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Diversity and composition of tropical secondary forests recovering from large-scale clearing: results from the 1990 inventory in Puerto Rico

J. Danilo Chinea*, Eileen H. Helmer

International Institute of Tropical Forestry, USDA Forest Service, P.O. Box 25000, Río Piedras, PR 00928, USA

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Abstract

The extensive recovery from agricultural clearing of Puerto Rican forests over the past half-century provides a good opportunity to study tropical forest recovery on a landscape scale. Using ordination and regression techniques, we analyzed forest inventory data from across Puerto Rico's moist and wet secondary forests to evaluate their species composition and whether the landscape structure of older forest affected tree species composition of recovering forests at this scale. Our results support conclusions from studies conducted in Puerto Rico at smaller scales and temperate forests at larger scales that timing of abandonment and land use history are of overwhelming importance in determining the species composition of recovering forests. Forest recovery is recent enough in Puerto Rico that previous land use is clearly evident in current species composition, and creates new forest communities. As demonstrated in other work, physical factors such as elevation and substrate co-vary with land use history, so that the species composition of the forest landscape results from the interplay between biophysical and socioeconomic forces over time. Our results also indicate that increasing the distance to the largest forest patches occurring in the landscape 12 years previous had a small negative impact on species richness but not species diversity or community composition. We conclude that land use history has as much influence in species composition as biophysical variables and that, at the scale of this study, there is no large influence of forest landscape structure on species diversity or composition.

Keywords: Forest fragmentation; Landscape dynamics; Tropical; Land use; Biodiversity

1. Introduction

Between 1950 and 1990, forest recovery in Puerto Rico has occurred over a greater proportion of lands previously cleared for agriculture than in any other nation (Rudel et al., 2000). The island was almost completely covered by forest at the time of European arrival in 1493 (Wadsworth, 1950). Deforestation occurred slowly during the next three centuries, then accelerated during the 19th century, as coffee and sugarcane plantations were established by a surge of immigrants, and it peaked in the middle of the 20th century, as sugarcane became the dominant cash crop (Franco et al., 1997). Forest cover reached a low of about 6% in the late 1940s and then increased to about 32% of the island's area by 1990 (Birdsey and

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[*] Corresponding author. Present address: Departamento de Biologia, Universidad de Puerto Rico, Recinto de Mayagüez, P.O. Box 9012, Mayagüez, PR 00681-9012, USA. Tel.: +1-787-832-4040x3431; fax: +1-787-265-1225.
E-mail address: jdchinea@yahoo.com (J.D. Chinea).

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Weaver, 1987; Franco et al., 1997). This forest recovery has provided an exceptional opportunity to study the impacts on forest ecosystems of large-scale tropical deforestation and subsequent forest recovery. Another advantage of studying Puerto Rico's secondary forests is that many secondary stands are now older than those found in areas of the world experiencing large-scale deforestation in the last few decades (Zimmerman et al., 1995; Aide et al., 1996).

In temperate zones, ecologists have had the opportunity to study over large scales the spatial correlates of forest species composition following widespread disturbances, such as clearing for agriculture or logging, and subsequent forest recovery (Foster, 1992; Mladenoff et al., 1993; Ohmann and Spies, 1998). Their research has shown that species composition of recovering forests relates to physical factors, such as climate, as well as socioeconomic processes, that occur over local to regional scales, and that there are significant interactions between forest successional processes, land use history and the physical constraints or influences on land use (Foster, 1992; Pan et al., 1999). In tropical zones, however, most information on forest recovery is restricted to smaller scales (Purata, 1986; Uhl et al., 1988; Zimmerman et al., 1995; Aide et al., 1996; Rivera and Aide, 1998; Oosterhoorn and Kappelle, 2000) or to studies that only investigate the spatial pattern of secondary forest cover as opposed to its species composition (Wilkie and Finn, 1988; Thomlinson et al., 1996; Kramer, 1997; Helmer, 2000). Recent studies have shown that in both temperate and tropical regions, secondary forests develop at the edges of remaining forest fragments from local (Purata, 1986; Uhl et al., 1988; Bierregaard et al., 1992; Oosterhoorn and Kappelle, 2000) to landscape (Foster, 1992; Turner and Corlett, 1996; Thomlinson et al., 1996; Spies et al., 1994; Kramer, 1997) to regional scales (Helmer, 2000) in a coalescing pattern. These older forest fragments may be in less accessible, less arable, and sometimes less populated areas (Foster, 1992; Chomitz and Gray, 1996; Helmer, 2000), and where alternative income sources become available such as wage labor (Behrens et al., 1994; Moran et al., 1994; Rudel et al., 2000). Landscape structure refers to the spatial relationships between ecosystems (Turner, 1989). Whereas the spatial pattern of older tropical forest relative to agricultural lands apparently affects patterns of forest recovery, the impact of landscape structure on secondary forest species composition at broader scales is unknown.

The USDA Forest Service surveyed the forests within the island's two major life zones in 1980 and 1990 (Birdsey and Weaver, 1987; Franco et al., 1997), and documented species composition over a large proportion of Puerto Rico's secondary forest. These surveys excluded urban areas, the best agricultural lands, dry coastal areas, critical watershed areas, and areas with extremes of slope or rainfall (Franco et al., 1997). Although these surveys were restricted to the area with potential for commercial timber production, the data cover more than half of the island's area and provide an opportunity to study the species composition of forests recovering from large-scale clearing for agriculture. In this study we describe in detail the geophysical and historical correlates of the tree species composition and diversity of the forests sampled in the 1990 survey. We also evaluate landscape structure as a potential factor influencing tree species composition and diversity of recovering forests.

2. Methods

2.1. Study area

Puerto Rico lies between about 17°45′N and 18°30′N and its longitude ranges from about 66°15′W to 67°15′W (Fig. 1). The main island occupies about 8900 km^2. Proceeding from northeast to southwest, in the direction of the trade winds, one first encounters semideciduous forests along Puerto Rico's north and east coasts. As three major mountain ranges force moisture-carrying trade winds to higher altitudes, submontane and lower montane wet and rain forests, including cloud forest formations, occur. Proceeding southern and west, rainfall decreases in the rain shadow of the major cordilleras, resulting in increasingly drier forest formations in southern and southwestern Puerto Rico. Upland forests have developed over alluvial, sedimentary, volcanic, limestone, and serpentine substrates.

2.2. Forest inventory data

The 1990 forest inventory included 167 forested sampling sites out of 437 sites located at the intersections of a 3 km × 3 km grid within the subtropical

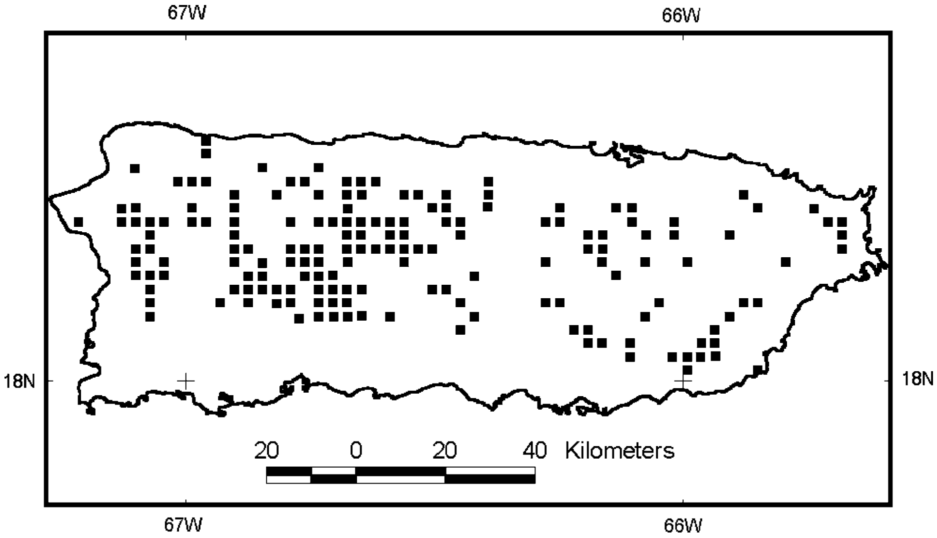

Fig. 1. Map of Puerto Rico and the location of the 167 forested sampling sites.

moist and subtropical wet forest life zones of Puerto Rico (Franco et al., 1997; Fig. 1). These two life zones cover 85% of the island (Ewel and Whitmore, 1973). The samples were established on the ground by running a computed azimuth and distance from a selected starting point. Each sample consisted of a cluster of three subplots spaced 25 m apart. The middle subplot was located at the center of the site while the other two subplots were aligned north and south of the middle subplot. Each sample tree >12.5 cm in diameter at breast height (dbh) in the variable radius subplots represented 0.83 m^2 of basal area. Sample trees 2.5–12.5 cm in dbh (bh = 1.3 m above the ground on uphill side of tree) were tallied on fixed radius plots of approximately 40 m^2 around each of the three subplot centers. Species were identified in the field by two local botanists. Nomenclature follows Little and Wadsworth (1964) and Little et al. (1974). Tree density and basal area were calculated for every sample and an importance value index per species in every sample was calculated based on the average of relative density and relative basal area.

We related species composition and diversity of forest inventory plots in 1990 to environmental variables potentially important to species composition including land use history, climate, slope, aspect, and the landscape structure of forest 12 years previous to 1990.

2.3. Geophysical and historical data

The land use data reported by the surveyors in 1980 and 1990, as defined in their manuals, were used as categorical variables. We also extracted environmental data from published and unpublished digital maps using the geographic coordinates of each sample. Environmental variables (Table 1) included rainfall (Calvesbert, 1970; PRAWA, 1971), elevation, aspect and percent slope (USGS, 1999), generalized geology (Krushensky, 1995), Holdridge life zone (Holdridge, 1967; Ewel and Whitmore, 1973) and “geoclimatic zone” (Figueroa-Colón, 1996), which resulted from a simple overlay of geology and life zone. Location of forest inventory plots relied on aerial photos and US Geological Survey topographic maps of scale 1:20,000. As a result, we estimated the spatial accuracy of sample coordinates to be within ±100–150 m and degraded the spatial resolution of these maps to a 240 m cell size before extracting environmental data for each sample.

In addition, to test the potential impacts of remaining forest landscape structure on species composition in 1990, we determined the distances from each sample to forest patches of various minimum sizes. Forest cover for this analysis derived from a land cover map developed from aerial photos dated about 1978 (Ramos and Lugo, 1994). This data also permitted

Table 1
Variables included in ordination and regression analyses

Variable	Description
Plot-level	
BA	Basal area ($m^2\ ha^{-1}$)
GUSE	Current ground use class (land use identified by the surveyors), including abandoned coffee shade[a], active coffee shade[b], secondary forest[c], young secondary forest, reversion[d], pasture[e] and idle farmland
PUSE	Past ground use class (land use identified by surveyors in the inventory of 1980), including abandoned coffee shade, active coffee shade, secondary forest, very young secondary forest, and pasture
Environmental	
RAINFALL	Annual rainfall (mm)
ELEVATION	Elevation (m)
ASPECT2	Aspect class, including *north* or *south*
ASPECT4	Aspect class, including northwest, northeast, southeast or southwest
PCTSLOPE	Percent slope
GEOLOGY	Geology of substrate, including alluvial, extrusive volcanic, intrusive volcanic or karst
GEOLOGY2	Geology of substrate, including *karst* and *non-karst*
LIFE ZONE	Holdridge life zone, including moist subtropical forest and wet subtropical forest
Forest landscape	
PATCH AREA 78	Area of forest patch in land cover map from 1978 within which inventory plot is located
DIST3801	Distance (km) to forest patches ≥3801 ha in size (0.1 percentile[f])
DIST362	Distance (km) to forest patches ≥362 ha in size (0.5 percentile[f])
DIST210	Distance (km) to forest patches ≥210 ha in size (1.0 percentile[f])
DIST42	Distance (km) to forest patches ≥42 ha in size (5.0 percentile[f])
DIST7	Distance (km) to forest patches ≥7 ha in size (25 percentile[f])
DISTP45	Distance (km) to forest patches ≥0.45 ha in size (75 percentile[f])

[a] Forest resulting from abandonment of coffee production under shade trees.
[b] Multi-story vegetation system with shade trees and well maintained coffee shrubs.
[c] Forest resulting from abandonment of cropland or pasture, or from regeneration of cutover or disturbed forest.
[d] Non-forest land in 1980 reverting to forest with 10–50% crown closure in 1990.
[e] Improved pasture with at least 10% tree crown closure.
[f] Percent of all forest patches greater than stated size.

estimation of the size of the forest patch in 1978 within which each plot was located. Plots that were not forested in the land cover map dated 1978 had a patch area of zero. Although the landscape structure of forest cover when it was at its minimum would also be desirable to evaluate, this map was the only map of forest cover available at the time at a scale appropriate to an island-level analysis. A contiguity analysis (ERDAS, 1997) first determined the distribution of forest patch sizes. In consideration of the log normal distribution of forest patch sizes, we selected minimum patch sizes that represented 0.1% (3801 ha), 0.5% (362 ha), 1.0% (218 ha), 5.0% (44 ha), 25% (7 ha) and 75% (0.45 ha) of all forest patches in the landscape. We then developed maps of all forest patches greater than or equal to each of the above minimum patch sizes and determined the proximity to forest of each site in each map. A map with minimum patch size of 362 ha, for example, included 0.5% of all forest patches. The variable DIST362 represented the distance from each site to the closest forest patch of ≥362 ha.

2.4. Vegetation analyses

Prior to the vegetation analyses, we removed unidentified and rare species (i.e., those occurring in fewer than 3% of the samples) and samples of under-represented land use types. This editing reduced the original 167 samples by 226 species data matrix to a matrix of 154 samples by 60 species.

A direct gradient analysis of species importance values, using canonical correspondence analysis (CCA version 4, ter Braak and Smilauer, 1998) determined the geophysical and land use history correlates of the compositional variability in these plots. We performed the CCA by forward selecting the independent variables and employing a Monte Carlo permutation test to evaluate their significance level. Each variable was tested at the 5% confidence level with 1000 random permutations.

The sample data matrix was also classified using the unweighted-pair groups method (UPGMA) with the Sorensen distance measure available in the PC-ORD package (McCune and Mefford, 1999). The resulting groups of plots (clusters) were then analyzed using the IndVal (indicator value) analysis proposed by Dufrene and Legendre (1997). In this analysis each indicator value is the product of two indices:

$$\mathrm{IndVal}_{ij} = A_{ij} \times B_{ij} \times 100,$$

$$A_{ij} = \frac{\text{number of trees}_{ij}}{\text{number of trees}_{i}}, \quad B_{ij} = \frac{\text{number of sites}_{ij}}{\text{number sites}_{j}}$$

where A_{ij} (a measure of specificity) is the mean abundance of species i in the sites of cluster j compared to all clusters in the classification, and B_{ij} (a measure of fidelity) the relative frequency of occurrence of species i in the sites of cluster j. A_{ij} is maximum where species i is only present in cluster j, and B_{ij} is maximum where species i is present in all sites of cluster j. The significance of each indicator value was tested at the 5% significance level by the difference between the observed value and the mean of the values obtained from 1000 random permutations weighted by the standard deviation of the values obtained randomly.

2.5. Evaluating landscape structure impact on species richness and diversity

We first used forward multiple regression, with backwards elimination, to determine which environmental and land use history variables significantly explained variations in both total and native species richness and diversity (H′). This evaluation excluded the distance to forest variables. As with the ordination analyses, information on land use history derived from the presumably more accurate categorizations by the plot surveyors rather than maps. The plot locations were somewhat imprecise, and the map from 1978, for example, included all coffee cultivation in the single agricultural class. We then added to the resulting multiple regression models the variables for distance to forest patches of various minimum sizes. An extra sum of squares F-test (Ramsey and Shafer, 1997) served to evaluate whether these landscape structure variables explained any additional variation in species richness or diversity. To assist in data interpretation, we also calculated mean species richness and diversity, basal area, elevation, and distance to selected minimum patch sizes by climatic zone, geology and land use at the time of sampling.

2.6. Limitations of the inventory data

The data used in this study was intended for evaluating the potential of the island's secondary timber resources and describe their ecological characteristics (Franco et al., 1997). While the data obtained in the fixed area plots is compatible with data gathering methods in many ecological studies, the data gathering procedures in the variable area plots were quite different than in most ecological studies. Particularly, in some cases a large tree may have been tallied in two different subplots if its distance to the centers of the subplots was sufficiently close and its diameter was sufficiently large. This particularity may overestimate the importance of those species in a sample. However, such overestimates would be minimized by using relative instead of absolute abundance.

Another limitation was that the survey intended to sample only one stratum: the commercial forest region of Puerto Rico. Therefore, no consideration was given to sample with similar intensity the potentially different forest communities. However, considering the vast amount of information contained in this extensive data set of a tropical country, this data was worth analyzing for the purposes of our study, and we believe some very useful insights can be obtained. Moreover, data of much poorer quality from Grand Land Office presettlement records in many portions of the United States have been used adequately to determine the composition of presettlement forest communities and the abundances of their tree species (e.g., Schwartz, 1994; Fralish et al., 1991).

3. Results

3.1. Species composition

The following variables were forward selected by CANOCO prior to the ordination: four geophysical variables (longitude, distance to forest, elevation, rainfall, and karst substrate), four current land use types (reversion, abandoned coffee, active coffee, and pasture), and one past land use type (very young forest; Fig. 2). This combination of variables explained 16% of the total variance in species abundances. The first axis of the ordination explained 4.8% of the total variance ($P = 0.001$; Monte Carlo permutation test with 1000 permutations), while the second axis explained an additional 2.6%. The first axis is strongly negatively correlated with elevation and positively correlated with prior history of other types of agricultural use (i.e., reversion from crops or pasture). The second axis is positively correlated with karst substrate and negatively correlated with longitude. Geophysical variables accounted for 46% of the explained variance, land use history variables accounted for 42, and 11% was shared between these two sets of variables.

The IndVal analysis of the UPGMA classification identified 11 significant sample clusters (Table 2;

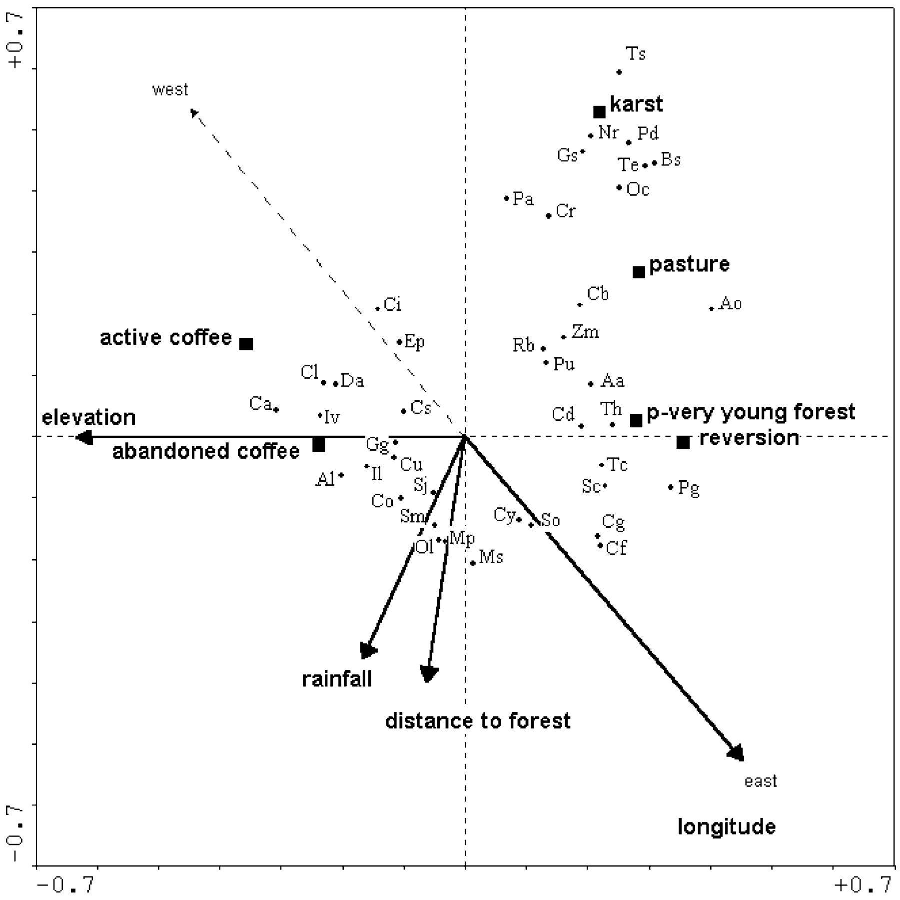

Fig. 2. Canonical correspondence analysis ordination diagram showing relationship among species with the forward selected geophysical and land use variables. Dashed line was added to highlight west to east longitudinal gradient. The centroids of categorical variables are indicated by solid squares. Variables preceded by the letter "p" indicated land use types determined in the 1980 forest inventory. Only species with a fit of 2% or larger are included in the diagram: ***A**lchornea **l**atifolia*, ***A**rdisia **o**bovata*, ***A**rtocarpus **a**ltilis*, ***B**ursera **s**imaruba*, ***C**alophyllum **b**rasiliense*, ***C**asearia **a**rborea*, *C. **d**ecandra*, *C. **g**uianensis*, *C. **s**ylvestris*, ***C**ecropia **s**hreberiana*, ***C**itharexylum **f**ruticosum*, ***C**itrus **s**inensis*, ***C**lusia **r**osea*, ***C**offea **a**rabica*, ***C**ordia **a**lliodora*, *C. **s**ulcata*, ***D**endropanax **a**rboreus*, ***E**rythrina **p**oeppigiana*, ***G**uarea **g**uidonia*, ***G**uettarda **s**cabra*, ***I**nga **l**aurina*, ***I**nga **v**era*, ***M**iconia **p**rasina*, ***M**yrcia **s**plendens*, ***N**eolaugenia **r**esinosa*, ***O**cotea **c**oriacea*, ***O**. **l**eucoxylon*, ***P**ersea **a**mericana*, ***P**etitia **d**omingensis*, ***P**iper **a**duncum*, ***P**sidium **g**uajava*, ***R**oystonea **b**orinquena*, ***S**chefflera **m**orototoni*, ***S**pathodea **c**ampanulata*, ***S**pondias **m**ombin*, ***S**yzygium **j**ambos*, ***T**abebuia **h**eterophylla*, ***T**erminalia **c**atapa*, ***T**etrazygia **e**laeagnoides*, ***T**houinia **s**triata*, and ***Z**anthoxylon **m**artinicense*.

Table 2
Two-way indicator table showing the species indicator power for the site clustering hierarchy[a]

Species	Ind val	Cluster (no. of plots)										
		1 (5)	2 (6)	3 (15)	4 (8)	5 (33)	6 (58)	7 (13)	8 (3)	9 (8)	10 (2)	11 (3)
A. inermis	57	232/5	52/3	136/12	48/3	63/11	342/33	12/3	4/1	6/2		
No indicator species												
T. heterophylla	67	14/2	256/6	50/4	47/5	68/10	8/2			29/4	3/1	4/1
C. guianensis	61		17/1	367/13	32/3	45/7	72/8	26/2		1/1		
T. pallida	35			87/6			23/5			3/1		
Ocotea sintenisii	26		3/1	43/6		13/3	53/5					
No indicator species												
P. guajava	95	3/1	6/1	20/2	367/8	7/1	49/7	6/2				
Calophyllum brasilensis	26			8/2	40/3	35/1	12/3			12/1		
I. laurina	52	10/1		25/2		331/24	74/13				3/1	
S. jambos	44		17/3	17/3		413/17	48/9					
O. leucoxylon	40		5/2	9/3		230/19	54/10	16/1		3/1		
C. arborea	26					88/9	11/2					
I. vera	58	6/1	5/1	11/3		123/12	1201/50	4/1	11/1		3/1	
G. guidonia	54	36/3	6/1	35/4	15/1	114/14	1111/47	8/2		6/1		
C. arabica	51			1/1		54/10	685/34					
C. sylvestris	31	22/1	5/2	119/9	21/1	73/10	143/16	14/4				
S. campanulata	96		18/3	9/3	57/3	26/5	214/18	980/13		4/1		
T. elaeagnoides	95	23/1	41/2	14/2	6/1	9/1	15/3	2/1	165/3	13/2		
G. scabra	54		8/1	6/1		4/1			12/2	61/4		
O. coriacea	36			2/1		2/1	3/1		4/1	20/3		
P. domingensis	35		6/1			6/1	5/1	14/2	11/1	40/3		
C. rosea	87			24/1						126/7		
T. striata	75					9/1	2/1			111/6		
N. resinosa	62			2/1			17/1			91/5		
C. decandra	50			75/7	29/2	17/3	19/3			38/5		
A. obovata	34		13/2	1/1	33/1		3/1			31/3		
C. schreberiana	34		3/1	4/1		294/22	233/24	15/1	24/1	16/2	12/11	
C. arborea	98			5/1		38/5		14/2			11/2	
Byrsonima spicata	47					29/7					6/1	
A. latifolia	40					74/11	16/5	3/1			8/1	
T. catapa	40	8/1		3/1		1/1	14/2			6/1	6/1	
S. morototoni	37			16/1		98/12	78/8	6/1			12/1	
A. altilis	34					28/1	68/5	3/1	40/1	6/1	21/1	
P. americana	30			3/1			11/3			13/1	4/1	
C. umbrosa	90		5/1	13/2	2/1	110/13	59/11	23/2			12/1	238/3
Myrsine coriacea	63		3/1			37/4	4/2					16/2
B. simaruba	25		49/2				9/2			43/3		36/1

[a] The gray shading indicates the level or cluster at which the indicator value for a species was maximum. Species in bold had significant indicator values at $P < 0.05$. Only species with indicator values ≥25% are included. In the columns for each species, the first number indicates the sum of importance values and the second number indicates the number of plots where the species is present within a cluster.

Fig. 3). These clusters are quite variable internally in terms of their environmental and land use history conditions. The following are the main patterns suggested mostly by the land use conditions in 1980 and the indicator species.

Sites of clusters 1 and 2, identified mostly as reversions from pastures by the surveyors, were differentiated by *Andira inermis* and *Tabebuia heterophylla*, respectively. Most of the plots in these two clusters had basal areas <15 $m^2\ ha^{-1}$. Sites of cluster 3

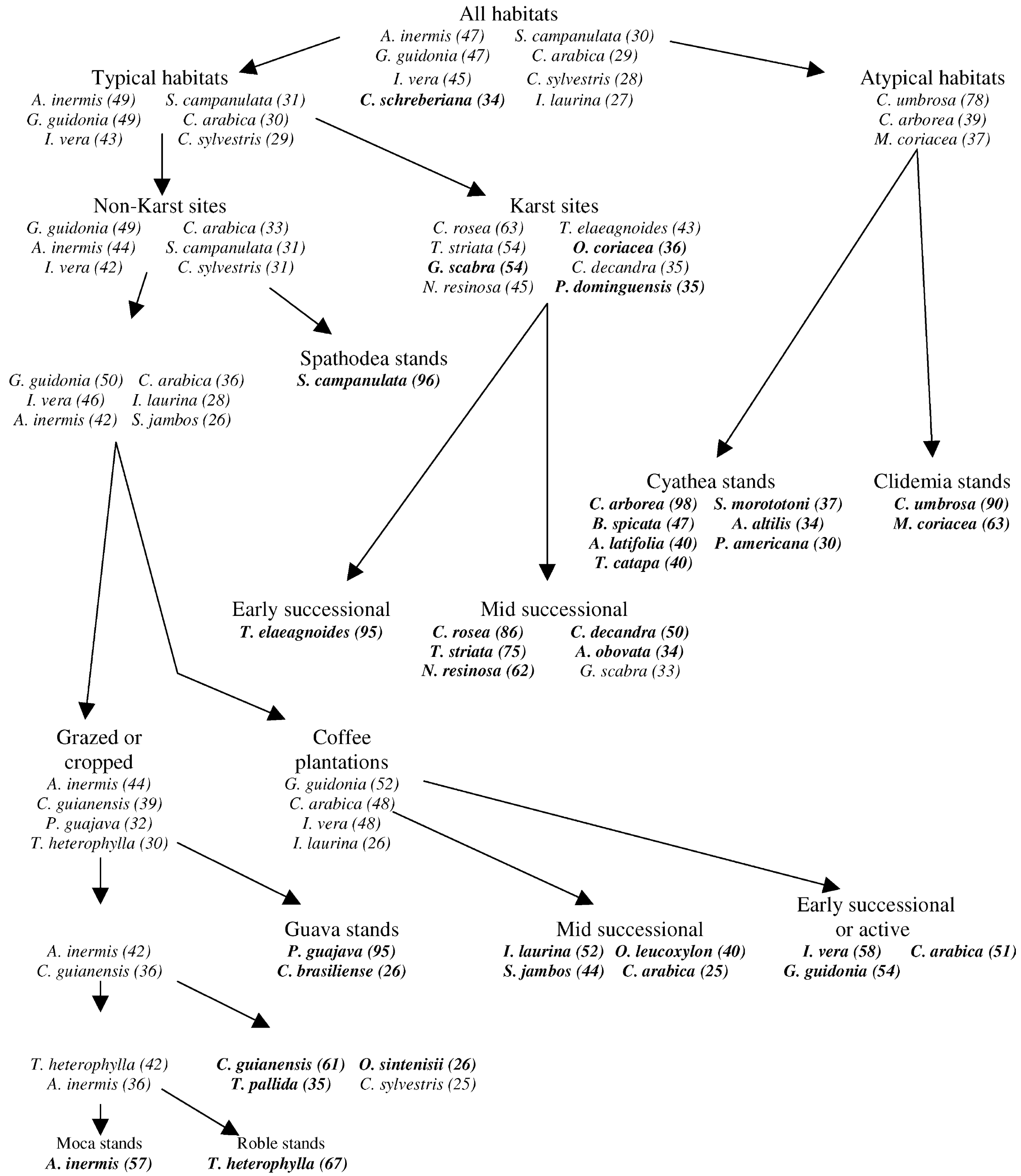

Fig. 3. Site clusters obtained with the UPGMA method, but with the associated indicator species and indicator values in parentheses. Only species with an indicator value ≥25% are included for each site cluster. Maximum indicator values for a given level are indicated in bold.

were identified mostly as mid-secondary forests while sites of cluster 4 were mostly early-secondary forests. Cluster 3 was characterized by two fairly shade tolerant shrubs or midsized trees, *Casearia guianensis* and *Trichilia pallida*, and a mean basal area of 15 $m^2\,ha^{-1}$. Cluster 4 was characterized by the shade intolerant guava (*Psidium guajava*) and had a mean basal area of 8.2 $m^2\,ha^{-1}$. Clusters 5 and 6 contain the largest number of samples (21 and 38%, respectively). Most of these sites corresponded to coffee plantations either active or at some stage of abandonment. Cluster 5 had a mean basal area of 21.1 $m^2\,ha^{-1}$, while cluster 6 had a mean basal area of 16.9 $m^2\,ha^{-1}$. These differences in basal area suggest that sites belonging to cluster 5 were at a more advanced stage of secondary succession than sites of cluster 6. Cluster 6 included the only active coffee sites sampled (four sites). Cluster 5 was characterized by the commonly planted coffee shade tree *Inga laurina*, and the shade tolerants *Sysygium jambos* and *Ocotea leucoxylon*. The shade trees *Inga vera* and *Guarea guidonia*, and coffee characterized cluster 6. Nearly all sites of cluster 7 were identified as improved pastures in 1980 and as reversions in 1990. The light-demanding exotic, *Spathodea campanulata* characterized this cluster. Even though these sites were at an early stage of succession, the mean basal area (16.8 $m^2\,ha^{-1}$) was nearly the same as that of cluster 6 and included the site with the largest basal area of all plots (47.1 $m^2\,ha^{-1}$). Nearly all sites of clusters 8 and 9 occurred on karst substrate. Sites of cluster 8, characterized by *Tetrazigia elaeagnoides*, are very early successional stands (mean $BA = 3.4\,m^2\,ha^{-1}$), while most sites of cluster 9 were in a more advanced stage of succession (mean $BA = 15.4\,m^2\,ha^{-1}$). Clusters 10 and 11 contain the fewest number of sites (two and three, respectively) and their physico-historical conditions cannot be distinguished. Yet, they are floristically very distinct, characterized by the early successional species *Cyathea arborea* (cluster 10), and *Clidemia umbrosa* (cluster 11).

3.2. Relationships between forest landscape variables and species diversity

All the regression models that estimated species diversity (Table 3) selected basal area first in forward variable selection, which showed positive relationships with species diversity measures. Current land use also appeared in all the final models. Current land uses of pasture, reversion from pasture and active coffee, significantly decreased both total and native species richness and Shannon's diversity indices relative to secondary forest and abandoned coffee. In

Table 3
Variables significant to measures of species diversity in multiple regressions derived by forward variable selection[a]

Species diversity model[b]	N[c,d]	R^2	Extra sum of squares Pr > F for DIST3801[e]
$(\text{RICHNESS})^{-2}$ (natives + non-natives) = $f\{\text{BA}^{***}, \text{GUSE}^{***}, \text{GEOLOGY2}^{***}, \text{DIST3801}^{*}\}$	158	0.64	<0.05
$(\text{SHANNONS})^{1.5}$ (natives + non-natives) = $f\{\text{BA}^{***}, \text{GUSE}^{***}, \text{GEOLOGY}^{***}\}$	153	0.51	
$(\text{RICHNESS})^{-2}$ (natives only) = $f\{\text{BA}^{***}, \text{GUSE}^{***}, \text{GEOLOGY}^{**}, \text{DIST3801}^{*}\}$	158	0.61	<0.05
SHANNONS (natives only) = $f\{\text{BA}^{***}, \text{GUSE}^{**}, \text{GEOLOGY2}^{*}\}$	141	0.40	

[a] All models are highly significant ($P < 0.0001$), based on F-tests for overall significances of the regressions. Also shown are significance levels resulting from extra sum of squares F-tests of the variable DIST3801 when it was significant, which tests the importance of the landscape structure of forest patch variable to species diversity. After accounting for stand and environmental variables, distance to forest patches 3801 ha or larger was the only significant landscape variable, and only for regressions on species richness.

[b] Asterisks indicate probabilities of erroneously rejecting the null hypothesis that coefficient estimates are zero, based on a two-sided t-distribution.

[c] Plots with Shannon's diversity index of zero were eliminated from regressions as they qualified as outliers.

[d] Excludes plots of rare land use (GUSE or PGUSE), including *scrub*, *urban/industrial*, *roads*, or *other*.

[e] Pr > F. Probability of erroneously rejecting the null hypothesis that the coefficient estimates for the variable DIST3801 are zero, after accounting for the other variables.

* $P \leq 0.05$.

** $P \leq 0.005$.

*** $P \leq 0.0005$.

addition, plots on karst substrate showed slightly greater species richness and Shannon's diversity than other substrate types. Although previous land use (PUSE) of improved pasture significantly decreased species richness and diversity, this variable became insignificant when the regressions included current land use (GUSE).

After accounting for the most important variables mentioned above basal area, land use and substrate, distance to the largest 0.1% of forest patches (≥3801 ha) was a significant factor explaining variation in total and native species richness. However, at an average loss of 0.28 ± 0.26 native species and 0.25 ± 0.22 total species per 10 km increase in distance from the largest patches, the effect was small. Basal area, land use and substrate related significantly to Shannon's diversity, but no forest landscape variables explained significant variation in the diversity measure. None of the other forest landscape variables that we tested were significant in the diversity regressions.

4. Discussion

Results both from ordination and species diversity analysis highlighted that land use history and substrate are important determinants of both recovering forest communities and their diversity. We discuss each in turn below.

4.1. Relationship between explanatory variables and species composition

The ordination diagram (Fig. 2) summarizes the geographical distribution of tree species composition in the forests of Puerto Rico. Sites currently or formerly under coffee cultivation are found mostly at the highest elevations. Active coffee sites can be distinguished by their higher abundances of shade tree species like *I. vera* and *Erythrina poeppigiana*, while abandoned coffee sites tend to include vertebrate dispersed species like *Alchornea latifolia*, *Casearia arborea*, and *Cecropia schreberiana*.

Contrasting land use types occur at the lower end of the elevation gradient, as is the case for pastures and very young secondary forests. Some grazed sites were sampled in 1990 because they were sufficiently stocked with trees. The surveyors identified very young secondary forests sampled in 1990 as reversions from previous agriculture. Such sites tend to be dominated by light-demanding species like *S. campanulata*, *P. guajava*, and *T. heterophylla*. Rainfall added significantly to the explained variation. The strong and opposing effect of karst substrate in the ordination magnified this contribution by rainfall.

Substrate type also provided a clear separation of species. Tree species like *Thouinia striata*, *O. coriacea*, and *T. elaeagnoides* were nearly restricted to karst sites. Plant communities over karst have long been described as having unique species composition resulting from the contrasting soil moisture gradients within limestone hills and the clear differences between soil chemical conditions on karst and other substrate types within similar climate conditions (Gleason and Cook, 1927; Chinea, 1980). Longitude (actually, the cube of longitude, indicating that the relationship is not linear) was ranked fourth in amount of variance explained. This west to east geographic gradient may result from at least three sources of variability in species composition. Karst areas are nearly restricted to the western two-thirds of the northern half of the island. In addition, coffee plantations, with fairly distinct species composition as well, are mostly restricted to the western half of the Central Mountain Range. Moreover, the disturbance produced by Hurricane Hugo in September 1989 was nearly restricted to the northeastern section of the island. Although this hurricane did not alter species composition to a large extent, it reduced considerably the density of some species less resistant to wind damage, like *C. schreberiana* (Francis and Gillespie, 1993).

A landscape structure variable, distance to forest patches at least 362 ha in size, was negatively correlated with the second axis. This result may be an artifact of karst areas having significantly shorter distances from patches at least 362 ha (Table 4). A more clear effect of this variable on species composition may have been missed because the ordination only included the most frequent species. Older forests are more likely to affect species composition by providing propagules of infrequent or rare species.

Geophysical and land use history variables contributed almost equally to the variability in species composition in these forests. Roche et al. (1998) obtained similar results in a French rural landscape. Also,

Table 4

Spatial attributes (mean and 95% confidence intervals) of forest inventory plots by current ground use, Holdridge life zone and geology

	N[a]	Species richness (natives + non-natives)	Species richness (natives)	Shannon's diversity index (natives + non-natives)	Shannon's diversity index (natives)	Basal area (m^2 ha^{-1})	Elevation (m)	Distance to nearest patch[b] ≥3801 ha (km)	Distance to nearest patch[b] ≥362 ha (km)	Distance to nearest patch[b] ≥0.45 ha (km)
Ground use										
Abandoned coffee	33	11.6 ± 1.4	9.2 ± 1.2	2 ± 0.14	1.8 ± 0.15	21.1 ± 2.1	456 ± 89	3.27 ± 1.25	2.45 ± 0.92	0.44 ± 0.2
Active coffee	20	5.7 ± 1.5	3.8 ± 1.1	1.39 ± 0.21	0.98 ± 0.27	10.1 ± 2.2	499 ± 115	2.17 ± 1.78	1.12 ± 0.47	0.5 ± 0.23
Idle farmland	4	7.8 ± 4.2	6 ± 2.6	1.87 ± 0.55	1.65 ± 0.38	7.7 ± 3.1	182 ± 162	3.72 ± 6.77	3.46 ± 6.95	0.32 ± 0.7
Pasture	7	6.3 ± 2	4.9 ± 1.4	1.52 ± 0.38	1.27 ± 0.29	7.9 ± 7.2	185 ± 47	4.95 ± 4.23	3.56 ± 4.57	0.04 ± 0.05
Reversion	36	5.5 ± 1.4	4.1 ± 1.4	1.09 ± 0.25	0.85 ± 0.27	8.3 ± 3.1	272 ± 59	6.65 ± 2.36	1.74 ± 0.81	0.22 ± 0.11
Secondary forest	45	14.3 ± 1.5	12.1 ± 1.6	2.22 ± 0.14	2.02 ± 0.17	22.6 ± 2.4	348 ± 70	2.79 ± 1.12	2.03 ± 0.84	0.24 ± 0.13
Young secondary forest	13	11.8 ± 2.3	10 ± 2.6	1.99 ± 0.24	1.84 ± 0.33	14.6 ± 3.8	318 ± 128	4.1 ± 2.29	2.69 ± 1.57	0.38 ± 0.34
Holdridge life zone										
Moist subtropical forest	78	9.7 ± 1.3	7.7 ± 1.3	1.7 ± 0.16	1.47 ± 0.18	13.4 ± 2.2	243 ± 34	4.97 ± 1.4	1.76 ± 0.61	0.12 ± 0.05
Wet subtropical forest	81	10.3 ± 1.2	8.4 ± 1.2	1.82 ± 0.14	1.59 ± 0.16	18 ± 2	467 ± 54	2.85 ± 0.61	2.39 ± 0.57	0.5 ± 0.12
Geology										
Alluvial	2	10 ± 88.9	6 ± 76.2	1.14 ± 4.99	1.01 ± 12.81	28.6 ± 107.5	112 ± 488	2.67 ± 33.93	2.67 ± 33.93	0.00
Extrusive volcanic	103	9.3 ± 1	7.4 ± 0.9	1.68 ± 0.14	1.45 ± 0.15	16.5 ± 1.9	404 ± 50	5.03 ± 1.06	2.56 ± 0.55	0.41 ± 0.1
Intrusive volcanic	25	11.4 ± 2.2	9.5 ± 2.2	1.99 ± 0.23	1.78 ± 0.25	16.4 ± 3.7	326 ± 80	2.69 ± 1.27	2.22 ± 1.14	0.26 ± 0.18
Karst	29	11.1 ± 2.5	9.2 ± 2.5	1.89 ± 0.27	1.64 ± 0.31	11.7 ± 3.4	232 ± 35	0.97 ± 0.65	0.23 ± 0.17	0.04 ± 0.03

[a] Number of observations in each category.

[b] Largest 0.1% of patches ≥3801 ha; largest 0.5% of patches ≥362 ha; largest 75% of patches ≥0.45 ha.

several North American investigators have stressed the importance of land use history factors in determining the species composition at local to regional scales (e.g., Fuller et al., 1998). These factors may even obscure or modify the impact of geophysical variables on species composition (Fuller et al., 1998). Comparisons of forest communities recovering from several human activities in Puerto Rico (e.g., Zimmerman et al., 1995; Chinea, 2002) have also demonstrated the importance of land use history variables on species composition at local scales. Our results provide further evidence of the importance of land use history on community structure at a larger spatial extent.

4.2. Relationship between explanatory variables and species diversity

Our results, that stand structure and land use history are important predictors of secondary tropical forest species diversity, agree with other work in Puerto Rican secondary forests. Aide et al. (1996) found a positive relationship between stand age and species richness in northeast Puerto Rico, and these attributes were also positively related to basal area.

In contrast to our results, distance to forest was not significant in the analysis of species diversity in Aide et al. (1996). The greatest forest distances in that study were mostly less than 50 m and did not exceed 450 m. These distances are similar to the average distances of plots to forest patches of at least 0.45 ha of 100–500 m (Table 4), which was not significant in multiple regressions. In a landscape-scale study, Chinea (2002) found that distance to older forest was an important predictor of species richness and diversity in eastern Puerto Rico.

Nevertheless, the effect on species diversity of distance to large forest patches appeared small. This result may have occurred because the inventory included only trees >2.5 cm dbh, thereby excluding potential variations in understory herbaceous or woody seedling diversity that might be related to distance from older forest. In addition, the forests present in 1978 would have included much secondary forest that was <30 year old, because forest cover on the island increased substantially between about 1950 and 1980. Landscape structure variables that better isolate potential influence of forest patches older than that, or perhaps remnant old-growth forest patches, might exhibit more influence on species diversity.

The fact that distance to the largest forest patches present in 1978 was not significant to Shannon's diversity but was significant to species richness could indicate that this landscape variable becomes important in explaining the presence of species that are rare relative to other species in a given plot.

Forest patch area in 1978 may not have been significant in the models of species diversity because the map from 1978 categorized 55% of them as agriculture or pasture.

4.3. Conservation value of these secondary forests

Restoration ecologists have established that plantations can catalyze forest succession on degraded lands through creating more favorable microclimatic conditions, stimulating surface soil accumulation of organic carbon and attracting seed-dispersing wildlife (Parrotta et al., 1997). Plantations that create deep shade or physical barriers to seed establishment may not have these effects (Parrotta, 1995). However, the secondary forests developing on abandoned pastures in Puerto Rico may have beneficial effects on forest recovery. Indeed, Aide et al. (1996) concluded that, as compared with abandoned coffee plantations, the higher species diversity of *S. campanulata* stands developing on abandoned pastures could be due to *S. campanulata*'s deciduousness during the dry season, which permits more light in the understory and potentially more opportunities for colonization. Our data indicates that stands in which *S. campanulata* had importance values between 10 and 50% had an average of 7.1 native species (±4.0 S.D., $n = 16$) and an average importance value for native species of 59.4%. However, the average species richness for all stands was just slightly higher with 8.1 species (±5.3 S.D., $n = 165$); the average importance value of native species was 73.3%. Although this comparison must be more restricted to particular habitat conditions, it suggests that some common exotic species may be tolerated by or even benefit natives.

5. Conclusions

This study demonstrated for the first time that even at a landscape scale that encompassed differing geologic substrates and a range of climatic conditions, land use history had a similar impact on the species composition of Puerto Rico's secondary forests in 1990. Light-demanding, wind-dispersed early successional species (e.g., *S. campanulata*) colonize pastures and reversions from pasture, while vertebrate dispersed species characterize abandoned coffee plantations.

At the same time, environmental factors strongly control patterns of land use history, so that land use and physical variables are generally confounded when evaluating the relationships between these variables and recovering forest community composition (Foster, 1992; Ohmann and Spies, 1998; Pan et al., 1999; Crow et al., 1999). However, our results confirm those of Foster (1992) and Ohmann and Spies (1998), that biophysical-vegetation community relationships are still visible in recovering forests. The unique aspects of recovering forests in Puerto Rico's karst region demonstrate this pattern, as do the differences between early successional communities and high vs. low elevations.

At this stage in the development of Puerto Rico's forest landscape and at this scale of investigation, we did not see a large influence of forest landscape structure on species diversity or composition. Forest landscape structure probably indirectly influences species composition through influencing rates of forest recovery, but this influence is likely difficult to separate from the tendency of humans to abandon sites earlier that are in the same locations where potential returns from land are lower and more remnant forest remains. Still, the significance of landscape structure in 1978 to species diversity warrants further investigation that incorporates information on understory diversity, or diversity in relation to locations of very old or remnant old-growth forest.

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