

## Effects of land management and a recent hurricane on forest structure and composition in the Luquillo Experimental Forest, Puerto Rico

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### Abstract

We compared the long-term effects (60 years) of land use practices and short-term effects (5 years) of a hurricane on forests in abandoned pastures, abandoned coffee plantations, and forested stands in the Luquillo Mountains of eastern Puerto Rico. There was no effect of management practices on species richness of trees and shrubs, nor on species diversity, species evenness, stem density, or basal area. However, there was a strong effect of management on tree species composition. *Myrcia deflexa* and *Palicourea riparia* dominated the former pastures, as well as *Tabebuia heterophylla*, a species which naturally invades pastures and which was subsequently established in many of the pasture areas by the USDA Forest Service. Abandoned coffee plantations were dominated by *Guarea guidonia*. *Cecropia schreberiana*, a pioneer species in the forest, was almost completely lacking in the old pastures indicating that this species is not an important component of forest recovery in abandoned pastures in the Luquillo Mountains. The abundance of *Cecropia schreberiana* in coffee and forest sites was inversely related to distance from the path of Hurricane Hugo (September 1989). Although the recent hurricane strongly affected the forest, it was unable to erase the signature of land use history on the species composition of these sites.

**Keywords:** Abandonment; Coffee plantation; Pasture; *Cecropia*; Land use history; Secondary succession; Tropics

### 1. Introduction

Protecting primary forest is one approach to reduce human effects on tropical forests. A comple-

mentary approach is to manage secondary forests to maintain biodiversity and sustain timber production (Wadsworth, 1987; Brown and Lugo, 1990). Understanding the ability of tropical forests to regenerate from human disturbance is one step for formulating management strategies for secondary forests (Brown and Lugo, 1994). However, humans affect tropical forest in many ways and the type of land use can

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strongly influence the way in which forests will recover (Brown and Lugo, 1990, 1994; Aide et al., 1995). Rates of tropical deforestation have increased dramatically in the last 20 years, but humans have influenced these ecosystems for centuries. Forests that were once thought to be 'primeval' are known to have supported large populations of humans in the past (Gómez-Pompa et al., 1987; Bush et al., 1990; Bush and Colinvaux, 1994). In many areas it is difficult to attain such a long-term perspective of recovery due to the lack of information on the land use history or because areas have only recently been abandoned.

Although the importance of past land use, particularly in 'old forests' has been ignored, recent studies have shown that the type of land use can explain a large proportion of the variation in forest structure and composition in temperate (Foster, 1992; Bratton and Miller, 1994) and tropical forests (García-Montiel and Scatena, 1994; Reiners et al., 1994). What aspect of the forest is most affected by previous use? We might expect that ecosystem processes, e.g. nutrient cycling and water retention, might recover faster than biodiversity and the previous species composition (Lugo, 1992; Brown and Lugo, 1994). How long do these signatures of previous land use persist? The answers to these questions will help us determine management plans and evaluate restoration efforts in tropical secondary forests.

Given that previous land use may have a lasting impact on a recovering forest ecosystem, will the recovery process be affected by ensuing natural disturbances? Do natural disturbances retard or augment the recovery process, or are human effects so pervasive as to resist the effects of the natural disturbance regime? In the extreme cases where there has been overgrazing and soil erosion, and where fires are frequently set by humans, recovery will be inhibited (Gómez-Pompa et al., 1972; Aide and Cavelier, 1994). However, natural disturbance may eliminate the land use signature in areas that have not been severely affected (e.g. slash and burn agriculture, coffee production) by promoting the establishment of native forest species. Few studies have addressed these questions in a tropical setting, but investigations conducted by Foster and his colleagues in New England strongly suggest that human impacts often persist through natural disturbances (Foster et al.,

1992). More importantly, human land use can, as a result of its effects on the species composition of forested stands, determine landscape patterns of damage due to disturbances such as hurricanes (Foster and Boose, 1992).

On the Caribbean island of Puerto Rico, forest cover has increased from 15% (including shade-grown coffee) to over 30% during the last 50 years (Birdsey and Weaver, 1987). After World War II, the economic basis of Puerto Rico shifted from mainly agriculture to small industries (Dietz, 1986). This resulted in the abandonment of agricultural lands throughout the island. The availability of detailed information on land use, particularly aerial photographs dating to 1936, provides a unique opportunity to determine the long-term effects of human impacts on regenerating forests (García-Montiel and Scatena, 1994; Aide et al., 1995).

We report on the effects of land use and management of forest stands in the Luquillo Experimental Forest (LEF) in eastern Puerto Rico. In particular, we compare 60 years of forest regeneration in abandoned shade coffee plantations to forested areas of the same age not used for coffee production and to forest stands in abandoned pastures. We predicted that abandoned coffee plantations would regenerate quickly and contain a biomass, biodiversity, and species composition similar to forested areas because the shade trees planted with the coffee provide habitat and resources for birds and bats that disperse seeds of native trees. In contrast, forest regeneration in pastures is inhibited at least for the first 10 years by the dominance of herbaceous species (Aide et al., 1995). The slower regeneration in the abandoned pastures might be reflected in relatively low species diversity. In addition to potential differences in rate of regeneration we were also interested in the effect that the different land uses would have on the species composition of the regenerating forests. *Cecropia schreberiana*, which becomes abundant following many natural disturbances in forests of the LEF (Crow, 1980; Weaver, 1989; Guariguata, 1990), is virtually absent in recovering pastures aged 10–35 years (Aide et al., 1995). In the context of a disturbance regime dominated by a high hurricane frequency, we sought to determine if *Cecropia schreberiana* would eventually be able to invade the abandoned pastures.

## 2. Methods

### 2.1. History of the Luquillo Mountains

The Luquillo Mountains began to be settled by Europeans in the early 1800s (Wadsworth, 1951; Scatena, 1989; García-Montiel and Scatena, 1994). Cattle production, shade coffee, timber extraction, and subsistence farming were common on the lower parts (below 600 m) of the mountains by the latter part of the century. In 1876, the Spanish declared large areas of the mountains a crown preserve. In 1898 Spain ceded Puerto Rico to the United States and the former crown preserve became a US forest preserve, which was eventually placed under the authority of the USDA Forest Service. Hurricanes in 1899 and again in 1928, 1931, and 1932 caused extensive property damage to the area and many residents abandoned the area. In the 1930s, the USDA Forest Service purchased much of the lower elevations of the Luquillo Mountains.

Charcoal production, conducted by local residents under the direction of the USDA Forest Service, was a major industry in the Luquillo Mountains in the 1940s, for which coffee shade trees (*Inga vera*) and other species present in the abandoned coffee plantations (*Inga laurina* and *Guarea guidonia*) were the preferred tree species. Secondary forest management, including timber improvement, selective harvesting, and plantation forestry were the other main land use activities until the 1970s. This included, in the late 1940s and 1950s, the planting of over 225 000

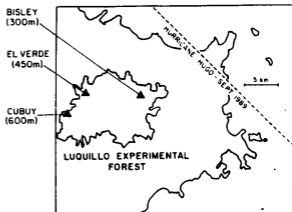


Fig. 1. Location of study sites in the Luquillo Experimental Forest, Puerto Rico, and their relationship to the path of Hurricane Hugo (18 September 1989).

seedlings of *Tabebuia heterophylla* in many of the abandoned pastures (F.H. Wadsworth, personal communication, 1995). This planting was based on results reported by Marrero (1947) indicating that *T. heterophylla* established readily in abandoned pastures. Hurricane Hugo, with peak winds exceeding  $200 \text{ km h}^{-1}$  near the eye, passed over the Luquillo Experimental Forest in September 1989 (Walker et al., 1992; Fig. 1).

### 2.2. Study sites

We studied three sites (Bisley, El Verde, Cubuy) in the Luquillo Mountains located between 300 and

Table 1

Location of stands sampled in the Luquillo Experimental Forest, Puerto Rico, and their distance to the center of Hurricane Hugo on 18 September 1989 and estimated peak sustained winds as predicted by the HURRECON model (E. Boose, personal communication, 1994; Boose et al., 1994)

Site	Land use	Latitude	Longitude	Elevation (m)	Distance to Hugo (km)	Peak sustained winds ( $\text{km h}^{-1}$ )
Bisley	Forest	18°19'01"	65°45'03"	300	10.2	140
	Coffee	18°18'57"	65°44'48"	300	10.0	140
	Pasture	18°19'23"	65°44'40"	260	9.3	140
El Verde	Forest	18°19'27"	65°48'42"	430	14.3	126
	Coffee	18°19'19"	65°48'55"	440	14.8	126
	Pasture	18°19'51"	65°48'34"	440	13.7	126
Cubuy	Forest	18°17'34"	65°50'15"	600	18.7	119
	Coffee	18°17'19"	65°50'54"	610	19.8	115
	Pasture	18°17'31"	65°51'06"	570	19.8	115

600 m and at increasing distances from the path of Hurricane Hugo (Fig. 1, Table 1). Undisturbed forests below 600 m are dominated by *Dacryodes excelsa*, *Manilkara bidentata*, and *Sloanea berteriana* (Brown et al., 1983). Above 600 m the forest is typically dominated by *Cyrtia racemiflora*, *Croton poecilanthus*, and *Micropholis garciniaefolia*. *Cecropia schreberiana* is an important pioneer tree in both forest types (Crow, 1980; Weaver, 1989).

At each site we located three areas of different land uses: pasture, shade coffee, and forested areas not used for coffee production. The land use history of specific areas was determined by interviewing local residents and reviewing historical documents (García-Montiel and Scatena, 1994; D.C. García-Montiel, personal communication, 1993; A. Estrada-Pinto, personal communication, 1993). All sites were cross checked with the 1936 aerial photographs. In the aerial photographs, areas designated as pastures had less than 10% forest cover. Forest cover in the coffee plantations ranged from 20 to 50%. Only sites with over 80% cover were considered for forest sites. Soils at each of the sites were derived from volcanoclastic sandstones and are all complexes of Zarzal clay, an oxisol, and either Cristal or Humatas clays, which are ultisols (Huffacker, 1995).

The Bisley area was purchased by the USDA Forest Service in 1934 (Scatena, 1989; García-Montiel and Scatena, 1994). The forested area in Bisley was a mature stand that had never been planted in coffee (García-Montiel and Scatena, 1994). The area was subject to stand improvement thinning and selective logging of both *D. excelsa* and *Manilkara bidentata* in the 1940s and 1950s. The former coffee plantation was located in Bisley experimental watershed No. 2 (Scatena, 1989) and the pasture site was located near the former residence (see García-Montiel and Scatena, 1994, fig. 2).

The El Verde Tract was also purchased in 1934. We sampled a forest site that had been selectively cut prior to the 1930s (USDA Forest Service, unpublished data, 1992). In this area, large (over 50 cm diameter at breast height (DBH)) *D. excelsa* (equal to about 10% of stand volume) had been removed in the 1950s following stand improvement thinning in the 1930s and 1940s (Odum, 1970). The coffee plantation was located in the area of the El Verde

Field Station. The pasture site was located approximately 1.2 km northeast of the El Verde Field Station at the upper elevational limit of a large pasture that appears in the 1936 air photos.

The forest site at Cubuy was located in the original Spanish crown lands, for which there is little detailed information on land use in the early part of the century. The crown lands were not surveyed in the 1930s as were lands eventually purchased by the USDA Forest Service. The presence of a few individuals of bamboo near our transects and the presence of a single coffee plant and *Hibiscus pernambucenus* (a species cultivated as an ornamental) in our samples (see Appendix) indicated that the area was not entirely free of human disturbance. This indicates the area may be near a former homestead illegally established in the crown lands and abandoned sometime before 1936. The coffee plantation we sampled was located on land purchased in 1937 and, although not actively maintained, local inhabitants continued to harvest coffee from the site until the 1950s (A. Estrada-Pinto, personal communication, 1993). The pasture site was located within the former crown lands near a residence that was just outside the reserve boundary.

### 2.3. Sampling and data analysis

Between October 1993 and February 1994, we sampled trees (over 1 cm DBH) in four 1 m × 50 m belt transects within each land use type. We located all transects in the center region of the land use area (to avoid possible edge effects) and away from plantations of *Swietenia* established by the USDA Forest Service in the 1950s and again in the 1970s. Species area curves were determined using 40 1 m × 5 m quadrats from each set of transects and generated by taking 500 randomly ordered selections of the quadrats and then taking the average of the 500 randomly generated curves (McCune, 1993). Species diversity among stands was compared using the Shannon–Weiner index and species evenness was calculated using the modified Hill's ratio (Ludwig and Reynolds, 1988). Species richness, diversity, and evenness, as well as tree basal area and density were compared using a two-way ANOVA. Basal area and density were analyzed using log transformed values. An ordination among stands was conducted using the

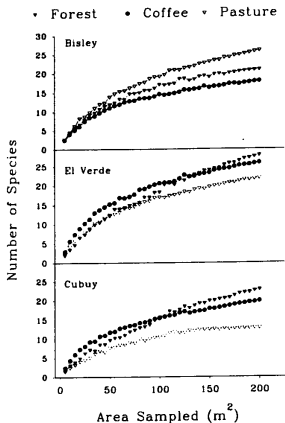


Fig. 2. Average species area curves (resulting from 500 random selections of  $5 \text{ m}^2$  quadrats) for each forest stand.

importance values for each species. Importance values were calculated using the average of relative basal area and relative density for each species and, therefore, ranged from 0 to 100%. Importance values were arcsin-square root transformed prior to analysis. The ordination was performed using principal components analysis on the variance-covariance matrix (Grieg-Smith, 1983). The number of interpretable axes from PCA was determined using the recommendations of Jackson (1993).

### 3. Results

The number of species ( $S$ ) varied from only 12 in the Cubuy pasture to 27 in the El Verde forest (Fig. 2). The species area curves for the El Verde and Cubuy site show a similar pattern with  $S$  increasing from abandoned pastures to shade coffee to forested areas (Fig. 2). The Bisley site (site nearest the path of Hurricane Hugo), showed a different pattern with the greatest number of species occurring in the pasture site. Overall, there were no significant differences in  $S$  among land use types ( $F_{2,4} = 0.22$ ,  $P = 0.81$ ). Similarly, there were no significant effects of land use history on the Shannon-Weiner index of species diversity ( $H'$ ; Fig. 3;  $F_{2,4} = 1.38$ ,  $P = 0.35$ ), the species evenness ( $E$ ;  $F_{2,4} = 2.19$ ;  $P = 0.23$ ),

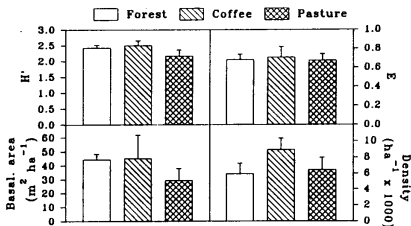


Fig. 3. Forest stand characteristics averaged by land use type. Included are the Shannon-Weiner diversity index ( $H'$ ), Hill's modified ratio for evenness ( $E$ ), basal area, and stem density.

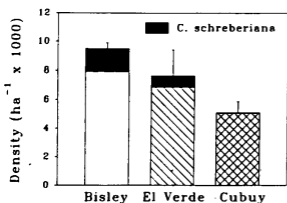


Fig. 4. Variation in stem density (trees  $\text{ha}^{-1}$ ) among sites. The dark portion of each bar represents the density of *Cecropia schreberiana*.

basal area ( $F_{2,4} = 1.05$ ,  $P = 0.26$ ), or stem density ( $F_{2,4} = 1.05$ ,  $P = 0.11$ ). The values of  $H'$  ranged from 2 to 2.5 and values of  $E$  for the three land use categories were all approximately 0.62. Basal area ranged from  $30 \text{ m}^2 \text{ ha}^{-1}$  in abandoned pastures to  $45 \text{ m}^2 \text{ ha}^{-1}$  in forest and coffee stands. Average stem density of trees over 1 cm DBH ranged from about 6000 to over 8000  $\text{ha}^{-1}$  (Fig. 3).

One effect of the recent hurricane (Fig. 1) was to cause an increase in woody stem density in sites near the hurricane path (Fig. 4,  $F_{2,4} = 9.03$ ,  $P = 0.033$ ). Differences in density among the three sites is partially explained by changes in the density of the pioneer species, *Cecropia schreberiana*. Differences among sites in the other components of stand structure ( $S$ ,  $H'$ ,  $E$ , and basal area) were not significant ( $P = 0.13-0.26$ ).

Axis I of the PCA ordination explained 37% of the variance in species' importance values (Table 2) and gave high positive weightings to *T. heterophylla*, *Myrcia deflexa*, and *Palicourea riparia* and high negative weightings to *G. guidonia*, *Cecropia schreberiana*, *Psychotria berteriana*, *Sapium laurocerasus*, and *Urera baccifera*. This axis consistently ordered the land use types within each site from coffee to forest to pastures (Fig. 5). Axis II explained 24% of the variation and primarily explained differences in the occurrence of tabonuco (*Dacryodes excelsa*; Table 2) and other elements of virgin tabonuco stands (*Manilkara bidentata*, *Sloanea berteriana*). Axis III, explaining 15.5% of the variance, primarily

Table 2

Pearson correlations coefficients for importance values of species exhibiting at least one significant correlation with ordination axes I-III

Species	Axis I	Axis II	Axis III
<i>Tabebuia heterophylla</i>	0.836 **	-0.501	-0.007
<i>Myrcia deflexa</i>	0.827 **	0.011	0.144
<i>Palicourea riparia</i>	0.761 *	0.256	-0.522
<i>Guarea guidonia</i>	-0.927 ***	-0.229	0.002
<i>Cecropia schreberiana</i>	-0.886 **	0.361	-0.169
<i>Psychotria berteriana</i>	-0.863 **	0.278	-0.390
<i>Sapium laurocerasus</i>	-0.834 **	0.299	-0.123
<i>Piper glabrescens</i>	-0.831 **	0.063	-0.022
<i>Urera baccifera</i>	-0.800 **	0.075	-0.013
<i>Dacryodes excelsa</i>	-0.373	0.913 ***	-0.030
<i>Psychotria bracteata</i>	-0.393	0.787 *	-0.070
<i>Sloanea berteriana</i>	0.164	0.703 *	-0.122
<i>Manilkara bidentata</i>	0.336	0.683 *	-0.156
<i>Prestoea montana</i>	-0.079	0.140	0.972 ***
<i>Guarea glabra</i>	-0.200	-0.3730	0.809 **
<i>Hibiscus pernambucensis</i>	-0.200	-0.373	0.809 **
<i>Croton poecilanthus</i>	-0.142	-0.291	0.779 *
Percent variance	37.8	23.9	15.5

separated sites by the occurrence of the palm *Prestoea montana*. This axis (not shown) distinguished only among stands at the Cubuy site.

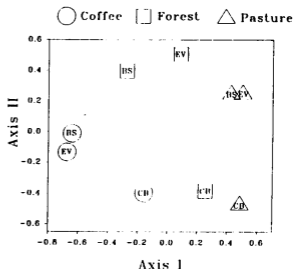


Fig. 5. Plot of first and second axes in an ordination (principle components analysis) of importance values of species occupying forest stands with differing land use histories.

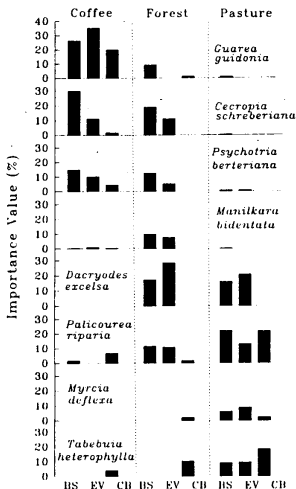


Fig. 6. Distributions of selected species (importance values range from 0 to 100%) by land use and site.

Former coffee plantations were dominated by *G. guidonia* (Fig. 6), a species used as coffee shade. *Inga vera* and *I. laurina* were not abundant in any of the former coffee plantations (see Appendix). Coffee and forest stands at Bisley and El Verde (sites nearest the hurricane path) were also dominated by *Cecropia schreberiana* (Fig. 6), a pioneer tree whose abundance increases after hurricanes (Crow, 1980; Weaver, 1989), as well as by *Psychotria berteriana* (Fig. 6). Abandoned pastures were almost completely lacking in these species at any elevation. The tree species *T. heterophylla* and *Myrcia deflexa* dominated the abandoned pastures at all elevations

(Fig. 6). The shrub *Palicourea riparia* was also common in abandoned pastures (Fig. 6). *Dacryodes excelsa*, *Manilkara bidentata* (Fig. 6), and *Sloanea berteriana* (Appendix) were found most abundantly in the forested stands at low elevations (Bisley and El Verde), but not at the high elevation site (Cubuy). *Dacryodes excelsa* was also present in pastures at the low elevation sites.

## 4. Discussion

### 4.1. Effects of land management

In this Caribbean forest the 'signature' of previous land use still exists after 60 years, even after a hurricane severely damaged the forest. Among the sites we sampled in the LEF, the effects of human land use was reflected in strong differences in the species composition of the forest stands. There was no apparent effects of land management practices on tree species richness, diversity, or evenness, nor were there any apparent effects on tree density or basal area.

Coffee stands were dominated by *G. guidonia*, a species often found in abundance in active and abandoned coffee plantations (Weaver and Birdsey, 1986). These stands lacked *I. vera* and *I. laurina*, nitrogen-fixing species also associated with the cultivation of coffee in Puerto Rico. This may reflect harvesting of *Inga* for charcoal production in the LEF in the 1940s, activities that we know occurred in both the Bisley and El Verde sites (García-Montiel and Scatena, 1994; D.C. García-Montiel, personal communication, 1993). Also, *I. vera* is a short-lived species that does not regenerate well in a forest understorey (Muñiz-Melendez, 1978). Birdsey and Weaver (1987) found that the basal area of *I. vera* declined following abandonment of shade coffee plantations, while that of both *I. laurina* and *G. guidonia* increased.

Areas formally in pastures were consistently dominated by two tree species, *T. heterophylla* and *Myrcia deflexa*, and the shrub, *Palicourea riparia*. The high abundance of *T. heterophylla* in abandoned pastures is probably due in part to planting efforts by the USDA Forest Service in the 1940s and 1950s (F.H. Wadsworth, personal communication, 1993),

but this species has also been shown to be one of the first tree species to establish naturally in overgrazed areas (Marrero, 1947). At the two lower elevation sites, *D. excelsa* was also common in pastures. However, the most striking feature of the pasture stands near the path of hurricane Hugo was the scarcity of *Cecropia schreberiana*, a pioneer tree that was very abundant in nearby coffee and forest stands. *Psychotria berteriana*, a pioneer shrub, was also rarely found in abandoned pastures at low elevations.

The forest stand at Cubuy appeared to have several important differences which distinguished it from the lower elevation stands at Bisley and El Verde. The stand was dominated by *Prestoea montana* and *Croton poecilanthus*, species that are known to be more abundant at higher elevations in the Luquillo Mountains (Brown et al., 1983). The forested stand was chosen because the 1936 air photos indicated that forest cover was over 80% at that time. However, as indicated, there was evidence of previous human occupation. The coffee stand at Cubuy had many more coffee plants in the understory than any of the other abandoned coffee plantations, perhaps due to occasional maintenance and harvesting for personal consumption by neighboring families (A. Estrada-Pinto, personal communication, 1993). Finally, the pasture site was dominated by *Syzygium jambos*, an introduced ornamental that can form dense thickets (Little and Wadsworth, 1991). However, as in the lower elevation sites, the coffee stand at Cubuy was dominated by *G. guidonia* and the abandoned pasture supported an abundance of both *Palicourea riparia* and *T. heterophylla*.

#### 4.2. Hurricane disturbance

Hurricane Hugo struck the LEF on 18 September 1989 with winds exceeding  $200 \text{ km h}^{-1}$  at the wall of the hurricane eye, which had a diameter of 25 km. The strength of the winds declined as the storm began to pass over land (Table 1) which was reflected in a gradient of damage across the LEF (Boose et al., 1994). At Bisley, over 60% of trees were broken or uprooted (Basnet et al., 1992) while at El Verde only 17–20% trees were damaged (Walker, 1991; Walker et al., 1992; Zimmerman et al., 1994). Although damage was not quantified at

the Cubuy site, we observed very little evidence of hurricane damage.

Overall stem density and the abundance of *Cecropia schreberiana* were correlated with proximity of the sites to the hurricane in coffee and forest stands. While distance to the hurricane path and elevation are confounded in our data set, we feel that the increases in abundance of pioneer species *Cecropia schreberiana* and *Psychotria berteriana* in forest and coffee stands were due to the effects of the hurricane. The absence of *Cecropia schreberiana* and *Psychotria berteriana* in pastures near the hurricane may reflect the low stature of forests in the abandoned pastures and a low frequency of tree uprooting, resulting in less soil disturbance. Following the hurricane at El Verde, most *Cecropia schreberiana* and *Psychotria berteriana* were found near soil mounds caused by tree uprooting (L.R. Walker, unpublished data). In addition, if the soils in the abandoned pastures are relatively nutrient poor, this may impede the growth of the nutrient-demanding pioneer species (Jordan, 1985).

Do the differences that we observed in species composition among land use types represent stable assemblages (cf. Ewel, 1980; Reiners et al., 1994)? The experience in central New England strongly suggests that widespread deforestation that occurred in the 1800s permanently changed the composition of most forests (Foster, 1992; Foster et al., 1992). Bratton and Miller (1994) have recently attributed differences in the structure of maritime oak forests in southern Georgia (an area frequently struck by hurricanes) to land use patterns dating to the early 1800s. The abandonment of agricultural lands in the Luquillo Mountains (Scatena, 1989), provides the opportunity to determine if the same pattern holds true in a tropical area.

#### 4.3. Recovery at the ecosystem level

Although the species composition in abandoned coffee plantations and pastures has been slow to recover, other forest characteristics have recovered more rapidly. Tree density and basal area in 60-year-old abandoned coffee plantations were not distinguishable from secondary forests of much greater age. Abandoned pastures, some of which were planted with *T. heterophylla*, also had a similar

forest structure. Similar forest structure could indicate that the ecosystem properties of the stands of variable species composition might be similar. Lugo (1992) has shown that plantations and secondary forests in the LEF, paired by age and site, exhibit strikingly similar attributes in terms of biomass distributions, litter production, and nutrient cycling. These similarities occurred despite large differences in the species composition of the overstory. If stands of differing land management are also similar in terms of their ecosystem attributes, it would suggest that ecosystem function recovers more quickly from human disturbance than species composition, whether the recovery is aided by management or not.

#### 4.4. Implications for forest management

What are the implications of our findings for the management of secondary forests? The answer depends on whether the goal is reclamation of a forest with ecosystem properties similar to primary forests versus restoring the forest to its former species composition (Brown and Lugo, 1994). Weaver and Birdsey (1986) concluded that abandoned coffee plantations offered many management opportunities, including timber harvesting, plantation forestry, and a variety of agroforestry alternatives. However, if the goal is to restore abandoned coffee plantations to a state similar to relatively undisturbed forests (Brown and Lugo, 1994), our results suggest that a directed effort to establish such species as *D. excelsa* and *Manilkara bidentata*, which are removed when coffee plantations are established (García-Montiel and Scatena, 1994), will be necessary. We have previously shown that pastures appear resistant to invasion by woody species and impart a selective filter on the species that are able to establish (Aide et al., 1995). Our current results indicate that establishment of *T. heterophylla* in abandoned pastures can lead to

forest stands with a structure similar to less disturbed forests in as little as 40 years and attests to this species' utility in forest reclamation (Marrero, 1947; Little and Wadsworth, 1991). The apparent ability of *D. excelsa* to establish in low elevation pastures offers some hope that, if desirable, these areas could be restored to something similar to undisturbed stands. However, the overall implication is that management of abandoned pastures in wet tropical sites require a high degree of intervention to overcome barriers to forest establishment (Aide and Cavalier, 1994; Aide et al., 1995) and provide a more natural species composition.

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## Appendix

Species encountered among the nine stands studied and their importance values. Only species with importance values of over 1% in at least one stand are included. Nomenclature follows Little and Wadsworth (1991) and Little et al. (1974)

Species	Coffee			Forest			Pasture		
	BS	EV	CB	BS	EV	CB	BS	EV	CB
<i>Alchornea latifolia</i>	1.8	0.5					1.8		
<i>Andira inermis</i>	1.8								
<i>Buchenavia capitata</i>			0.5	1.0		0.6			
<i>Casearia arborea</i>	0.3		4.7		1.9		0.6	1.4	1.8
<i>Casearia guianensis</i>						0.7	0.9	4.8	
<i>Casearia sylvestris</i>		2.3	13.2		1.3		0.3		2.4
<i>Cecropia schreberiana</i>	30.2	11.2	1.7	19.2	7.0		0.5		
<i>Citrus sinensis</i>			10.1						
<i>Coffea arabica</i>	0.3	1.2	11.4			0.8			
<i>Cordia alliodora</i>	2.2	0.9	7.8	0.9	1.5	8.4		1.7	1.4
<i>Croton poecilanthus</i>			1.2	0.9	0.9	20.0			
<i>Dacryodes excelsa</i>				17.4	28.7		16.1	20.9	
<i>Drypetes glauca</i>					1.0	0.6			
<i>Faramea occidentalis</i>							2.6		
<i>Guarea glabra</i>						1.2			
<i>Guarea guidonia</i>	26.5	35.4	20.2	9.5		1.3	1.0		
<i>Guatteria caribaea</i>					1.3				
<i>Hibiscus pernambucensis</i>						3.8			
<i>Hirtella rugosa</i>								3.1	
<i>Inga vera</i>		1.1							
<i>Manilkara bideniata</i>	0.3	1.1	0.4	10.2	8.0		0.3		
<i>Miconia prasina</i>	0.5				0.9		6.5	1.0	1.8
<i>Miconia racemosa</i>					1.3				
<i>Miconia tetrandra</i>					0.5			1.1	
<i>Myrcia deflexa</i>						2.3	6.3	9.0	2.6
<i>Myrcia splendens</i>		0.3	0.4			0.6	2.0	1.0	
<i>Palicourea riparia</i>	2.0		7.0	11.7	11.0	1.9	22.2	13.2	22.1
<i>Piper balatanum</i>						1.2			1.7
<i>Piper glabrescens</i>	5.9	8.9		1.5				0.4	
<i>Prestoea montana</i>	7.1	8.2	2.4	4.8	10.6	37.9	8.2	13.7	
<i>Psychotria berteriana</i>	15.0	10.3	4.6	12.8	5.4		0.9	0.9	1.7
<i>Psychotria bracteata</i>				1.5	1.3		4.5	0.9	
<i>Ocotea leucoxydon</i>			5.3	1.5	3.4	2.6	6.8	11.0	
<i>Samyda spinulosa</i>		0.2							1.4
<i>Sapium laurocerasus</i>	3.2	0.9		1.0	0.4				1.4
<i>Schefflera morototoni</i>	2.0	0.5	2.5	1.9	3.6		5.1	3.0	6.3
<i>Sloanea berteriana</i>	0.3			2.9	6.5				
<i>Swietenia macrophylla</i>		1.1					1.7		
<i>Syzygium jambos</i>			1.0			1.9			37.6
<i>Tubeuia heterophylla</i>			4.2			10.5	9.4	9.6	18.7
<i>Tetragastris balsamifera</i>		1.6							
<i>Urera baccifera</i>	1.4	7.1		0.4	0.5				

BS, Bisley; EV, El Verde; CB, Cubuy.

## References

- Aide, T.M. and Caveller, J., 1994. Barriers to tropical lowland forest restoration in the Sierra Nevada de Santa Marta, Colombia. *Restoration Ecol.*, 2: 219–229.
- Aide, T.M., Zimmerman, J.K., Herrera, L., Rosario, M. and Serrano, M., 1995. Forest recovery in abandoned tropical pastures in Puerto Rico. *For. Ecol. Manage.*, 77: 77–86.
- Basnet, K., Likens, G.E., Scatena, F.N. and Lugo, A.E., 1992. Hurricane Hugo: damage to a tropical rain forest in Puerto Rico. *J. Trop. Ecol.*, 8: 47–55.
- Birdsey, R.A. and Weaver, P.L., 1987. Forest area trends in Puerto Rico. Res. Note SO-331. US Forest Service, New Orleans, LA. 13 pp.
- Boose, E.R., Foster, D.R. and Fluet, M., 1994. Hurricane impacts to tropical and temperate landscapes. *Ecol. Monogr.*, 64: 369–400.
- Bratton, S.P. and Miller, S.G., 1994. Historic field systems and the structure of maritime oak forests, Cumberland Island National Seashore, Georgia. *Bull. Torrey Bot. Club*, 121: 1–12.
- Brown, S. and Lugo, A.E., 1990. Tropical secondary forests. *J. Trop. Ecol.*, 6: 1–32.
- Brown, S. and Lugo, A.E., 1994. Rehabilitation of tropical lands: a key to sustaining development. *Restoration Ecol.*, 2: 97–111.
- Brown, S., Lugo, A.E., Silander, S. and Lielig, L., 1983. Research history and opportunities in the Luquillo Experimental Forest. Gen. Tech. Rep. SO-44, US Forest Service, New Orleans, LA. 128 pp.
- Bush, M.B. and Colinvaux, P.A., 1994. Tropical forest disturbance: paleoecological records from the Darien, Panama. *Ecology*, 75: 1761–1768.
- Bush, M.B., Piperno, D.R. and Colinvaux, P.A., 1990. A 6000 year history of Amazonian maize cultivation. *Nature*, 340: 303–305.
- Crow, T.R., 1980. A rainforest chronicle: a 30 year record of change in structure and composition at El Verde, Puerto Rico. *Biotropica*, 12: 42–55.
- Dietz, J.L., 1986. *Economic History of Puerto Rico*. Princeton University Press, Princeton, 337 pp.
- Ewel, J.J., 1980. Tropical succession: manifold routes to maturity. *Biotropica*, 12: 2–7.
- Foster, D.R., 1992. Land-use and vegetation dynamics in central New England: an historical perspective. *J. Ecol.*, 80: 753–772.
- Foster, D.R. and Boose, E.R., 1992. Species and stand response to catastrophic wind in central New England, USA. *J. Ecol.*, 76: 135–151.
- Foster, D.R., Zebrzyk, T., Schoonmaker, P. and Lezberg, A., 1992. Post-settlement history of human land-use and vegetation dynamics of a *Tsuga canadensis* (hemlock) woodlot in central New England. *J. Ecol.*, 80: 773–786.
- García-Montiel, D.C. and Scatena, F.N., 1994. The effect of human activity on the structure and composition of a tropical forest in Puerto Rico. *For. Ecol. Manage.*, 63: 57–78.
- Gómez-Pompa, A., Vasquez-Yanes, C. and Guevara, S., 1972. The tropical rain forest: a nonrenewable resource. *Science*, 117: 762–765.
- Gómez-Pompa, A., Flores, J.S. and Sosa, V., 1987. The 'Pet Kot' a man-made tropical forest of the Maya. *Interciencia*, 15: 10–15.
- Grieg-Smith, P., 1983. *Quantitative Plant Ecology*, 3rd edn. Blackwell, Oxford, 359 pp.
- Guangata, M.R., 1990. Landslide disturbance and forest regeneration in the upper Luquillo Mountains of Puerto Rico. *J. Ecol.*, 78: 814–832.
- Huffacker, L., 1994. Soil survey of the Caribbean National Forest and Luquillo Experimental Forest. US Forest Service, in press.
- Jackson, D.A., 1993. Stopping rules in principal components analysis: a comparison of heuristical and statistical approaches. *Ecology*, 74: 2204–2214.
- Jordan, C.F., 1985. *Nutrient Cycling in Tropical Forest Ecosystems*. Wiley, Chichester, UK.
- Little, E.L. and Wadsworth, F.H., 1991. Common trees of Puerto Rico and the Virgin Islands. Handbook 249. USDA, Washington DC.
- Little, E.L., Woodbury, R.O. and Wadsworth, F.H., 1974. Trees of Puerto Rico and the Virgin Islands. Vol. 2. Handbook 449. USDA, Washington DC.
- Ludwig, J.A. and Reynolds, J.F., 1988. *Statistical Ecology: A Primer on Methods and Computing*. John Wiley, New York, 337 pp.
- Lugo, A.E., 1992. Comparison of tropical tree plantations with secondary forests of similar age. *Ecol. Monogr.*, 62: 1–41.
- Marrero, J., 1947. A survey of the forest plantations of the Caribbean National Forest. MS Thesis, University of Michigan, Ann Arbor.
- McCune, B., 1993. Multivariate analysis on the PC-ORD system. Oregon State University, Corvallis, 139 pp.
- Muñiz-Melendez, E., 1978. Demographic analysis of the life history of *Inga vera* subspecies *vera*. MS Thesis, University of Tennessee, Knoxville.
- Odum, H.T., 1970. The El Verde study area and the rain forest systems of Puerto Rico. In: H.T. Odum and R.F. Pigeon (Editors), *A Tropical Rain Forest*. NTIS, Springfield, VA, pp. B3–B32.
- Reiners, W.A., Bouwman, A.F., Parsons, W.F.J. and Keller, M., 1994. Tropical rain forest conversion to pasture: changes in vegetation and soil properties. *Ecol. Appl.*, 4: 363–377.
- Scatena, F.N., 1989. An introduction to the physiography and history of the Bisley Experimental Watersheds in the Luquillo Mountains of Puerto Rico. Gen. Tech. Rep. SO-72. US Forest Service, New Orleans, LA. 22 pp.
- Wadsworth, F.H., 1951. Notes on the climax forests of Puerto Rico and their destruction and conservation prior to 1900. *Caribb. For.*, 11: 38–56.
- Wadsworth, F.H., 1987. A time for secondary forestry in tropical America. In: J. Figueroa, F.H. Wadsworth and S. Branham (Editors), *Management of the Forests of Tropical America: Prospects and Technologies*. Institute of Tropical Forestry, Rio Piedras, pp. 189–198.
- Walker, L.R., 1991. Tree damage and recovery from Hurricane Hugo in the Luquillo Experimental Forest, Puerto Rico. *Biotropica*, 23: 379–385.

- Walker, L.R., Voltzow, J., Ackerman, J.D., Fernández, D.S. and Fetcher, N., 1992. Immediate impact of Hurricane Hugo on a Puerto Rican rain forest. *Ecology*, 73: 691-694.
- Weaver, P.L., 1989. Forest changes after hurricanes in Puerto Rico's Luquillo Mountains. *Interciencia*, 14: 181-192.
- Weaver, P.L. and Birdsey, A., 1986. Tree succession and management opportunities in coffee shade stands. *Turrialba*, 36: 47-58.

- Zimmerman, J.K., Everham, III, E.M., Waide, R.B., Lodge, D.J., Taylor, C.M. and Brokaw, N.V.L., 1994. Responses of tree species to hurricane winds in subtropical wet forest in Puerto Rico: implications for tropical tree life histories. *J. Ecol.*, 82: 911-922.