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Landscape effects on structure and species composition of tabonuco forests in Puerto Rico: Implications for conservation

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ABSTRACT

We studied the structure and species composition of nine residual forest stands of *Dacryodes excelsa* (tabonuco), a dominant vegetation type in the moist and wet lower montane forests of the Caribbean. The stands were scattered over three different landscapes with different degrees of anthropogenic disturbance: forested, shade coffee, and tobacco. We compared our results with data from undisturbed stands inside a protected and forested landscape to see how the type of landscape that surrounded them affected the structure and species composition of the residual forest stands. In the process we sought conservation lessons that would help restore degraded tabonuco forests to original conditions. Tree density, basal area, and species density all increased with elevation. We found 98 tree species, including 50 of the 83 species that we identified as belonging to undisturbed tabonuco forests (including 13 of 18 endemic tree species), 41 tree species not reported for undisturbed tabonuco forests, eight primary forest species, and six introduced species. When ordered by species Importance Value by site, the stands in nine sites separated into three general groups corresponding to landscape type: (1) Heavily used for tobacco production. (2) Shade coffee, and (3) Forested. The importance of introduced species increased, and the abundance of tabonuco forest indicator species and endemic species decreased with increased anthropogenic disturbances. When restoring tabonuco forests, it is necessary to understand the landscape forces that influence the species composition of these forests. It appears that particular species combinations are natural outcomes of the level of anthropogenic activity in the landscape and reversing those tendencies might be impractical or too costly.

1. Introduction

Successional studies have shown that the structure and species composition of resulting mature stands vary with the landscape context in which succession takes place. For stands of tabonuco (*Dacryodes excelsa*), a major forest type in Puerto Rico and the Caribbean (Beard, 1949; Wadsworth, 1950), the outcome of succession after natural disturbances such as hurricanes is the maintenance of the same structure and native species composition as before the disturbance event. Heartsill Scalley et al. (2010) found that after the passage of a hurricane about 20 years of succession are required for the re-establishment of the pre-hurricane species assemblage of tabonuco forests. This generalization holds true if the stand is in a forested landscape matrix. Usually this cyclic succession in the Caribbean occurs when anthropogenic disturbances are insignificant. However, if the succession begins on an abandoned pasture on a deforested landscape, the outcome of the succession is different from that of the cyclic succession. In these landscapes forest successions develop structurally as expected but they differ in two important ways (Aide et al., 1995; Lugo and Helmer, 2004; Lugo and Brandeis, 2005; Zimmerman et al., 2007). First, they exhibit different species composition, and second, the type of agricultural activity prior to abandonment influences species composition and speed of recovery (Molina Colón and Lugo, 2006). This successional phenomenon occurs throughout the world as documented in Cramer and Hobbs (2007) and the new forests that emerge after abandonment of agricultural lands have been termed novel forests by Hobbs et al. (2006).

A third successional scenario that we will focus on, however, is that of remnant stands of native forests scattered on a variety of landscape conditions that range from forested landscapes to agricultural landscapes such as those of shade coffee and tobacco. These remnant forest fragments are important to conservation because they represent forested islands where the natural biota might gain refuge during the agricultural activity and from which propagules might disseminate to power forest regeneration after the abandonment of agriculture. The question that we pose is whether the fragment itself undergoes changes in structure and

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species composition depending upon the type of landscape under which it stands.

The importance of the type of landscape in the regulation of species composition of affected forests is associated with its level of degradation. Landscape degradation is a complex phenomenon that was discussed in detail by Barrow (1991). In this study our focus on landscape degradation is associated with the combined effects of deforestation and conversion to agricultural use, specifically coffee and tobacco production. Deforestation and agricultural use not only remove biomass and forest cover from affected sites, but they also have long-term effects on site fertility due to soil erosion and depletion of nutrients (Nye and Greenland, 1960). The presence of tabonuco forest residual stands in a variety of landscape conditions in Puerto Rico gave us an opportunity to explore any effects that landscapes might have on the structure and species composition of these forest stands.

Abundant straight-bole trees and root-grafted tree unions characterize tabonuco forests (Basnet et al., 1993). Root grafting, i.e., the interconnection of trees by lateral roots (Photo) provides resistance to hurricane winds to groups of tabonuco trees growing on ridges. Also, root grafting allows sharing of resources among trees, thus contributing to group resilience after disturbances. Tabonuco forests occur on subtropical moist to subtropical wet life zones (*sensu* Holdridge, 1967) and are valued for their timber qualities, complex structural and biotic development, and other useful products such as resins (Lugo and Wadsworth, 1990). The original distribution of this forest type in Puerto Rico ranged across most of the central mountains and lowlands (Little and Wadsworth, 1964; Álvarez Ruiz, 2002; Fig. 1), but a large proportion of the region was fragmented by extensive agricultural activity that eventually deforested over 95% of the island (Birdsey and Weaver, 1982). Deforested lands remained under agricultural use for over a century after which progressive and extensive land abandonment that began in the 1940s led to the reestablishment of forests to over 50% of the landscape (Brandeis et al., 2007).

Our objective was to study tabonuco forest stands under three landscape conditions (from undisturbed to degraded): forested, coffee, and tobacco in order to gain insight into the feasibility of restoring tabonuco forest fragments to their original condition. We were also interested in exploring the species composition threshold at which tabonuco forests shifted from stands of native species to stands with numerous introduced species. Our expectation was that the species composition and structural characteristics of tabonuco stands would change in a direction determined by the type of human activity that prevailed on the landscape, and that it would be difficult to restore stands to their original native species composition.

Photo. Residual stand of tabonuco (*Dacryodes excelsa*) forest where the lateral roots that connect trees into tree unions are exposed due to past erosion (foreground). On the back and to the right, a stump is kept alive by a lateral root from the tree on the upper right corner of the photo (photo by A.E. Lugo).

2. Methods

Locating tabonuco stands was made difficult by the magnitude of past deforestation and agricultural activities such as shade coffee and tobacco. We systematically traversed a 95-km corridor through Puerto Rico between Adjuntas and Luquillo along the known range of the tabonuco forest in search of remnant tabonuco stands. The fieldwork was conducted between June 1994 and June 1995. A GPS unit was used to locate the position of remnant stands. We located and studied nine tabonuco stands representing a range of elevations, past land uses, and landscape conditions (Fig. 1, Table 1). All our study sites had experienced some degree of human intervention such as cultivation of coffee and tobacco or selective stand thinning. For information on undisturbed sites, we depended on previously published data.

At each site we randomly established four 0.1 ha plots, or 36 plots for the study. At each plot all trees with diameter at breast height (dbh) at 1.37 m were identified, and their dbh and height measured. We constructed diameter distribution histograms for each plot from which we inferred past selective cutting by the presence of gaps in the distribution of size classes. All plots, except those at Bisley Biodiversity Plot (Bisley BP) and El Verde 3, were circular plots with a radius of 17.85 m. At Bisley BP and El Verde 3, plots were rectangular. From these data we estimated stand structure (density and basal area), species richness or species density (number of species per sampled area), species Importance Value (IV) based on relative density and relative basal area, and tabonuco tree diameter distribution. We also checked for the presence of tabonuco tree unions (root grafts) by poking the soil between individual trees and tracing the direction and destination of their lateral roots. When a stand contained trees with and without root grafting, we measured them separately to characterize any differences between trees within or without a union. Species were classified as native or introduced using Little and Wadsworth (1964), Little et al. (1974), and Francis and Liogier (1991).

From the information gathered, we were able to assess the degree of maturity and species composition of the vegetation by comparing results with those of the best-conserved tabonuco forests in the Luquillo Experimental Forest. For this comparison, we used the list of species typical of tabonuco forests in the Luquillo Mountains and Central Cordillera of Puerto Rico (Little and Wadsworth, 1964; Gleason and Cook, 1926). From Smith (1970), Weaver (1994), and long-term records for the El Verde 3 plot (Briscoe and Wadsworth, 1970) we developed an indicator species list for undisturbed tabonuco stands with the species ranked-ordered by relative density. This ranking was used as the basis to compare similar species lists for our remaining eight study sites. The area sampled by Smith (1970), Weaver (1994), and Briscoe and Wadsworth (1970) was 1.6, 0.4, and 0.7 ha, respectively. We also used other information in Briscoe and Wadsworth (1970) and Smith (1970) as additional reference for the species expected to occur in undisturbed tabonuco stands.

The history of land use on each of the study sites was reconstructed using all or a combination of the following materials, depending on availability. We used aerial photography (coverage from 1936 to the present), historic documents and maps, interviews with land owners and older people in the immediate communities, literature accounts of land use and agricultural activity, examination of historical records, and/or discussions with experienced professionals. The professionals interviewed were: F.H. Wadsworth, USDA Forest Service; C. Buitrago, University of Puerto

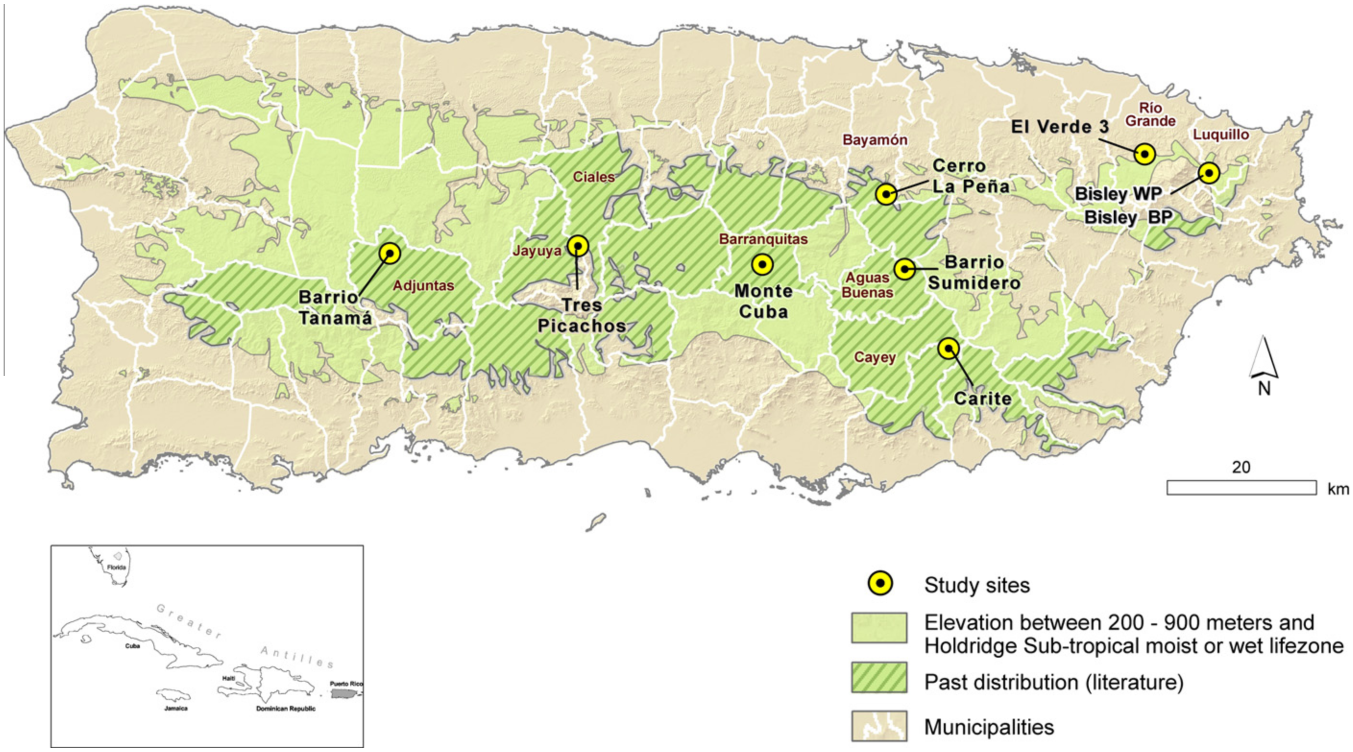

Fig. 1. Historical and present distribution of tabonuco (*Dacryodes excelsa*) forests and the location of study sites. The historical data cover from 1770 to 2001.

Table 1
Study sites and their location, elevation, landscape setting, and tenure. The sites in the municipalities of Río Grande and Luquillo are within the Luquillo Experimental Forest. Within Bisley, WP is a watershed plot and BP is a biodiversity plot.

Site	Municipality	Elevation (m)	Landscape setting	Tenure
El Verde 3	Río Grande	510	Forested	Public
Bisley WP	Luquillo	450	Forested	Public
Bisley BP	Luquillo	405	Forested	Public
Carite	Cayey	710	Forested	Public
Tres Picachos*	Jayuya	951	Forested	Private
Monte Cuba	Barranquitas	670	Fragmented coffee	Private
Barrio Tanamá	Adjuntas	637	Fragmented coffee	Private
Cerro La Peña	Bayamón	568	Fragmented tobacco	Private
Barrio Sumidero	Aguas Buenas	104	Fragmented tobacco	Private

* This site was recently protected under the public domain.

Rico Río Piedras; and M. Valdés, University of Puerto Rico Mayagüez. The interviews with landowners and workers (70–85 years old) that had worked farms in the 1950s, and community members were based on a questionnaire developed in collaboration with the Center for Applied Social Sciences Research, University of Puerto Rico at Mayagüez. From the interviews, we also tried to reconstruct the historic uses and species composition of tabonuco stands as well as farming activities and other relevant information about land use and land cover. Álvarez Ruiz (2002) contains details on land use and land cover for each site.

We used the Statistics 7 program of Analytical Software Publishers in Tallahassee, FL for the statistical analyses. All data were tested for normality and then analyzed with One-way Analysis of Variance (ANOVA), linear regression, or chi square tests. Significance was set at $p \leqslant .05$. When ANOVA results were significant, a Tukey multiple comparison test was performed using $p \leqslant .05$ for significance. A two-tailed Kolmogorov–Smirnov test was performed on frequency distribution of tree relative density values. Species classes were established as follows: dominant (>10%), common (9.9–1%), and rare (<1%). A Canonical Correspondence Analysis (CCA) ordination for species IV, elevation, and precipitation was conducted with CANOCO Ordination Program version 4 (Ter Braak and Smilauer, 1998).

3. Results

Tree density, basal area, and species density all increased with elevation for stand data (Table 2). The increase was not significant for tree species density ($r^2 = 0.3$, $p = .16$) but was significant for tree density ($r^2 = 0.46$, $p = .04$) and basal area ($r^2 = 0.5$, $p = .03$). However, when all 36 individual tree plots were used in the species density vs. elevation regression, the relationship was significant at $p < .05$ ($r^2 = 0.5$). For tabonuco trees, the differences in Table 2 had no relationship to elevation. Nevertheless, stands with tree unions had higher tabonuco tree densities than those without tree unions (Table 2). The diameter class distributions varied among stands (Table 3). Most had missing large trees except Tres Picachos. Bisley sites had truncated distributions. Cerro La Peña and Carite had L-shaped distributions, but lacking large trees. Barrio Sumidero and Tres Picachos had gaps in their diameter distributions. Monte Cuba, Barrio Tanamá, and El Verde 3 had bell-shaped distributions but El Verde 3 had larger size classes.

Table 2
Mean species density, mean tree density, and basal area of tabonuco (*Dacryodes excelsa*) stands, and mean tree diameter at breast height (dbh) and mean tree density of tabonuco trees in nine study stands. Standard deviation is in parenthesis and means with the same letter are not different at $p \leqslant .05$. Sites with the largest mean tabonuco tree density had tree unions. Data are for trees with dbh $\geqslant$ 9 cm and mean values are rounded. Site characteristics are given in Table 1. Within Bisley, WP is a watershed plot and BP is a biodiversity plot.

Site	Stand			Tabonuco	
	Species per 0.1 ha	Density (trees/ha)	Basal Area (m^2/ha)	dbh (cm)	Density (trees/0.1 ha)
El Verde 3	14^{c} (3)	632^{d} (65)	33.7	31.6^{b} (17.5)	17.0^{a} (4.0)
Bisley WP	22^{b} (3)	752^{c} (94)	42.3	35.9^{a} (23.4)	13.0^{a} (6.0)
Bisley BP	9^{d} (3)	267^{e} (46)	8.7	45.6^{a} (21.0)	3.7^{b} (4.3)
Carite	18^{b} (3)	1200^{a} (320)	33.6	18.1^{c} (7.5)	13.2^{b} (9.5)
Tres Picachos	23^{a} (6)	1057^{b} (148)	52.5	41.2^{a} (24.7)	2.7^{b} (2.9)
Monte Cuba	13^{c} (1)	847^{c} (53)	76.1	29.8^{b} (12.1)	23.2^{a} (7.9)
Barrio Tanamá	9^{d} (4)	577^{d} (88)	36.2	30.2^{b} (12.0)	29.2^{a} (19.0)
Cerro La Peña	11^{c} (1)	1082^{b} (366)	21.5	17.3^{c} (6.2)	14.7^{b} (26.9)
Barrio Sumidero	7^{d} (3)	305^{e} (156)	17.6	41.8^{a} (14.9)	2.5^{b} (2.1)

Table 3
Stem diameter size distribution of tabonuco (*Dacryodes excelsa*) trees in different locations in Puerto Rico. Site information is given in Table 1. The number in parenthesis is the total number of tabonuco stems per 0.4 ha. The Luquillo Experimental Forest is LEF. El Verde 3 is EV3, BWP is Bisley Watershed Plot, and BBP is Bisley Biodiversity Plot. Diameters were measured at breast height (1.37 m).

	Adjuntas (116)	Jayuya (29)	Barranquitas (92)	Bayamón (49)	Aguas Buenas (10)	Cayey (52)	LEF EV3 (67)	LEF BWP (52)	LEF BBP (15)
Diameter class (cm)	Percent of total stems								
9–16	8.6	10.3	15.2	53.1	10.0	51.9	16.4	25.0	13.3
16.1–24	25.9	3.4	20.7	26.5	10.0	30.8	28.4	15.4	6.7
24.1–32	30.2	13.8	21.7	18.4	0.0	11.5	13.4	11.5	6.7
32.1–40	13.8	13.8	25.0	2.0	50.0	3.8	17.9	3.8	6.7
40.1–48	12.9	24.1	9.8		10.0	1.9	10.4	13.5	20.0
48.1–56	4.3	6.9	4.3		20.0		1.5	13.5	6.7
56.1–64	4.3	3.4	3.3				1.5	7.7	20.0
64.1–72		3.4					9.0	1.9	6.7
72.1–80		6.9					1.5	3.8	13.3
80.1–88								0.0	
88.1–96		6.9						3.8	
96.1–104									
104.1–112		3.4							
112.1–120		3.4							

Of the 83 native tree species that we identified as belonging to undisturbed tabonuco forests (including 18 endemic tree species), we found 50 in our study sites (Table 4). We found 41 tree species not reported for undisturbed tabonuco forests and 92 native tree species, including 12 endemic species and eight primary forest species *sensu* Smith (1970). We also found six introduced species. The majority of the species (33–60%) were rare species and the least number of species were the dominant ones (2–16%). Common species ranged from 32% to 50% of the total count for each site. These ranges do not include Barrio Sumidero, which had 69% of its species in the common category and 19% in the rare category.

Most species were arranged along elevation and precipitation gradients (Fig. 2), except for 10 species that were outliers: *Byrsonima spicata* (BYRSPI), *Chionanthus domingensis* (CHIDOM), *Dipholis bellonis* (DIPBEL), *Drypetes alba* (DRYALB), *Matayba domingensis*∗ (MATDOM), *Miconia tetranda*∗(MICTET), *Symplocos martinencensis* (SYMMAR), *Syzygium jambos* (ZYZJAM), *Tabebuia heterophylla*∗ (TABHET), and *Tetrazygia urbanii* (TETURB) (asterisk means the species has been recorded in undisturbed tabonuco stands). The nine sites separated into three general groups when ordered by species Importance Value by site (Fig. 2) or by floristic composition and homogeneity of dominance by individual plot (data not shown). The groups were those in landscapes heavily used for tobacco production (Barrio Sumidero and Cerro La Peña), those in the coffee region (Monte Cuba, and Barrio Tanamá), and the forested sites in public lands (Tres Picachos, Carite, El Verde 3, Bisley BP, and Bisley WP).

4. Discussion

Most of the lands harboring tabonuco forests in Puerto Rico were deforested and converted to other uses, usually agriculture. Wadsworth (1950), Briscoe and Wadsworth (1970), and Weaver (1994) described the structure and species composition of undisturbed mature tabonuco stands in the Luquillo Mountains. All our study sites and all other remnant stands that we found are residual stands that somehow survived deforestation but did so in the context of landscapes with different intensities and kinds of human activities. Our results show that the study sites maintain levels of tree density, basal area, and species density that vary with gradients of precipitation and elevation (Fig. 2, Table 2), which suggest that the residual stands are responding as expected to environmental gradients. Stands also reflect past selective cutting (Table 3), which affects present basal area and tree density due to the selective removal of particular size classes. The diameter distribution pattern expected of mature and undisturbed tabonuco forests is the classic L-shape distribution (Briscoe and Wadsworth, 1970), but those in Table 3, even the L-shaped ones, show missing or a small range of diameter classes. All the distributions that we found reflect past tree cutting events.

Table 4
Species ranking by relative tree density in eight tabonuco (*Dacryodes excelsa*) stands throughout Puerto Rico. Data corresponds to trees ⩾9 cm diameter at breast height and a sampling of 0.4 ha per site. The species in column 1 are listed in their density rank order in three undisturbed tabonuco forests in the Luquillo Experimental Forest, including El Verde 3 (methods). Species with an asterisk (∗) are primary forest species (*sensu* Smith, 1970), those with double asterisk (∗∗) are introduced, and (E) means the species is endemic (*sensu* Little, 1970). Empty spaces means the species was not recorded. Species codes were used in Fig. 2. Table 1 contains information on sites, and Bisley WP and BP correspond to watershed and biodiversity plots, respectively.

Species	Species Code	Bisley, WP	Bisley, BP	Carite	Tres, Picachos	Monte, Cuba	Tanamá	Cerro, La Peña	Barrio, Sumidero
Dacryodes excelsa∗	DACEXC	17.28	13.15	11.04	2.6	29.56	50.65	14.48	8.26
Prestoea montana∗	PREMON	15.61	39.44	55.63	24.11	30.05	10.82	0.25	
Manilkara bidentata	MANBID	2.33	2.79						
Tetragastris balsamifera∗	TETBAL	0.66	1.2		8.04				1.65
Sloanea berteriana∗	SLOBER	21.59	15.14	0.83	0.95	0.36	1.3		
Cecropia schreberiana	CECSCH	1.66	0.4	1.67	2.13	2.8			
Drypetes glauca	DRYGLA		0.4	0.42	0.71	1.22	0.43		
Andira inermis	ANDINE	0.33	0.8						
Micropholis guyanensis	MICGUY			2.08	7.57		6.06		
Guarea guidonia	GUAGUI		4.78		0.47	1.22			
Miconia tetrandra	MICTET	0.66		3.33	0.47		1.3	7.39	
Ormosia krugii∗	ORMKRU	1.33		0.83	4.96			1.72	0.83
Buchenavia tetraphylla	BUCTET	0.33	0.4	0.42	3.07	0.36	3.9	1.72	2.48
Alchorneopsis floribunda	ALCFLO		2.79		1.89		0.43	1.97	0.83
Didymopanax morototoni	SCHMOR	1.99	2.39	1.67	3.78	2.07	0.43	0.99	5.79
Casearia arborea	CASARB	1.66	0.4	4.17	2.6	3.28	1.73	0.25	4.96
Laetia procera	LAEPRO	1.99			7.33				
Matayba domingensis∗	MATDOM			0.63			0.43	9.61	
Alchornea latifolia	ALCLAT	1.99	0.4	2.5	5.2		0.87	0.25	
Tabebuia heterophylla	TABHET						0.43	3.94	
Inga vera	INGVER	1	0.4	0.63					
Cordia sulcata	CORSUL			0.42	2.13	1.22			
Hirtella rugosa (E)	HIRRUG	0.33		0.83					
Inga fastuosa	INGFAS				0.47				
Guettarda valenzuelana	GUEVAL						0.43		
Myrcia leptoclada	MYRLEP				0.47			0.25	
Guatteria caribaea	GUACAR	2.66					0.87		
Ocotea leucoxylon	OCOLEU	3.65	0.4	2.5	0.24	2.43	0.43	0.49	1.65
Eugenia stahlii∗ (E)	EUGSTA			0.21	0.24				
Casearia sylvestris	CASSYL				1.18				
Ocotea moschata∗ (E)	OCOMOS			0.42	0.24			0.74	
Homalium racemosum	HOMRAC			1.25	1.65			1.23	
Meliosma herbertii	MELHER	2.33	0.4		0.24	2.07			
Casearia guianensis	CASGUI	0.33							
Ficus citrifolia	FICCIT				0.47	0.36	0.43		
Guarea glabra	GUAGLA	1.33	0.4		0.47	0.36			
Ixora ferrea	IXOFER			0.21			0.87		
Inga fagifolia∗	INGFAG		6.77	0.42					
Sapium laurocerasus (E)	SAPLAU	1	2.79						
Magnolia splendens (E)	MAGSPL	0.33							
Miconia prasina	MICPRA	0.33	0.4						
Myrcia deflexa	MYRDEF				0.47				
Cordia borinquensis (E)	CORBOR			1.88					
Inga laurina∗	INGLAU	2.66				0.85			
Laplacea portoricensis (E)	LAPPOR	0.66							
Byrsonima wadsworthii (E)	BYRWAD			0.42	0.47				
Antirhea obtusifolia (E)	ANTOBT			0.63					
Cyathea arborea	CYAARB	0.33							
Dendropanax arboreus	DENARB	0.66	0.4		0.47				
Trichilia pallida	TRIPAL		0.4						
Musa sp.∗∗	Musasp	4.98							
Cyathea portoricensis (E)	CYAPOR	2.66							
Miconia racemosa	MICRAC	1							
Psychotria berteriana	PSYBER	0.66		0.21					
Aniba bracteata	ANIBRA	0.33							
Henriettea squamulosa	HENSQU	0.33							
Khaya nyasica∗∗	KHANYA	0.33	0.8						
Nectandra sp.		0.33							
Chrysophyllum argenteum	CHRARG	2.8	1.2						
Nephelea portoricensis	NEPPOR		0.8						
Pterocarpus officinalis	PTEOFF		0.4						
Pouteria multifora	POUMUL		0.4						
Syzygium jambos∗∗	SYZJAM			0.83	4.96	18.25	11.26	40.39	64.46
Coccoloba borinquensis	COCBOR			0.63					
Coccoloba sintenisii	COCSIN			0.63					
Ficus sintenisii (E)	FICSIN			0.63				0.74	
Magnolia portoricensis (E)	MAGPOR			0.42	3.07				
Tabebuia schumanniana	TABSCH			0.42					
Miconia laevigata	MICLAE			0.21					
Phoebe elongata	PHOELO			0.21					

Table 4 (*continued*)

Species	Species Code	Bisley, WP	Bisley, BP	Carite	Tres, Picachos	Monte, Cuba	Tanamá	Cerro, La Peña	Barrio, Sumidero
Zanthoxylum martiniciense	ZANMAR			0.21					
Eugenia confusa	EUGCON				1.42				
Byrsonima spicata	BYRSPI				1.18	1.22	4.33	4.19	
Eugenia eggersii	EUGEGG				0.71				
Clusia rosea	CLUROS				0.47				
Myrcia fallax	MYRFAL				0.47				
Myrcia splendens	MYRSPL				0.47				
Nectandra membranacea	NECMEM				0.47				
Tetrazygia urbanii	TETURB				0.47			7.64	
Chionanthus domingensis	CHIDOM				0.24			0.74	
Eugenia biflora	EUGBIF				0.24				
Nectandra coriacea	NECCOR				0.24				
Nectandra turbacensis	NECTUR				0.24	0.85			
Cyathea borinquena (E)	CYABOR					0.36			
Guapira fragans	GUAFRG					0.36			
Persea urbaniana	PERURB					0.36			
Symplocos martinicensis	SYMMAR					0.36			0.83
Genipa americana	GENAME						1.3		
Casearia decandra	CASDEC						0.87		
Ditta myricoides	DITMYR						0.43		
Licaria triandra	LICTRI							0.74	
*Citrus sinensis***	CITSIN								2.48
Dipholis bellonis	DIPBEL								1.65
Hymenaea courbaril	HYMCOU								1.65
*Artocarpus altilis***	ARTALT								0.83
Drypetes alba	DRYALB								0.83
*Persea americana***	PERAME								0.83

In spite of the obvious effects of past selective cutting on all our study stands, the results also reflect a clear influence of the landscape context on the species composition and in some cases on the successional dynamics of sites. We start this discussion with sites in the protected areas.

4.1. Mature tabonuco forests in protected forested landscapes

In general, most of the species present in these forests were native tree species (Table 4). Nevertheless, because the level of selective cutting was not uniform (greater in Carite and Bisley BP; lower at El Verde 3, intermediate at Bisley WP), we found negligible relative densities of introduced species at some sites. For example, the planted *Khaya nyassica* had a 0.33% relative density at Bisley WP while *S. jambos* had the highest relative density for introduced species (0.83%) among protected stands in Carite (Table 4). Smith (1970) reported an individual of this species at the nearby El Verde forest. These stands, along with Tres Picachos, also had the highest density of the most common species in undisturbed tabonuco forests, the highest number of primary species such as *Sloanea berteriana* and prime timber species such as *Manilkara bidentata* (Fig. 3). With the exception of Bisley BP, protected forests also had the highest number of endemic tree species (Table 4).

After the passage of two strong hurricanes (Hugo and Georges), studies of stand succession showed a continuity of native tree species and very small changed in the IV value of these species in the Bisley and El Verde 3 plots (Scatena and Lugo, 1995; Fu et al., 1996). In fact, dominant species such as tabonuco, *S. berteriana*, and *M. bidentata* were favored by the hurricane and no new species invaded the sites. This succession outcome after hurricane disturbance of mature tabonuco forests in protected forested landscapes was confirmed by Thompson et al. (2002) in a 9-ha permanent plot adjacent to El Verde 3 and to Smith's (l970) El Verde plot. Moreover, an analysis of the population dynamics of introduced species over the nine hectares, confirmed that they occur in very low densities and do not spread following the hurricane (Thompson et al., 2007). The individuals of introduced species that regenerated after canopy opening by the hurricane, died in the 5–10 years following each event, and the remnant populations of introduced species remained as rare components of the flora and only in areas with documented past deforestation and canopy opening for agricultural activities.

4.2. Tabonuco forests in the shade coffee landscape

Tabonuco forests in the coffee region lacked timber species, such as *M. bidentata* and had very low density of *S. berteriana*. Both of these species occur in relatively high density in the tabonuco forests of the protected forested region (Fig. 3). The complement of primary forest species in the shade coffee landscape is generally lower than in the protected forested landscape with the exception of Tres Picachos, which had the highest species density among all study sites and a high count of native species typical of undisturbed tabonuco stands (Table 4). However, Tres Picachos, although in the coffee region, was within a forested landscape and has recently been designated as a public forest (Table 1).

More notable, however is that forest stands in the shade coffee region had an increased presence of introduced species like *S. jambos* as well as other species not found in the stands within the forested landscape. These other species were not only the rare native ones expected to appear in response to the elevation increase in species density, but also tree species not reported for undisturbed tabonuco stands (Table 4).

4.3. Tabonuco stands in the tobacco landscape

Tabonuco stands in the tobacco region had the highest representation of *S. jambos* (Table 4, Fig. 3). In fact, this introduced species exhibited greater density than that of tabonuco trees (Fig. 3). These tabonuco stands were considerably different from those in the protected forested and shade coffee landscapes. The species composition of tabonuco stands in the tobacco landscape was impoverished relative to stands in other landscapes, and the kinds of species associated with these stands were very different from those in the other two types of landscape. These species fell out of the ordination that included all other tabonuco species, which

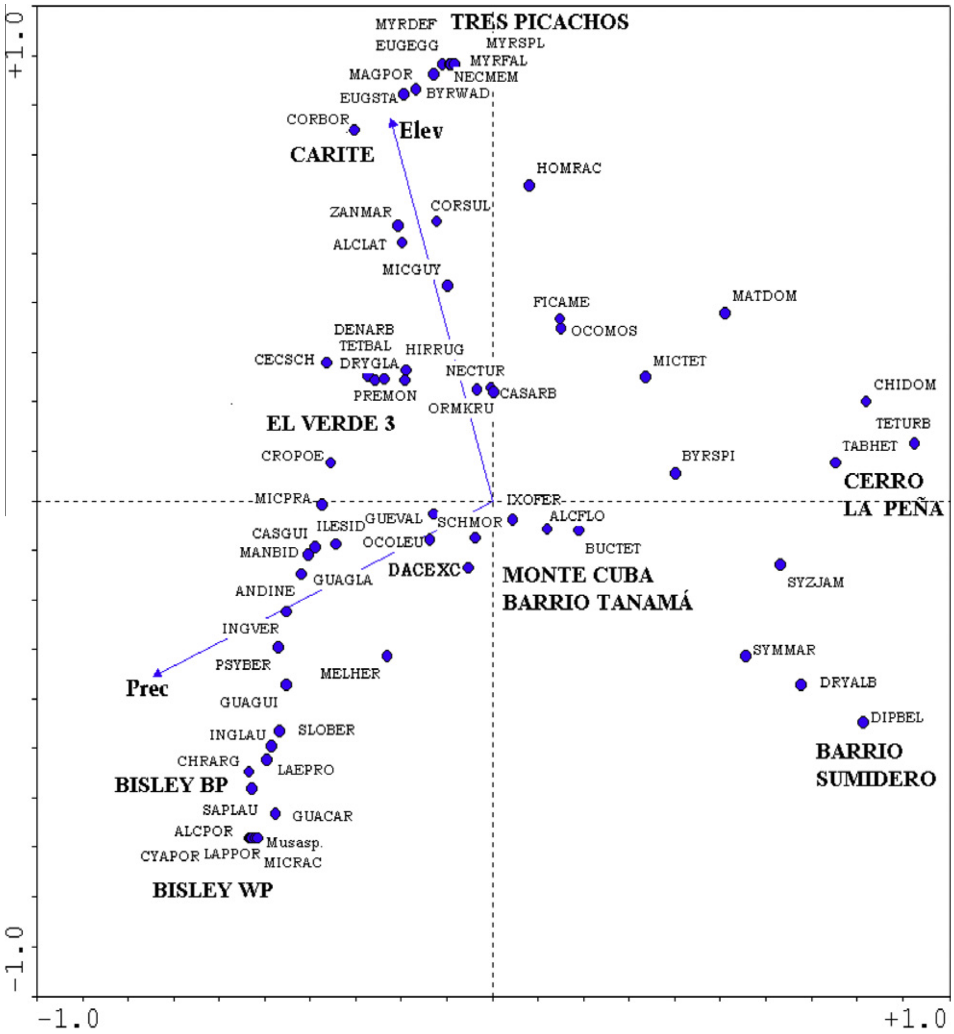

Fig. 2. Canonical Correspondence Analysis ordination for tree species Importance Value in tabonuco (*Dacryodes excelsa*) stands in Puerto Rico (Table 1). The ordination is along precipitation and elevation gradients with a sampling area of 3.6 ha. Bold face identifies sites by municipality. Species codes contain three characters each for genus and species.

suggests that the conditions on these tabonuco stands are somewhat different from those of undisturbed tabonuco forests. In addition, Barrio Sumidero had the highest number of introduced species, the lowest number of species from undisturbed tabonuco forests, and with Monte Cuba, the lowest number of primary forest species. One possible explanation is the soil degradation associated with tobacco farming and the extreme fragmentation of this landscape.

Tobacco farming exposes the soil to erosion and infertility (Picó, 1969) and the cultivation of short tobacco plants maintains an open landscape where forest fragments are exposed to a different mesoclimate than stands in forested or shade coffee landscapes. Under these conditions, it is probably as difficult for native species associated with tabonuco forests to regenerate, as it is for tabonuco. In the tobacco landscape, tabonuco forest might be closer to the threshold beyond which it cannot prevail as a tabonuco forest. For example, tabonuco seedlings are intolerant of high light intensity and require intermediate light, moderate temperature, and soil humus to develop into poles (Lugo and Wadsworth, 1990). Moreover, when mature tabonuco trees are exposed to the open after heavy logging, they lose vigor, exhibit crown dieback, and mortality within a decade (Lugo and Wadsworth, 1990). A highly fragmented landscape with eroded soils, exposes tabonuco trees on the perimeter of the fragment to adverse conditions for their growth and survival, and exposes the perimeter to invasion by introduced and other native species not usually associated with tabonuco forests.

4.4. Synthesis

Table 4 and Fig. 3 show a transition of species density as the landscape changes from continuous forest cover with protection to isolated residual tabonuco stands on a fragmented landscape with exposed soil and unfavorable temperature and light conditions. A shade coffee landscape is intermediate in terms of the environmental conditions it offers for the growth of native species associated with tabonuco stands. While elevation and precipitation explain much of the distribution of native species (Fig. 2), they do not explain the shift from a native tree species-dominated tabonuco forest to a tabonuco forest dominated by an introduced species and the presence of 41 tree species not shared with undisturbed tabonuco forests (Table 4).

We attribute this shift in species composition to human activity. We propose the following sequence of events representing changes in species composition with increasing intensity of human use. Humans first cutover forests and alter the diameter class distributions and in some instances eliminate the tree unions. In spite of these effects, native species associated with undisturbed tabonuco trees remain dominant in protected stands and few if any introduced

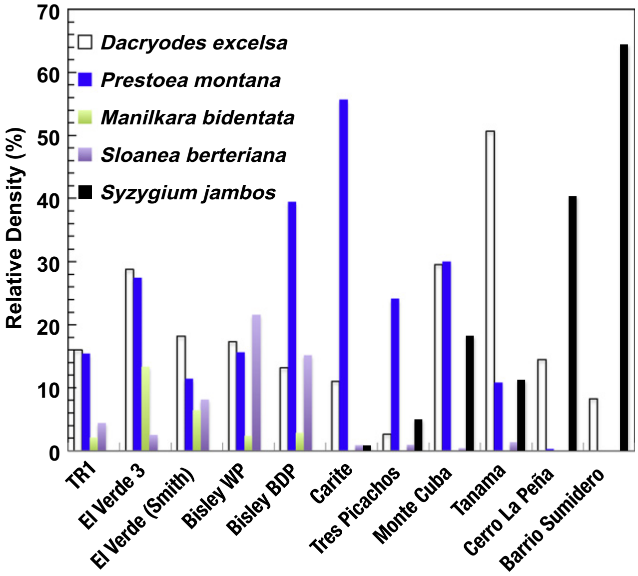

Fig. 3. Relative density of indicator native tree species and an introduced species (*S. jambos*) in tabonuco (*Dacryodes excelsa*) stands in Puerto Rico. Data are for trees with diameter at breast height (dbh) ⩾ 9 cm, except for Smith and Weaver who used ⩾4 cm dbh. Sites a Cerro La Peña and Barrio Sumidero are in tobacco landscapes, while Tanamá and Monte Cuba are in shade coffee landscapes. All other sites are in forested and protected landscapes. Site identification corresponds to those in Table 1 plus TR 1 (Weaver, 1994), and El Verde (Smith, 1970).

species reach one percent of the relative density. The level of anthropogenic disturbances increases in the coffee region. Humans alter the species composition of the forest understory, select for different species for shading coffee, and trample the understory. These anthropogenic influences begin to shift the species composition of stands. However, because the shade coffee region is a forested landscape, it is possible for tabonuco stands to maintain similarities in both species composition and structure with stands in the protected forest region. Tres Picachos is a prime example of this generalization. In tobacco landscapes, soil erosion, fragmentation, and absence of nearby forest cover expose the remnant tabonuco stands to different meso- and microclimate and to invasion by introduced species that eventually dominate the stands. Under these extreme environmental conditions, tabonuco trees no longer dominate stands, and dominance shifts to other species including introduced species. The resulting mature stands are novel forests unlikely to return to the species composition of undisturbed forest stands (Fig. 4).

4.5. Implications for ecosystem dynamics and conservation

Smith (1970) suggested that succession in tabonuco forests was not cyclical but directional. He based his observation on the abundance of secondary forest species in tabonuco stands, which he interpreted as a response to periodic hurricane disturbances. However, Heartsill Scalley et al. (2010) showed that after the passage of hurricanes succession is cyclical in unconverted forested landscapes with native species. Moreover, as anthropogenic disturbances modify conditions through deforestation, conversion to agriculture, and site degradation the succession becomes directional, as we have shown for tabonuco stands in shade coffee and tobacco landscapes. In each case, succession leads to a different mature state of tabonuco forest (Fig. 4).

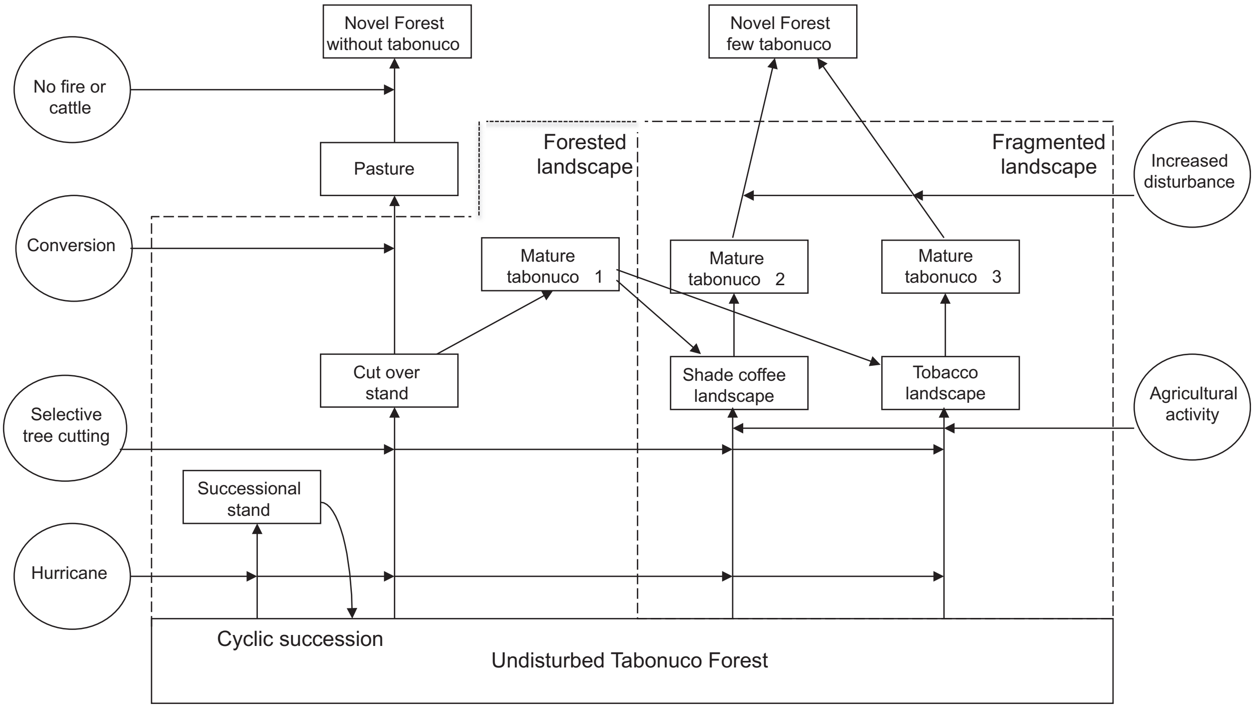

Fig. 4. Diagram of the four types of succession of tabonuco (*Dacryodes excelsa*) forest stands discussed in this study. All successions are shown to originate from undisturbed tabonuco forest in the bottom of the diagram. These forests are subject to hurricanes, which in the absence of anthropogenic disturbances activate a cyclic succession that returns stands to initial conditions after several decades (bottom left side of the diagram). Undisturbed forests are subject to selective tree cutting, which leads to cut over tabonuco stands. Cut over stands can mature within the forested landscape (Mature tabonuco 1) or can be converted to pasture. In the absence of fire and cattle, these pastures develop into novel forests without tabonuco trees (Lugo and Helmer, 2004). Mature cutover stands can occur in other landscapes such as the two fragmented landscapes on the right side of the diagram. These landscapes are a result of agricultural activity (shade coffee and tobacco landscapes). Overtime, and after cessation of human activities in the forest stands, mature tabonuco stands with different species composition develop on these landscapes (Mature tabonuco 2 and 3). If these forests are disturbed even more, a novel forest with few tabonuco trees is possible. Circles in the diagram represent outside forces that drive succession, boxes represent different states of forests and vegetation, and lines show the pathways of succession (between boxes) or influence (from the circles).

The species composition of tabonuco stands on different landscapes reflects different solutions through self-organization to prevailing environmental conditions. In the extreme conditions of the tobacco landscape, 10 species fell as outliers in the ordination along precipitation and elevation, reflecting their response to unique conditions in these remnant stands (Fig. 2). Environmental conditions have changed in these landscapes, even if the cultivation of tobacco and shade coffee is no longer practiced near these sites. It is improbable that these forests will return to species assemblages typical of the original undisturbed conditions, which are now present only in a small fraction of the original distribution of the tabonuco forest (Fig. 1). However, from a structural perspective, all tabonuco stands have indices that suggest that this forest attribute is in the process of restoration. In time, tree diameter distributions can change and fill the gaps left by past selective tree cutting but we do not know to what degree the tree unions will be reestablished in the future.

One can also foresee future environmental changes in the form of increased urbanization (Martinuzzi et al., 2007), continued natural disturbances, and potential climate change. These changes will continue to interact with the legacy of land covers of the three landscapes that we examined and direct the species composition of tabonuco stands into unpredictable trajectories. Establishing plantations of tabonuco trees is not an alternative to the restoration of these forests because the regeneration of tabonuco through plantations has not proven successful (Marrero, 1950). Tabonuco regenerates best under its own canopy, which means that the conservation of remnant stands is critical for expanding the cover of this forest type. However, restoring these stands to the initial species composition of undisturbed forests might be too costly and impractical. For this reason any restoration proposal requires a clear objective so that its feasibility can be evaluated. We propose that a management strategy for these residual tabonuco stands is to allow natural processes to dictate species composition and continued development of forest structure, i.e., biomass, basal area, tree density, etc. Our proposal would also protect tabonuco trees by limiting harvesting. Over time, this strategy leads to forest stands that:

- Increase in basal area and tree size.
- Restore L-shape stem diameters classes.
- Retain tabonuco trees and hopefully enhance their populations through new regeneration under closed canopies.
- Slowly increase the presence of native timber species.
- Develop naturally a new mix of tree species, which evolves in the direction that prevailing conditions allow.

Such management strategy requires less intrusive interventions and is compatible with investments to select for, or encourage, desirable species for particular functions, but always in the context of prevailing environmental conditions to minimize costs and opportunities for failure.

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