by providing ingredients necessary for the maintenance of species diversity, such as spatial connectivity, habitat and resources for seed dispersing fauna, and favorable conditions for plant growth. Local planning and public policy efforts aimed at conserving or restoring threatened species and promoting agroforestry should take advantage of the ecological benefits that novel forest ecosystems provide.

Novel forests are emerging throughout the world as nature's response to human land use, degradation and abandonment, and human-mediated species transport and introductions. In Puerto Rico, land managers must face decisions concerning the fate of *Spathodea* forests and the lands they occupy. One alternative has been to use these sites for urban development, which may have unwanted consequences for the island's food security in a future where climate change may increase the frequency of droughts and hurricanes, and where economic prosperity is uncertain (Carro, 2002; Comas, 2009; Henareh et al., 2016). Another and perhaps wiser alternative has been to revert *Spathodea* forests to agricultural production. Crops established on these lands will benefit from soil structure and fertility improvements resulting from *Spathodea* forest growth. *Spathodea* forests can thrive and perform this supporting service until there is a need to clear these novel forests to feed the island's population with local production. If this happens, a key to managing these lands sustainably for socio-economic resilience is to develop end uses for *Spathodea* biomass and tissues in ethnobotany, energy production and construction, for example, and not to let this resource go to waste.

Another alternative can be to use *Spathodea* forests as sites to carry out adaptive management interventions for threatened tree species restoration, agroforestry crops or timber production. *Spathodea's* deciduousness allows for seasonal pulses of increased sunlight, litterfall mass and nutrient inputs to soil, which, in turn, can favor the growth of trees and, potentially, the productivity of crops planted in the forest understory (Abelleira, 2011; Lugo and Abelleira, 2018). Early-successional tree species or agroforestry crops that thrive on exposed forest edges and in gaps due to greater incoming sunlight may be more suitable for enrichment plantings in novel *Spathodea* forests of smaller area and high P/A, such as those on alluvial riparian lands formerly used for sugarcane, which potentially contain more sun-exposed microclimates (Tables 1 and 2, Figures 4-6; Benítez and Ramos, 2003). Late-successional hardwood species adapted to shade may be better suited for enrichment plantings and subsequent stand management for thinning and timber crop release in novel *Spathodea* forests on volcanic extrusive substrate, which are of larger area and lower P/A ratio. A caveat is that perimeters estimated in this study do not always correspond to forest edges exposed to pastures but to vegetation that can include other forests. Nevertheless, P/A remains a proxy for spatial irregularities that create edge environments, such as ecotones and gaps, and for edges exposed to other types of vegetation (Turner et al., 2001), which are mostly pasture around *Spathodea* forests on alluvial valleys previously used for sugarcane. More attention should also be paid to understanding the ecological roles and devising interventions suitable for novel forests dominated by other species that possess traits, such as the capacity to fix nitrogen, that may influence the outcome of in-situ restoration or agroforestry interventions that involve the planting of trees and shade crops.

As an example of an adaptive intervention aimed at native species restoration, coworkers and I have experimentally planted rare *Pterocarpus officinalis* wetland trees in periodically flooded riparian *Spathodea* forests in alluvial valleys formerly used for sugarcane in the municipalities of Manatí and Vega Baja. Preliminary data suggests that between a third to half of the 108 individual trees planted across three sites survived up to 2018, withstanding the fury of Hurricane María on 20 September 2017, with some having attained a height of up to 5m from an initial planting height of 1 m in 2010. In another experiment aimed at testing adaptive interventions for establishing agroforestry crops in novel forests, juveniles of six fruit tree species, including avocado, breadfruit, cacao and coffee, were planted in the understory of novel forests dominated by *Spathodea* and other introduced species such as *Albizia procera*, a nitrogen-fixing leguminous tree, across sites in the moist life zone of Puerto Rico. Planting and long-term monitoring was begun a few weeks before the arrival of Hurricane María. Preliminary pre and post-hurricane assessments generally showed low (<10%) mortality of planted trees due to the hurricane, and high vigor and good form in the following months (Túa and Abelleira, 2019). The preliminary results from these experimental interventions suggest that biodiversity conservation and agroforestry crop production can take advantage of high-energy novel forest environments found in agricultural landscapes in

Puerto Rico and elsewhere, either by direct intervention, as in the case of threatened species restoration or agroforestry crops, or indirectly by landscape-level management for spatial connectivity of forested lands in tandem with lands under agricultural use (Hobbs et al., 2009 and 2014; Gould et al., 2017). If and when needed, a portion of these novel forests may be cleared for agriculture to sustain the island's human population, which now depends mostly on food imports. However, we should be careful not to repeat the massive forest clear-cuts that gave way to agriculture in the past. This will bring detrimental ecological consequences and the reversal of the ecological processes that have led to the rehabilitation of abandoned lands invaded by *Spathodea* forests. It may be better and wiser to develop management strategies that integrate ecological restoration and agroforestry interventions into novel forests so that Puerto Ricans can take steps towards using valuable resources in ways that guarantee the lowest tradeoffs between biodiversity conservation, food security and socio-economic development.

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