Plant Ecology **174:** 49–58, 2004.

Effects of land use history on hurricane damage and recovery in a neotropical forest

M. Uriarte[1,4,*], L.W. Rivera[2], J.K. Zimmerman[3], T.M. Aide[2], A.G. Power[1] and A.S. Flecker[1]

*[1]Cornell University, Department of Ecology and Evolutionary Biology, Ithaca, New York 14853; [2]University of Puerto Rico, Department of Biology, PO Box 23360, San Juan, Puerto Rico; [3]Institute for Tropical Ecosystem Studies, University of Puerto Rico, PO Box 363682, San Juan, Puerto Rico 00936-3682; [4]Current address: Institute of Ecosystem Studies, P.O. Box AB, Millbrook, New York 12545; *Author for correspondence (e-mail: UriarteM@ecostudies.org)*

Received 22 October 2001; accepted in revised form 27 July 2003

Key words: Hurricane effect, Human disturbance, Hispaniola, Land use history, Los Haitises

Abstract

Prior land-use history might influence damage and recovery of plant communities from natural disturbance. We examined effects of previous agricultural land use on damage and recovery of plant communities affected by Hurricane Georges. The study was conducted in the karst region of Los Haitises National Park, Dominican Republic. We compared pre- and post-hurricane stem density, basal area and diversity of woody vegetation in sites within the park that had been subject to different land use histories. The type of land uses included a wide range of histories, ranging from abandoned pastures and *conucos* (mixed plantings) to cacao plantations, intact forests and *mogote*s (hilltop communities) with no recent history of land use. Previous land use and the amount of basal area present prior to the hurricane determined effects of, and recovery from hurricane disturbance. Systems with high pre-hurricane basal area lost many large trees, whereas the basal area hardly changed in systems without large trees. Thus, basal area decreased at forested sites, *mogotes,* and cacao plantations and remained comparable to pre-hurricane figures in all other land uses. Shifts in species diversity paralleled to some degree reductions in basal area. Species diversity increased in *mogotes* and cacao plantations, perhaps as a result of hurricane damage to the forest canopy, which facilitated regeneration of heliophilic species. Finally, regeneration of cacao seedlings in former cacao plantations, and growth of pioneer species in young *conucos* (mixed plantings) more than doubled post-hurricane stem densities for these two types of land use. Previous agricultural land use left a lasting impression on the structure and composition on plant communities, which persisted even after hurricane damage.

Introduction

The leading cause of tropical forest destruction today is agriculture. As socioeconomic conditions change, large areas used for agriculture and ranching are abandoned and undergo secondary succession (Birdsey and Weaver 1987; Skole et al. 1994). Prior agricultural activity can alter ecosystem properties and leave long-term traces on the landscape after abandonment (Padoch and Vayda 1983; Hamburg and Sanford 1986; Foster 1992; Zou et al. 1995; Shukla et al. 1990; Saunders et al. 1991; Waide and Lugo 1992). The intensity of past agricultural exploitation has a large effect on the direction of changes in a community after abandonment. For instance, cattle ranching compacts the soil and alters hydrological regimes (Uhl 1987; Uhl et al. 1988). Such land use history accounts for a large proportion of the variation in structure and composition as forests recover following abandonment (Foster 1992; Garcia-Montiel and Scatena 1994; Reiners et al. 1994; Burslem et al. 2000; Boose et al. 2001).

The effects of previous land use on forest structure and composition can be discernable even after natural disturbances such as hurricanes and landslides (Zimmerman et al. 1995; Foster et al. 1992). In Caribbean forests, hurricanes are the most important natural disturbance. They cause tree defoliation, breakage and uprooting and can have dramatic, short-lived effects on ecosystem processes (Tanner et al. 1991). Historically, hurricane return frequency has ranged from 15 to 22 years at any given site (Alaka 1976; Neumann et al. 1999; Weaver 1986). Understanding how previous agricultural land use, an anthropogenic long-term disturbance, affects recovery from hurricane damage, a natural disturbance, can help clarify important aspects of successional dynamics of tropical forests and provide insight for the development of adequate management strategies for secondary forests in the Caribbean.

There is mounting evidence that the effects of multiple disturbances are not merely additive and may have unexpected consequences on ecological patterns and processes (Paine et al. 1998; Platt et al. 2001). For instance, Platt et al. (2001) found that anthropogenic changes to fire regimes in the Everglades pine savannas greatly influenced the effects on subsequent hurricanes on the mortality of pines. These effects could not have been predicted solely from hurricanes or fires. Increasing human pressure on forested landscapes coupled with global climatic change suggest that understanding the effects of multiple compounded disturbances may become even more important in the management of forests.

The goal of this study was to determine the effects of previous agricultural land use, an anthropogenic disturbance, on short-term recovery from hurricane damage as reflected in forest structure and composition. To this end, we compared pre- and post hurricane diversity, species turnover, stem density and basal area in plots with different agricultural land use history in Los Haitises National Park, Dominican Republic. The type of land uses included a wide range of histories ranging from abandoned pastures and *conucos* (mixed plantings) to cacao plantations, intact forests and *mogote* hilltop communities with no recent history of land use. Previous sampling at the study site provided a unique opportunity to examine how previous agricultural land use affects forest recovery from hurricane damage (Rivera et al. 2000).

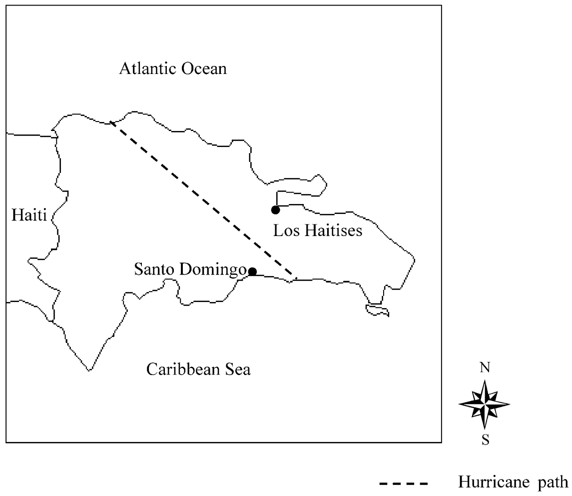

Figure 1. Trajectory of Hurricane Georges with respect to Los Haitises National Park, Dominican Republic.

The effects of hurricane damage on forest recovery may be compounded by historical land use. Previous agricultural exploitation can produce low initial levels of diversity and alter nutrient cycling processes (Aide et al. 1996). These effects may limit the number of species in seed banks or hinder seedling recruitment after the hurricane. Similarly, previous agricultural use may determine the amount of initial basal area present prior to the hurricane. Sites with a recent history of land use typically contain few large trees and low basal area. These sites may be less susceptible to hurricane damage, displaying only minor changes in community structure and composition in response to hurricane damage (but see Robertson and Platt 2002). Land use history may determine the initial density of woody stems at a site. In secondary forests in the Caribbean, stem density increases steadily for the first 20-30 years after abandonment, followed by thinning in more mature stands not subjected to hurricanes (Brown and Lugo 1994; Aide et al. 1995; Aide et al. 1996). Thus, time since abandonment may influence the potential range of changes in stem density that hurricane damage can effect.

Methods

Los Haitises National Park is located in the northern part of the Dominican Republic, south of Samana Bay (Figure 1). The average annual rainfall in this area is approximately 2,000 mm evenly distributed through the year (Zanoni et al. 1990). The limestone parent rock was formed during the Miocene, and resulted in the topographic features characteristic of the karst region: sinkholes, caves, cliffs, karst valleys (long and narrow valleys) and mogotes (long and narrow tops) (Kelly et al. 1988; Zanoni et al. 1990). Typical elevations are 150-250 m with maximum elevation of 467 m. The vegetation of the park is classified as subtropical broadleaf forest with strong differences in vegetation composition between the karst valleys and the *mogotes* (Zanoni et al. 1990).

On the 22nd of September 1998, hurricane Georges crossed the island of Hispaniola with sustained wind speeds of 210 Km/hour (approx. 50 m/s) causing extensive damage throughout the island (Mejia and Rodriguez 1999). As part of a previous study on the effects of previous land use on vegetation structure and composition, we had conducted extensive vegetation surveys in the park in January of 1997 (Rivera et al. 2000). We re-sampled our study sites in July, 1999, nine months after hurricane Georges crossed the study site in Los Haitises.

Study sites were distributed in 3 areas within the park that were accessible by road or from the sea: Trepada Alta (TA), Caño Hondo (CH), and Los Naranjos (LN). Interviews with park guards were used to determine the land use history of each site (Rivera et al. 2000). In consultation with park guards, sites were chosen to represent the variation in land use within each of the three study areas. We used guards' specific knowledge of previous land use and not the current status of the vegetation as selection criteria. Particular *mogote* tops were largely chosen for their relative accessibility, and all were covered by closed forest prior to the hurricane.

In valleys we surveyed five pasture sites, eleven *conucos* (mixed plantings of root crops, citrus and other annual and perennial crops), two former cacao plantations, and two sites that we termed "old forest" because they have characteristics of mature forests and there is no historical information on previous land use). We also surveyed six *mogote* tops. All pasture sites were abandoned at the time settlers were removed from the park (~ 5 years), and all cacao plantations and forests had been abandoned for a longer time ($>$25 years). *Mogote* tops were never cultivated. There was sufficient variation in time since abandonment in *conucos* to justify dividing these sites into two groups ("young", ~ 5 yr., and "old", $>$ 5 yr.). Although we observed some evidence of selective logging in *mogote* tops (e.g., removal of *Manilkara bidentata*), these sites showed little evidence of human effects. The two "old forest" sites were identified by park guards as having had little human use in recent times. However, the presence of cultivated plants (e.g., *Citrus sp., Persea americana, Artocarpus altitis*) indicated past human influences.

Some of these sites are old enough to have been damaged during previous hurricanes. The last two important hurricanes crossed Hispaniola in 1979 (David) and 1987 (Emily). Thus, the condition of the vegetation before the hurricane may have reflected long-term recovery from previous damage.

As part of a previous study on the effects of previous land use on vegetation structure and composition, we had conducted extensive vegetation surveys in the park in January of 1997 (Rivera et al. 2000). We had previously established and marked with pvc tubing 4 transects 1×50 m (50 m^2) in length at each site. Prior to the hurricane we identified, counted, and measured each stem $>$1.0 in dbh (diameter at breast height) in all of these transects. Variation between sites with the same prior land use was captured by these pre-hurricane measurements (Rivera et al. 2000). Post-hurricane data were collected in 1999, nine months after Georges passed over the study site. Thus, our data reflect the early stages of post-hurricane changes in vegetation. After the hurricane, fallen trees prevented us from relocating and measuring some of the previously established transects. We handled this difficulty by using the endpoints of two out of the four pre-hurricane transects and extending the width of the area sampled along each transect to 2 m (2×50 = 100 m^2). For the cases in which we extended the width of the established transects, we were unable to determine which part of the transects had been sampled prior to the hurricane. However, we expect that wider, shorter transects may produce greater and smaller estimates of stem density and basal area with equal probability. The same argument cannot be used for species diversity. If there was clumping in the spatial distribution of some tree species, we expect that decreasing the number of transects and increasing their width would decrease our estimate of diversity after the hurricane. Consequently, any changes in diversity we observed when comparing pre- and post-hurricane figures are a conservative estimate. The limitations of our post-hurricane sampling scheme warrant the interpretation of pre- and post-hurricane data as two snapshots in time. For plant nomenclature, we followed Liogier and Martorell (1982) and Zanoni et al. (1990). In addition, each species was confirmed by comparison with specimens in the National Botanical Garden of the Dominican Republic.

We calculated relative abundance (proportion of density of stems/area) and relative basal area (proportion of total basal area) for each species for a given land use. We compared these figures for the top 5 ranking species before and after the hurricane. We classified species into three groups to facilitate data analyses: Heliophilic species are opportunistic species that grow under full sun and open canopies. Mature forest species usually are capable of growth under the shade of a closed canopy. Finally, cultivar species are planted for their fruit, shade, or wood. Some species (e.g., *Inga vera* or *Spondias mombin*) can exist in mature forest but are also grown for their agricultural value. We arbitrarily classified these species as mature because we were unable to determine their source at our study sites.

All data were analyzed using a mixed linear model nested Analysis of Variance (ANOVA). The Mixed Procedure (SAS Institute Inc. 1997) is designed to handle both fixed and random effects. Land use and hurricane (before and after) were considered fixed effects. Hurricane damage varied greatly between our three study areas, Trepada Alta, Los Naranjos, and Caño Hondo because they differed in their proximity to the path of the hurricane. As a result, we also included study area as a fixed effect in our model. Finally, site was considered a random (block) factor nested within land use. We used Fischer's LSD test for planned comparison between means to determine if hurricane damage had affected our response variables (i.e., species diversity, stem density and basal area) within each type of land use.

Results

Land use effects

Land use history strongly influenced the nature and severity of hurricane damage (Table 1). The most dramatic effects of land use history were observed in shifts in basal area after the hurricane. Hurricane damage substantially decreased basal area in old cacao plantations, old forests and *mogote,* sites with no recent history of agricultural land use. These three land use types also had a greater number of large, older trees, and higher total basal area than *conucos* or pastures prior to the hurricane (Rivera et al. 2000).

Table 1. ANOVA results for hurricane, study area and land use effects on the vegetation of Los Haitises. NDF=Numerator degrees of freedom. DDF= Denominator degrees of freedom.

Source	NDF	DDF	F	P
Number of stems per 200 square m.				
Landuse	5	18	14.72	0.0001
Hurricane	1	22	27.32	0.0001
Area	2	17	0.14	0.86
Hurricane*Area	2	17	4.69	0.02
Landuse*Hurricane	5	22	2.64	0.05
Landuse*Hurric*Area	10	17	2.26	0.06
basal area per ha (sq.m)				
Landuse	5	18	8.33	0.003
Hurricane	1	21	47.65	0.0001
Area	2	16	3.81	0.04
Hurricane*Area	2	16	1.94	0.17
Landuse*Hurricane	5	21	9.74	0.0001
Landuse*Hurric*Area	10	16	4.43	0.004
number of species/ha.				
Landuse	5	20	2.32	0.08
Hurricane	1	22	5.16	0.032
Area	2	17	0.57	0.57
Hurricane*Area	2	17	0.58	0.56
Landuse*Hurricane	5	22	2.44	0.06
Landuse*Hurric*Area	10	17	0.77	0.65

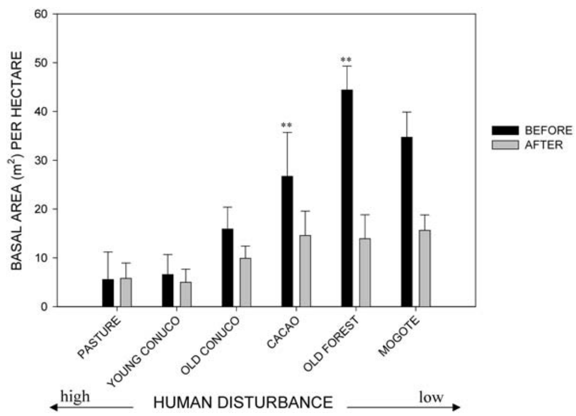

Figure 2. Mean basal area per hectare in each land use category before and after the hurricane. Bars represent standard errors. **indicates that mean values were significantly different before and after the hurricane for that land use type (p = 0.05). * indicates that values were significantly different at p=0.10.

Basal area per hectare decreased by more than 40% in cacao plantations, 50% in *mogotes*, and by more than 50% in old forest sites (Figure 2). In contrast, basal area after the hurricane was comparable to pre-hurricane Figures at sites with a more recent history of land use, such as young *conucos* or pastures (Fig-

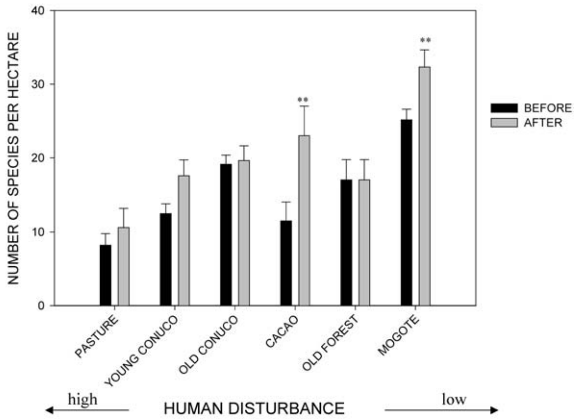

Figure 3. Mean number of species per hectare in each land use category before and after the hurricane. Bars represent standard errors. **indicates that mean values were significantly different before and after the hurricane for that land use type (p = 0.05). * indicates that values were significantly different at p=0.10.

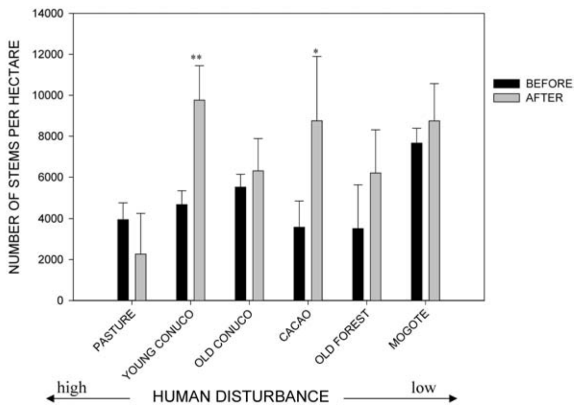

Figure 4. Mean number of stems per hectare in each land use category before and after the hurricane. Bars represent standard errors. **indicates that mean values were significantly different before and after the hurricane for that land use type (p = 0.05). * indicates that values were significantly different at p=0.10.

ure 2). Young *conucos* and pastures were dominated by many small stems < 4 cm in dbh and had the lowest amount of pre-hurricane basal area of all land use types included in our study (Rivera et al. 2000). Old *conucos* and cacao sites had intermediate basal area.

Changes in species diversity paralleled to some degree changes in basal area (Table 1). The total number of plant species had doubled in former cacao plantations and increased by 25% in *mogotes* compared to pre-hurricane Figures (Figure 4). The increase in the number of species for these two land use types was driven by the appearance of opportunistic, heliophilic species, such as *Cecropia scheberiana* in *mogotes*, which had not been present in the understory prior to the hurricane. Despite dramatic decreases in basal area as a result of hurricane damage, we did not observe an increase in species diversity in forest sites after the hurricane. One possible reason for the lack of change in diversity is the small sample size for forest sites (n = 2). Moreover, the two forest sites were in valleys, which were flooded by the hurricane (A. Balbuena, pers. comm.). This flooding may have killed many of the seedlings and seeds present in the forest floor prior to the hurricane.

Land use history had a smaller effect on changes in stem density after the hurricane (Table 1). With the exception of old *conucos* and pastures, stem density increased at the majority of sites after the hurricane. However this increase was only significant in young *conucos* and former cacao plantations where the number of stems doubled after the hurricane (Figure 4).

Community composition effects

Species composition also changed at many of the sites. In most cases, however, a large proportion of species ranking among the five most important in each community prior to the hurricane maintained these rankings after the hurricane (Table 2). However, the hurricane changed relative basal area and relative abundance for these high-ranking species (Table 2). With a few exceptions, the relative basal area of species within our three “habitat” groups, pioneer, mature and cultivar species, remained comparable to pre-hurricane Figures. The effects of the hurricane on species composition was idiosyncratic to each particular land use:

(a) In pastures, *Lepianthes* sp. accounted for a large proportion of species abundance after the hurricane, but the dominance of *Piper aduncum* was reduced. The hurricane also increased the relative basal area of *Hura crepitans* at these sites (Table 2). All of these species are heliophiles that thrive in open environments. Hurricane damage did not alter light availability at these already open sites. However, hurricane Georges flooded most of the pastures and may have favored those species with a greater capacity to survive in flooded soils. We observed many dead *Piper aduncum* stems in our transects.

(b) In young *conucos, Inga vera, Guarea guidonia* and *Coffea arabica* accounted for a larger portion of

Table 2. Five most important species before and after the hurricane in each type of land use. Species are classified into three classes: cultivar, heliophile or mature forest plants.

Before	Relative abundance	Relative basal area	After	Relative abundance	Relative basal area
PASTURE					
Piper aduncum (Heliophile)	46.5	44.4	*Psidium guajava* (Cultivar)	24.4	44.6
Psidium guajava (Cultivar)	24.1	28.5	*Piper aduncum* (Heliophile)	17.1	8.5
Lantana camera (Heliophile)	6.1	4.6	*Hura crepitans* (Heliophile)	2.7	36.4
Inga vera (Mature/cultivar)	1.6	8.3	*Lepianthes sp.* (Heliophile)	14.7	1.1
Piper leateviride (Heliophile)	6.1	4.2	*Guarea guidonia* (Mature)	5.4	0.3
Total	84.4	90.0	Total	64.3	90.8
YOUNG CONUCO					
Piper aduncum (Heliophile)	27.3	39.0	*Piper aduncum* (Heliophile)	12.7	2.7
Triumfetta sp. (Heliophile)	14.7	7.3	*Mangifera indica* (Cultivar)	0.5	41.6
Psidium guajava (Cultivar)	5.2	5.9	*Guarea guidonia* (Mature)	5.4	3.4
Piper leateviride (Mature)	6.4	3.0	*Inga vera* (Mature/cultivar)	3.5	8.6
Lantana camara (Heliophile)	5.1	3.3	*Coffea arabica* (Cultivar)	8.1	0.4
Total	58.7	58.5	Total	30.1	56.6
OLD CONUCO					
Piper leateviride (Mature)	27.1	15.0	*Guarea guidonia* (Mature)	16.1	11.8
Piper jacq. (Mature)	17.0	7.0	*Spondias mombin* (Mature/cultivar)	2.8	15.4
Guarea guidonia (Mature)	10.5	7.3	*Piper aduncum* (Heliophile)	10.3	3.0
Spondias mombin (Mature/cultivar)	2.7	7.5	*Coffea arabica* (Cultivar)	5.1	2.8
Citrus Spp. (Cultivar)	1.9	6.1	*Piper jacq.* (Mature)	6.5	1.6
Total	59.1	43.0	Total	40.9	34.7
CACAO					
Theobroma cacao (Cultivar	35.1	52.3	*Theobroma cacao* (Cultivar)	36.0	27.3
Psychotria pubescens (Heliophile)	13.0	5.2	*Guarea guidonia* (Mature)	7.1	54.6
Inga vera (Mature/cultivar)	6.5	10.2	*Inga vera* (Mature/cultivar)	10.0	15.1
Guarea guidonia (Mature)	10.4	6.4	*Ocotea spp.* (Mature)	6.3	0.1
Piper jacq. (Mature)	5.2	2.2	*Chrysophyllum argenteum* (Mature)	7.9	0.1
Total	70.0	76.4	Total	67.4	97.2
OLD FOREST					
Piper leateviride (Mature)	25.7	6.3	*Cecropia scheberiana* (Heliophile)	14.4	9.8
Piper jacq. (Mature)	16.6	3.7	*Guarea guidonia* (Mature)	4.8	18.2
Psychotria pubescens (Heliophile)	16.0	4.7	*Piper jacq.* (Mature)	14.4	6.0
Guarea guidonia (Mature)	4.8	22.1	*Piper leateviride* (Mature)	8.2	4.2
Artocarpus altitis (Cultivar)	3.4	23.2	*Artocarpus altitis* (Cultivar)	2.2	7.9
Total	66.5	60.0	Total	44.1	46.1
MOGOTE					
Ocotea coriacea (Mature)	27.1	14.8	*Coccoloba diversifolia* (Mature)	6.1	14.7
Bombacopsis emarginata (Mature)	11.0	10.7	*Mastochidendron deminguensis* (Mature)	6.3	5.4
Coccoloba diversifolia (Mature)	7.8	6.4	*Cecropia scheberiana* (Heliophile)	10.6	0.3
Cinamodendrum ekmanii (Mature)	3.0	9.9	*Bombacopsis emarginata* (Mature)	6.0	10.0
Prunus myrtifolia (Mature)	4.7	3.7	*Miconia laevigata* (Mature)	3.5	8.1
Total	53.6	45.5	Total	32.5	38.4

standing species after the hurricane, but *Psidium guajava* and *Lantana camara* decreased in importance. The latter species had trees with smaller diameter before the hurricane and may have been more susceptible to hurricane damage. The relative basal area of *Piper aduncum* decreased after the hurricane, replaced by an increase in the relative basal area of *Mangifera indica*. However, as we indicated before, we doubled the width of transects in our post-hurricane sampling. The new transects included a particularly large *Mangifera indica* individual which accounted for the large shift in relative basal area in favor of this species (Table 2). Thus, this particular result cannot be interpreted as a direct consequence of hurricane damage.

(c) In old *conucos, Guarea guidonia, Piper aduncum* and *Coffea arabica* increased in relative abundance while the abundance of *Piper laeteviride* and *Piper jacquemontianum* decreased. These two species of *Piper,* typically found in closed gallery forest under relatively closed canopy conditions, may have decreased in abundance following canopy opening during the hurricane. The relative basal area of *Guarea guidonia* and *Spondias mombin* increased after the hurricane while that of *Piper* sp. decreased (Table 2).

(d) In cacao plantations, *Ocotea* sp., *Chrysophyllum argenteum* and *Inga vera* increased in relative abundance while *Psychotria pubescens* and *Piper jacquemontianum* decreased after the hurricane. Dominance in relative basal area shifted from *Thebroma cacao* to *Guarea guidonia* (Table 2). The large shift in relative basal area in favor of *Guarea guidonia* could be attributed to several individuals from this species not included in our pre-hurricane transects.

(e) In old forest sites, hurricane damage decreased the relative abundance of both *Psychotria pubescens* and *Piper laeteviride*. These two species typically occur in the shaded understory, but can also survive in forest gaps under somewhat open canopy conditions. However, hurricane damage caused severe damage to the canopy at these forest sites, favoring aggressive pioneers such as *Cecropia schreberiana* which can easily outgrow more shade-tolerant species like *Psychotria pubescens* and *Piper laeteviride*. Post-hurricane census data showed that *Cecropia scheberiana* increased in both relative abundance and basal area at these old forest sites (Table 2). This species is usually well represented in the seed bank and can respond quickly to increased light availability (Lomascolo and Aide 2001).

(f) Finally, the relative abundance of mature forest species within the top 5 species decreased in *mogotes* while that of pioneer species increased (Table 2). Specifically, *Bombacopsis emarginata, Ocotea coriacea, Prunus myrtifolia* and *Cinamodendrum ekmani i* decreased in relative abundance in *mogotes* after the hurricane; *Cecropia scheberiana, Mastichodendron dominguensis, Miconia laevigata* and *Coccoloba diversifolia* increased in abundance. Paralleling changes in relative abundance, the relative basal area decreased slightly for mature species at *mogote* sites and the relative importance of species shifted as a result of hurricane damage. Specifically, relative basal area of *Ocotea coriacea, Cinnamodendrum ekmanii*, and *Prunus myrtifolia* decreased while the relative basal area of *Mastichodendron dominguensis* and *Miconia laevigata* increased (Table 2). Pioneer species only accounted for a small percentage of basal area among five top species because these individuals were primarily saplings of small diameter and their relative basal area did not change in any significant manner after the hurricane (Table 2).

Discussion

Prior agricultural use influenced both damage and recovery from hurricane disturbance. The effects of hurricane damage on basal area were most dramatic in sites with no recent history of agricultural exploitation, namely old cacao plantations, forests, and *mogote* tops. These three land use types had a greater number of large, older trees, and higher total basal area than *conucos* or pastures prior to the hurricane (Rivera et al. 2000). Tall trees of large diameter are more likely to be uprooted during a hurricane and to damage neighboring trees in the process (Walker 1991). Additionally, topography probably accounts for some of the drastic decrease in basal area in *mogote* hilltop communities. Previous studies in Caribbean forests found that hurricane damage was higher in exposed ridge tops than in adjacent valleys (Bellingham 1991, Brokaw and Grear 1991). However, one study in Puerto Rico found that damage from Hurricane Hugo was most severe in valleys and attributed this to differences in species composition between valleys and ridges (introduced vs. native), differences in soil stability and drainage between the two habitats, and big trees and branches falling from ridges into valleys (Basnet et al. 1992).

Land use history also affected species recruitment after hurricane damage. For most sites, hurricane damage increased the total number of species, although this trend was only significant in *mogotes* and old cacao plantations, paralleling to some degree changes in basal area. These two land use types had high basal area prior to the hurricane and had suffered greater hurricane damage. Treefall gaps and damage to the canopy increased light penetration in the understory (e.g., gaps) and enhanced recruitment of heliophilic species (e.g., *Cecropia scheberiana*) at these sites. Rates of tree growth in canopy gaps are usually very high, and recovery from a hurricane occurs from growth of trees that remain standing as well as new trees (Brokaw and Grear 1991).

Prior agricultural land use may have also affected the movement of seed dispersers and the potential for recovery after the hurricane. Dense shade canopies in *mogotes* and cacao plantations that would have prevented regeneration of heliophile species prior to the hurricane, may have also facilitated the increase in the number of species in cacao plantations and *mogotes* after the hurricane because a dense canopy provides perching and nesting sites for birds and enhances regeneration of species with bird-dispersed seeds (Saunders et al. 1991). Former cacao plantations and *mogotes* at this site harbor higher bird diversity than either pastures or traditional *conucos* (Power and Flecker, unpub. data). Seeds from bird-dispersed tree species might have already been present in the understory before the hurricane. Gap formation after the hurricane might have facilitated seed germination and seedling growth for these species.

Land use history was also the dominant factor determining community composition after the hurricane for all land use types. The maintenance of a large percentage of species basal area and abundance rankings within land use types after the hurricane suggests that human land use leaves a lasting trace on the landscape that persists through natural disturbance. Regeneration patterns within each land use might just reflect the "regeneration niches" of species present in the community prior to the hurricane (Vandermeer et al. 1997). Sites with a history of recent land use have a higher percentage of heliophilic species with high growth rates and little resprouting ability. On the other hand, sites with no recent history of agricultural use may have species with slower growth rates and capability to re-sprout after hurricane damage. Land use may affect recovery from natural disturbance by narrowing the pool of species that will re-sprout or regenerate after the hurricane. Our study demonstrates that hurricane damage may act to maintain the species composition characteristic of each land use type.

In some cases, however, the impact of past agricultural exploitation not only limits the pool of species present but also alters soil structure and hydraulic regimes making land more vulnerable to erosion and flooding. For instance, hurricane Georges flooded most of the pastures at Los Haitises. Soil compaction at these sites prevented rainwater from rapidly draining after the storm. Flooding, rather than direct hurricane damage, killed many of the existing *Psidium guajava* and *Piper* sp. (M. Uriarte, personal observation) and may have hindered regeneration of species present in these pastures prior to the hurricane. Slow dispersal of woody species into pastures or competition with ferns and herbaceous biomass, which occur at high densities in these sites, may have also prevented prevented or slowed?colonization by woody species after the hurricane (Aide et al. 1995).

Land use history can have important effects on plant community recovery from a natural disturbance. Past agricultural activity is not always detrimental to forest recovery. In our study, the total number of woody species increased in cacao sites after the hurricane. In traditional cacao plantations, trees are grown under a canopy of shade trees remnant of the original forest, providing habitat for plants, insects, and birds (Perfecto et al. 1997). As a result, we might expect high levels of diversity in these traditional plantations after a hurricane because the pool of species present in the understory is larger than in other agricultural systems. On the other hand, in pastures, diversity, basal area, and stem density remained low and unaltered by hurricane damage. In this case, the impact of previous land use is unaffected by natural disturbance. Forest recovery at these sites probably necessitates external inputs (e. g., chemicals, fertilizers, plantings).

Our examination of the interaction between natural and anthropogenic disturbance offers new insights into forest successional dynamics and suggests guidelines for the management of degraded lands and secondary forests. Hurricane disturbance may hinder the conversion of degraded lands to forests by flooding soils, leaching nutrients and uprooting initial colonizers. However, canopy opening as a result of hurricane damage can also accelerate the conversion of more benign agricultural land uses to forest. Increases in species diversity in the least degraded land uses, i.e., mogotes and cacao plantations, after the hurricane suggest that some land uses may facilitate recovery from hurricane damage. The selection of agroecosystems that mimic vegetation structure and composition of tropical forests and maintain the integrity of the soil can interact with natural disturbance to accelerate the conversion of agricultural landscapes to secondary forests.

Our study shows that anthropogenic disturbances can either facilitate or hinder recovery from a natural disturbance. This study adds to a growing body of evidence demonstrating that anthropogenic disturbances can override natural, infrequent disturbances with surprising or unpredictable ecological consequences (Paine et al. 1998). Several studies in the temperate areas and elsewhere in the tropics have demonstrated that land use history has long-lasting legacies that affect damage and recovery from natural wind disturbance (i.e., hurricanes and cyclones) (Boose et al. 2001; Burslem et al. 2000). The successional trajectories of secondary forests after hurricane damage may be largely unpredictable, particularly in areas with little knowledge of historical land use.

Acknowledgments

We would like to thank A. and S. Balbuena for assistance in locating the plots and plant identification, E. and R. Marcano for logistical support, and P.L. Marks for comments on the manuscript. We acknowledge the support of Cornell International Institute of Food, Agriculture, and Development (CIIFAD).

References

Aide T.M., Zimmerman J.K., Herrera L., Rosario M. and Serrano M. 1995. Forest recovery in abandoned tropical pastures in Puerto Rico. Forest Ecology and Management 2: 219–229.

Aide T.M., Zimmerman J.K., Rosario M. and Marcano H. 1996. Forest recovery in abandoned cattle pastures along an elevational gradient in northeastern Puerto Rico. Biotropica 28: 537–548.

Alaka M.M. 1976. Climatology of Atlantic tropical storms and hurricanes. In: Schwerdtfeger W. (ed.), Climates of Central and South America, World Survey of Climatology. Elsevier Scientific Publishing Company, Amsterdam, The Netherlands.

Basnet K., Likens G.E., Scatena F.N. and Lugo A.E. 1992. Hurricane Hugo: damage to a tropical rainforest in Puerto Rico. Journal of Tropical Ecology 8: 47–55.

Bellingham P.J. 1991. Landforms influence patterns of hurricane damage: evidence from Jamaica montane forests. Biotropica 23: 427–433.

Birdsey R.A. and Weaver P.L. 1987. Forest area trends in Puerto Rico. Us. Forest Ser. Res. Note SO-331. 13 pp.

Boose E.R., Chamberlin K.E. and Foster D.R. 2001. Landscape and regional impacts of hurricanes in New England. Ecological Monographs 71: 27–48.

Brokaw N.V.L. and Grear J.S. 1991. Forest structure before and after hurricane Hugo at three elevations in the Luquillo Mountains, PR. Biotropica 23: 386–392.

Brown S. and Lugo A.E. 1994. Rehabilitation of tropical lands: a key to sustaining development. Restoration Ecology 2: 97–111.

Burslem D.F.R.P., Whitmore T.C. and Brown G.C. 2000. Short-term effects of cyclone impact and long-term recovery of tropical rainforest on Kolombangara, Solomon Islands. J. of Ecology 88: 1063–1078.

Foster D.R. 1992. Species and stand response to catastrophic wind in central New England. Journal of Ecology 76: 135–151.

Garcia-Montiel D. and Scatena F.N. 1994. The effect of human activity on the structure and composition of a tropical forest in Puerto Rico. Forest Ecology Management 63: 57–78.

Hamburg S.P. and Sanford R.L. Jr. 1986. Disturbance, *Homo sapiens* and ecology. Bulletin of the Ecological Society of America 67: 169–171.

Kelly D.L., Tanner V.J., Kapos V., Dickinson T.A., Goodfriend G.A. and Fairbaim P. 1988. Jamaican limestone forest: floristics, structure, and environment of three examples along a rainfall gradient. Journal of Tropical Ecology 4: 121-156.

Liogier A.H. and Martorell L.F. 1982. Flora of Puerto Rico and adjacent islands. Rio Piedras, Puerto Rico. Editorial de la Universidad de Puerto Rico.

Lomascolo T. and Aide T.M. 2001. Seed and seedling bank dynamics in secondary forests following Hurricane Georges in Puerto Rico. Caribean Journal of Science 37: 259–270.

Mejia M.L. and Rodriguez L.P. 1999. Georges: 15-27 September 1998. 20 pp. Oficina Nacional de Metereología, Santo Domingo, Republica Dominicana.

Neumann C.J., Jarvinen B.R., McAdie C.J. and Elms J.D. 1999. Tropical Cyclones of the North Atlantic Ocean, 1871-1998. National Climatic Center, Asheville, North Carolina, USA.

Padoch C. and Vayda A.P. 1983. Patterns of resource use and human settlement in tropical forests. Eds. Tropical rainforest ecosystems, pp. 301–313. Elsevier, New York, New York, USA.

Paine R.T., Tagener M.J. and Johnson E.A. 1998. Compounded perturbations yield ecological surprises. Ecosystems 1: 535–545.

Platt W.J., Beckage B., Doren R.F. and Slater H.H. 2002. Interactions of large-scale disturbances: prior fire regimes and hurricane mortality of savanna pines. Ecology 83: 1566–1572.

Perfecto I., Vandermeer J., Hanson P. and Cartin V. 1997. Arthropod biodiversity loss and the transformation of tropical agroecosystems. Biodiversity and Conservation 6: 935–945.

Reiners W.A., Bowman A.F., Parsons W.F.J. and Keller M. 1994. Tropical rain forest conversion to pasture: changes in vegetation and soil properties. Ecological Applications 4: 363–377.

Rivera L.W., Zimmerman J.K. and Aide T.M. 2000. Forest recovery in abandoned agricultural lands in the karst region of the Dominican Republic. Plant Ecology 148: 115–125.

Robertson K.M. and Platt W.J. 2001. Effects of multiple disturbances (fire, hurricane) on epiphyte-host tree association in a subtropical forest, Florida, USA. Biotropica 33: 573–582.

SAS Institute 1997. SAS/STAT software: changes and enhancement through release 6.12. SAS Institute, Cary, North Carolina, USA.

Saunders D.A. and de Rebeira C.P. 1991. Values of corridors to avian populations in a fragmented landscape. In: Saunders D.A. and Hobbs R.J. (eds), Nature conservation 2: The role of corridors. pp 221-240. Surrey Beatty, Australia.

Shukla J., Nobre C. and Sellers P. 1990. Amazon deforestation and climate change. Science 247: 1322–1325.

Skole D.L., Chomentowski W.H., Salas W.A. and Nobre A.D. 1994. Physical and human dimensions of deforestation in Amazonia. Bioscience 44: 314–322.

Tanner E.V.J., Kapos V. and Healy J.R. 1991. Hurricane effects on forest ecosystems in the Caribbean. Biotropica 23: 513–521.

Uhl C. 1987. Factors controlling succession after slash and burn agriculture in Amazonia. Journal of Ecology 75: 377–407.

Uhl C., Buschbacher R. and Serrão E.A.S. 1988. Abandoned pastures in eastern Amazonia. I. Patterns of plant succession. Journal of Ecology 76: 663–681.

Vandermeer J.H., de la Cerda I.G. and Boucher D. 1997. Contrasting growth rate patterns in eighteen tree species from a post-hurricane forest in Nicaragua. Biotropica 29: 151–161.

Waide R.B. and Lugo A.E. 1992. A research perspective on disturbance and recovery of a tropical montane forest. In: Goldammer J.G. (ed.), Tropical forests in transition. pp. 173-190. Birkhauser Verlag, Basel, Switzerland.

Walker L.R. 1991. Forest structure before and after hurricane Hugo in Luquillo Experimental Forest, Puerto Rico. Biotropica 23: 379–385.

Weaver P.L. 1986. Hurricane damage and recovery in the montane forest of the Luquillo Forest in Puerto Rico. Caribbean Journal of Science 22: 53–70.

Zanoni T.A., Mejia M.M.M., Pimentel J.D. and Garcia R.G. 1990. La flora y la vegetación de los Haitises, República Dominicana. Moscosoa 6: 46–98.

Zimmerman J.K., Aide T.M., Rosario M., Serrano M. and Herrera L. 1995. Effects of land management and a recent hurricane on forest structure and composition in the Luquillo Experimental Forest, Puerto Rico. Forest Ecology and Management 77: 65–76.

Zou X., Zucca C.P., Waide R.B. and McDowell W.H. 1995. Long-term influence of deforestation on tree species composition and litter dynamics of a tropical rain forest in Puerto Rico. Forest Ecology Management 78: 147–157.