Chapter 9

CASE STUDY: GEOGRAPHIC DISTRIBUTION AND LEVEL OF NOVELTY OF PUERTO RICAN FORESTS

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A set of questions that emerge time and again during discussions of novel forests deal with the spatial cover of these systems. Are they dominant on landscapes? How broad is their geographic extent? Are they limited in ecological space to particular geoclimatic conditions? Responses to these questions require large-scale and georeferenced inventories of forests over a variety of geoclimatic conditions, regardless of level of human activity. The taxonomy of component trees also needs to be known so that questions about the nature of the species mix of forests, i.e. if the species are native or introduced as well as their relative importance, can be evaluated with confidence. Knowing the history of human activity over the same spatial scales as those of the forests being inventoried also helps to answer these questions.

Puerto Rico is an ideal place to address questions about the spatial distribution of novel forests. The island has been flown for aerial photography since the 1930s. This allows spatial as well as temporal analyses of its forest cover, which has experienced a dramatic change over the past centuries (Lugo 2004, fig. 1; see also Martinuzzi et al. 2009 for a 200-year analysis of mangrove forest cover change). The different land covers between the time when the island was mostly agricultural to today, with its 11% urban cover, is also well known (Helmer et al. 2002; Kennaway and Helmer 2007; Martinuzzi et al. 2007). In addition, forest cover of the island has been assessed several times in relation to climate and land cover (e.g. Lugo 2002; Helmer 2004; Lugo and Helmer 2004; Lugo and Brandeis 2005; Brandeis et al. 2009). Moreover, tree

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taxonomy in Puerto Rico is well known (Little et al. 1974; Francis and Liogier 1991) and the whole island has been inventoried three times between the 1980s and 2004 (Birdsey and Weaver 1982, 1987; Brandeis et al. 2007).

Given the wealth of information about forest cover and species composition available to us, we set out to develop a map of forest cover in Puerto Rico and to convert that map into novel forest cover maps. We used the presence of introduced tree species and their Importance Value (IV, a composite measure of abundance) as the criteria for novelty. We also included those locations where introduced species as a group accounted for 100% of the IV of vegetation in our mapping. As part of the mapping process we also estimated the extent of native, mixed native and introduced and purely introduced forest species assemblages present in the island. The mapping of novel forests allowed us to compare their distribution with that of native forests and to make observations about the relationship between human activity and forest cover in this tropical island.

9.1 METHODS

Our study combined recent land cover and forest inventory data. We used the results from the last forest inventory of Puerto Rico (Brandeis et al. 2009) to evaluate the abundance of introduced species across the different forest types of the island, which served as a surrogate for novelty. We also used a recent land cover map to spatially represent the information on introduced species. Our criteria for novelty included three different indexes, which we summarized by forest type: (1) the proportion of field plots belonging to tree species assemblages with any presence of introduced species; (2) the contribution of introduced species to the IV, for which we used the median across the plots (IV of a species included its relative basal area and stem density and its frequency, normalized to 100% for the sum of all species); and (3) the proportion of field plots belonging to assemblages composed entirely of introduced species. The higher these values, the more novel are the forests. These criteria were used to create maps of novel forests and to estimate the total area of native, mixed and purely introduced forest assemblages present in the island.

The forest inventory data were extracted from Brandeis et al. (2009) who identified the different tree species assemblages of the island and summarized their frequency by geoclimatic units, which are equivalent to forest types. Our plot data were at the species assemblage level. According to Brandeis et al. (2009) there are 14 major tree species assemblages whose presence and abundance change by geoclimatic unit or forest type. For each assemblage, the authors described the species composition including the distinction of native versus introduced species and the IV of each species. From knowledge of the assemblage species composition and the number of plots per geoclimatic unit, we were able to quantify our indexes for novelty for most forest types in the island. Forest types with low area coverage i.e. urban forests, forested wetlands, upper montane forests and abandoned palm plantations, were not well represented in the inventory. We therefore reviewed local studies to gain information about their species composition and hence their level of novelty (Figueroa et al. 1984; Lugo 1998; Lugo and Brandeis 2005; Gould et al. 2006; Table 9.1).

The forest cover map that we used to overlay species data (Fig. 9.1) was a simplification of a detailed land cover map developed by Gould et al. (2008). We added the classes 'urban forest' and 'upper montane forest' to distinguish two extreme conditions of anthropogenic presence, i.e. maximum for the urban, minimum for the upper montane. Urban forests were mapped by identifying the portion of the forest cover that was embedded in the island's urban areas (i.e. cities and towns, as mapped by Martinuzzi et al. 2007). Urban areas are hotspots for introduced species, and most of coastal Puerto Rico is urban. The upper montane forest, on the other hand, encompasses high-elevation wet and rain forests that have escaped from human disturbances due to their low suitability for agriculture, extreme rainfall and strong legal protection (see Helmer 2004; Kennaway and Helmer 2007). These areas include palo colorado, sierra palm and elfin forests, and other mature forest types located above the 600 m elevation (e.g. tabonuco forests; all of them mapped based on Gould et al. 2008). Finally, we were able to relate land cover and forest inventory data because both efforts used the same baseline information (i.e. geoclimatic units) to classify (with GIS) or sample (in the field) vegetation. In other words, the different forest types of the island were named, mapped and inventoried in a consistent fashion, making it possible to combine available data.

In summary, we first reclassified the forest cover map based on the three different criteria for novelty, using

Table 9.1 Abundance of introduced tree species in different forest types of Puerto Rico, as measured by three different plot-level inventory attributes. *N*: sample size; N/A: data not available; LM: lower montane; AVS: alluvial/volcanic/sedimentary substrate.

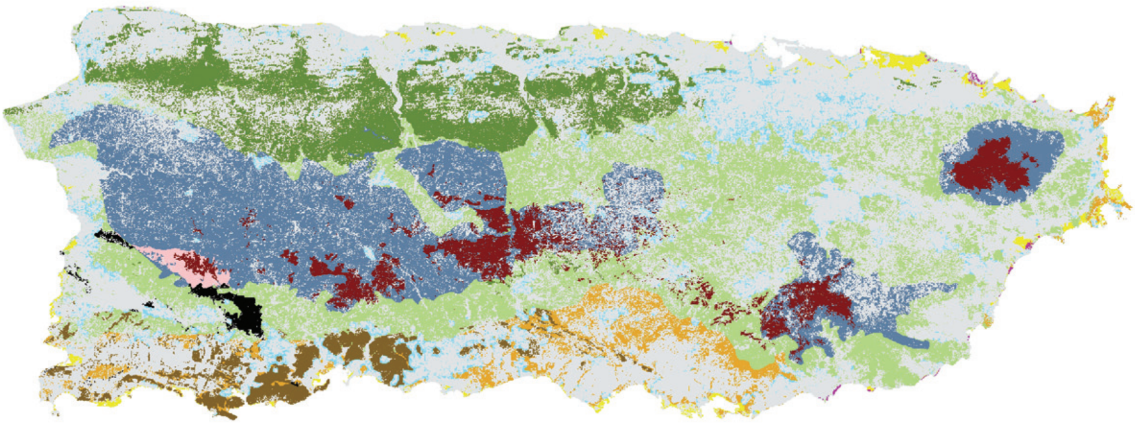
Forest type	Field plots belonging to assemblages with some introduced tree species (%)	Contribution of introduced species to IV (%)	Proportion of field plots belonging to assemblages composed entirely of introduced tree species (%)	*N*	Data source
Urban	N/A	66	N/A	6	Lugo and Brandeis (2005)
Dry/AVS	87	100	60	15	Brandeis et al. (2009)
Dry/limestone	86	13	43	14	Brandeis et al. (2009)
Dry, moist/ultramafic	63	10	38	8	Brandeis et al. (2009)
Moist/AVS	83	24	32	81	Brandeis et al. (2009)
Moist, wet/limestone	78	15	19	72	Brandeis et al. (2009)
Wet/AVS	82	24	18	68	Brandeis et al. (2009)
Wet, LM/ultramafic	17	0	0	6	Brandeis et al. (2009)
Upper montane	0	0	0	16	Gould et al. (2006); Brandeis et al. (2009)
Abandoned palm	100	53	N/A	2	Figueroa et al. (1984)
Forested wetlands	0	0	0	N/A	Lugo (1998)

the information for each species assemblage that we summarized by forest zone as described earlier. This resulted in three maps of novel forests where the original forest types are now represented by a value depicting the importance of introduced species. We used these maps to evaluate general patterns of forest novelty across the island and to compare forest types. We then quantified the extent of native, mixed and introduced forests by multiplying the proportion of plots in native, mixed or introduced species assemblages by the total area of the corresponding forest cover type. We considered species assemblages as native, mixed or introduced based on the contribution of introduced species to the IV: 0% for native; >0% and <100% for mixed; and 100% for introduced.

9.2 RESULTS AND DISCUSSION

9.2.1 Spatial patterns of novel forests

The novel forest maps (Fig. 9.2a–c) revealed two species composition attributes of Puerto Rican forests. First, introduced species exhibit a widespread distribution as they are present almost everywhere. Second, the maps depict the spatial patterns or spatial distribution of novelty. Only a few parts of the island contain forest types without introduced species. These locations with native forests include mountain peaks (upper montane forest type) and areas of land–ocean interface with forested wetlands. The rest of the island's forests all have some level of introduced species presence.



Forest type	Description	Hectares
Urban	Forests within urban areas	27,311
Dry/AVS	Dry forests on alluvial, volcanic and sedimentary substrates	21,592
Dry/Limestone	Dry forests on limestone substrate	19,822
Dry, Moist/Ultramafic	Dry and moist forests on ultramafic substrate	4,365
Moist/AVS	Moist forests on alluvial, volcanic and sedimentary substrates	143,543
Moist, Wet/Limestone	Moist and wet forests on limestone substrate	67,445
Wet/AVS	Wet forests on alluvial, volcanic and sedimentary substrates	125,408
Wet, LM/Ultramafic	Wet and lower montane forests on ultramafic substrate	3,364
Upper montane	Mature forests > 600 meters elevation	31,432
Abandoned palm	Abandoned coconut palm plantations	491
Forested wetlands	Mangroves and Prerocarpus swamps	7,946
	All forests	452,718
Non-forested lands		418,042

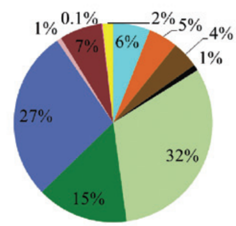


Figure 9.1 Forest land-cover types of Puerto Rico, including description and extent. From Gould et al. (2008).

The high presence of introduced species is particularly visible in Fig. 9.2a, which displays forest types based on the number of field plots belonging to species assemblages with introduced species. Most of the island's forests have many plots with introduced species, i.e. 80% or more. Upper elevation wet areas (i.e. regions for the upper montane and wet ultramafic forests) as well as forested wetlands were the only regions with very low or no presence of introduced species. The northern karst region (with the moist/wet limestone forest) had intermediate values.

In terms of the contribution of introduced species to IV, the highest values were observed in some of the lowlands including dry forests in the south (i.e. on alluvial/volcanic/sedimentary substrate or AVS), urban areas and abandoned palm plantations (Fig. 9.2b). In these forests the contribution of introduced species represented >50% of the IV. The areas with the lowest contributions of introduced species to the IV were located on limestone and ultramafic substrates, upland forests and forested wetlands.

The southern forests were the areas supporting the highest proportions of plots composed entirely of introduced species (i.e. 40–60%), followed by some of the eastern moist forests (i.e. on AVS substrate; Fig. 9.2c). The rest of the island contains typically lower values (<20% or zero).

9.2.2 Extension of native, mixed and introduced forests

Our study revealed that in Puerto Rico about 50% of the forest cover is mixed (i.e. corresponding to mixed

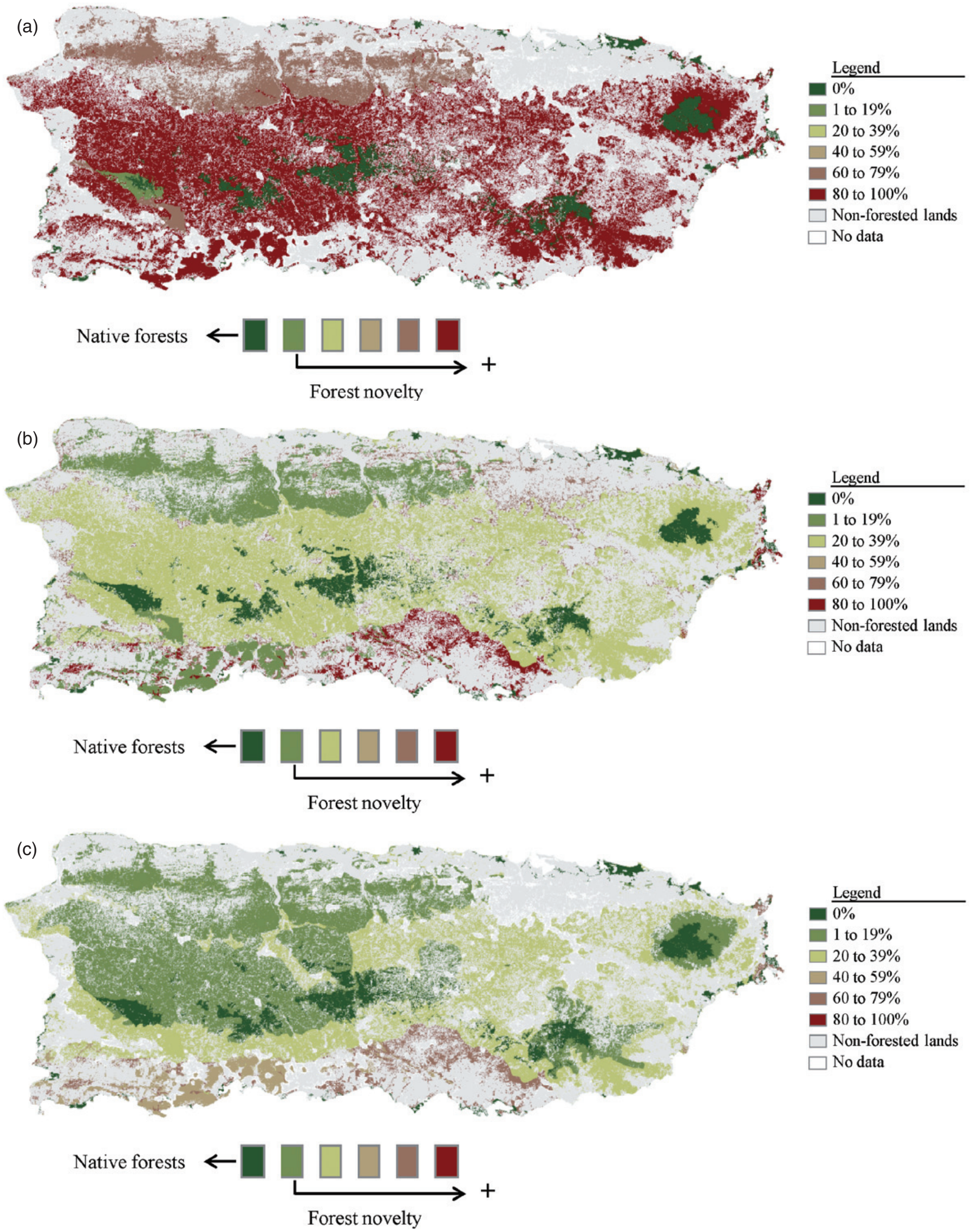


Figure 9.2 (a) Geographic patterns of forest novelty based on the proportion of field plots with some presence of introduced tree species. (b) Geographic patterns of forest novelty based on the contribution of introduced species to the IV estimator. (c) Geographic patterns of forest novelty based on the proportion of field plots composed entirely of introduced species. The values are calculated and displayed by forest type.

Table 9.2 Extension of native, mixed and purely introduced forests. Totals do not include urban forests.

Forest type	Hectares			In Percent		
	Native	Mixed	Introduced	Native	Mixed	Introduced
Urban	N/A	N/A	N/A	N/A	N/A	N/A
Dry/AVS	2,807	5,830	12,955	13	27	60
Dry/limestone	2,775	8,523	8,523	14	43	43
Dry, moist/ultramafic	1,615	1,091	1,659	37	25	38
Moist/AVS	24,402	73,207	45,934	17	51	32
Moist, wet/limestone	14,838	39,793	12,815	22	59	19
Wet/AVS	22,573	80,261	22,573	18	64	18
Wet, LM/ultramafic	2,792	572	0	83	17	0
Upper montane	31,432	0	0	100	0	0
Abandoned palm	0	491	0	0	100	0
Forested wetlands	7,946	0	0	100	0	0
Total	111,180	209,768	104,459	26	49	25

species assemblages), 25% is native (i.e. composed only of native species) and 25% is purely introduced (i.e. composed only of introduced species). For the mixed forests, the contribution of introduced species was about 25% of the IV (data not shown). If forest assemblages with any presence of introduced species are considered novel, then three-quarters of the island forests are novel (Table 9.2). Our study did not consider whether changes in forest species composition were reversible or not, and hence we did not distinguish potential hybrid systems from novel systems.

Upper montane forests, wet ultramafic and forested wetlands are the hotspots for native vegetation assemblages, totaling about 42,000 ha. These areas support very low presence of introduced species or no presence at all. Large extensions of native vegetation can also be found in moist and wet forests on limestone and AVS substrates (another 62,000 ha) however, but representing a small fraction (22% or less) of the total area of these forest types. Moist and wet forests on AVS and limestone substrates were however the hotspots for mixed forest assemblages. These forest types alone account for near 193,000 ha or 92% of all the mixed forests present in the island. Finally, dry forests were hotspots for introduced assemblages with >40% of their extent in this condition. However, large areas of introduced vegetation are also present in moist and wet forests. Information for urban forests was limited but, based on IV values in Table 9.1, we expect these forests to have a high presence of introduced species; they may therefore be composed mostly of mixed and/or introduced vegetation. Finally, based on the proportion of native, mixed and introduced tree species assemblages, upper wet forests and wetlands can be seen as mostly native, other wet and moist forests mostly mixed and dry forests mostly introduced.

The numbers presented in this study were based on field data of trees species expressed at the assemblage level and were valuable for assessing the geographic distribution and level of novelty of the Puerto Rican forests. However, the species assemblage level data excluded rare species and masked natural variations in species composition that may occur within each assemblage. Estimating the ultimate area of native, mixed and introduced forest vegetation will require analysis of the complete information for each individual plot. For these reasons, our numbers should be considered as an approximation.

9.3 CONCLUSIONS

Our study shows that introduced species have naturalized over most of the geographic space of Puerto Rico. However, forests in extreme environments, i.e. high rainfall, nutrient-poor soils (i.e. ultramafic substrate) or flooded, are still dominated by native vegetation; examples of areas dominated by native vegetation still occur on all forest types of the island. Novel forests do not appear to be restricted by geoclimatic conditions. Instead, they appear to be associated with the residual effects of past and present anthropogenic activity, which have in turn extended to most parts of the island. Two-thirds of the Puerto Rican forests may contain novel forest assemblages. We also found that the area of native forest species assemblages is now equaled by the area of forests that are classified as completely introduced. There is a critical need to study the functioning of novel forests in Puerto Rico and elsewhere in the tropics where they occur.

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