SIXTY-TWO YEARS OF CHANGE IN SUBTROPICAL WET FOREST STRUCTURE AND COMPOSITION AT EL VERDE, PUERTO RICO

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SUMMARY

A plot established in 1943 in a subtropical wet forest at the Luquillo Experimental Forest of Puerto Rico has been assessed periodically for changes in species and size of all trees >4cm diameter. Forest dynamics on a 0.72ha plot (EV-3) at 400masl at El Verde show recovery principally from hurricanes of 1928 and 1932, timber stand improvement in 1958, and from Hurricanes Hugo and Georges in 1989 and 1998. Damage from Hurricane Hugo only temporarily slowed aboveground biomass accretion of the developing forest. Stand increases in basal area and biomass continue to be due principally to growth of the dominant overstory species, Dacryodes excelsa and Manilkara bidentata, ingrowth of which was stimulated by Hugo. The pioneer species Cecropia schreberiana *filled gaps abundantly following the Hurricane and the understory tree* Psychotria berteriana *proliferated. Ingrowth of* Prestoea montana *has been greater than for all other species since 1976 and was stimulated by Hugo and Georges as well as prior hurricanes, so that by 2005 it was the most abundant species. Hurricane Hugo caused low mortality among the largest trees on the plot. As a few species have become more dominant species evenness has declined. Species richness is only slightly greater today than in 1943. Results are discussed in terms of "building" and "thinning" phases associated with major hurricanes. Hurricanes have stimulated the addition of species to the forest in "building years," but have maintained that richness in the intervening "thinning years", lending credence to the "intermediate disturbance hypothesis".*

Hurricanes are the dominant form of large scale disturbance in the Caribbean Basin and in Puerto Rico (Walker *et al*., 1991). In the 20th century, Hurricane San Felipe had passed to the southwest of the Mountains in 1928 and in 1931, Hurricane San Nicolas passed to the north over the ocean. Hurricane San Cipriano (September 26, 1932) passed directly over the Luquillo Mountains and the Luquillo Experimental Forest (LEF) in northeastern Puerto Rico with winds of 200km/h and >430mm of rain (Crow, 1980; Weaver, 1989). Hurricane Santa Clara produced 220mm of heavy rainfall at El Verde in 1956, but only "local or slight" damage, principally defoliation, over the Luquillo Mountains (Wadsworth and Englerth, 1959). In 1989, Hurricane Hugo passed just northeast of the LEF with winds of 166km/h and precipitation >200 mm over most of the LEF (Brennan, 1991; Scatena and Larsen, 1991). Hurricane Georges passed over southern Puerto Rico in 1998, but significantly affected the LEF to the north. Most noticeable in terms of defoliation, stem and branch breakage, and uprooting, however, were Hurricanes San Cipriano and Hugo.

In 1943, the U.S. Forest Service began establishing permanent plots on the LEF for monitoring forest and tree growth (Weaver, 1998). At El Verde, plot EV-3 was established by Frank Wadsworth at 400m elevation in the tabonuco forest type, the *Dacryodes-Sloanea* association *sensu* Beard (1949), and subtropical wet forest life zone (Ewel and Whitmore, 1973). The above-average site was chosen in order to assess stem growth of young trees of commercially valu-

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able species. In 1937, "a very light cutting in order to minimize the impact on the watershed" was conducted by the Forest Service of the area where the plot was subsequently sited (no records kept) and a timber-stand improvement treatment was applied in 1958 (F. Wadsworth, cited by Odum, 1970; Crow, 1980) which removed 146 stems, 109 from the 4-8cm diameter class, 26 from the 8-16cm class and 11 trees that were >16cm. *Sloanea berteriana*, *Dacryodes excelsa* and *Manilkara bidentata* were among the most common species removed. The plot has been monitored at 1 to 12 year intervals from establishment through 2005, making it one of the longest continuously monitored forest growth plots in the neotropics. Frequent hurricane activity in the area allowed for long-term assessment of species change and forest growth dynamics in response to catastrophic disturbance.

The University of Puerto Rico's El Verde Field Station was the general location for U.S. Atomic Energy Commission studies on effects of gamma irradiation on tropical forests (Odum, 1970) between 1963 and 1967, and has since served as the site for numerous field studies in tropical ecology (Reagan and Waide, 1996). The 16ha plot of tabonuco forest at El Verde, the Luquillo Forest Dynamics Plot (LFDP) established in 1990 ~0.5km from EV-3, is currently being monitored for woody species recovery from hurricanes (Thompson *et al*., 2004) and provides a nearby large scale example of changing forest dynamics to which EV-3 has been compared for the years following Hurricane Hugo. Although it is only a single plot, the long-term growth record provided by EV-3 is an invaluable supplement to the more recently established LFDP and provides information on the local forest that predates the larger 16ha plot. EV-3 has also served as the site for intensive studies of variation in oxisol soil series and vegetation according to topographic position (Johnston, 1992).

The purpose of this paper is to assess long-term forest changes to EV-3 from Hurricanes San Cipriano, San Nicholas and San Felipe in terms of forest structure, species community composition and tree growth during the 45 years following plot establishment (1943-88) and from Hurricanes Hugo in 1989 and Georges in 1998. The 62-year analysis of forest change updates a previous study of EV-3 (Crow, 1980) which was based on assessment dates of 1943, 1946, 1951 and 1976 and provides a longer term assessment of tropical forest dynamics where hurricanes are the principal form of "wind" disturbance initiating allogenic succession. Since EV-3 was already being monitored during Hurricanes Hugo and Georges, forest changes in the years immediately following hurricane disturbance are now evident, unlike the years following the hurricanes of 1928 and 1932 which impacted the Forest 11-15 years prior to plot establishment.

Methods

Site and species

Plot EV-3 at El Verde is 0.72ha in size, rectangular (60×120m) with a northwest aspect and is situated on a ridge on the south side of the Río Soñadora in the Luquillo Experimental Forest, a long-term ecological research site. The plot is ~0.5km from the site of the earlier irradiation studies and the 16ha Forest Dynamics plot. Between 1975 and 2003 the mean annual precipitation at El Verde Field Station was 3536mm and the mean annual temperature, 24.0°C. The minimum monthly precipitation usually occurs in January, averaging ~232mm. Soils on EV-3 are derived from marine deposited volcanic "sandstones" (Scatena, 1989) and are mostly acid clays of low cation exchange capacity (Soil Survey Staff, 1995).

Seven "indicator" species (sensu Crow, 1980) cover a wide range of ecologic functional niches within the tabonuco forest. These species (*Cecropia schreberiana* L., *Croton poecilanthus* Urb., *Dacryodes excelsa* Vahl, *Manilkara bidentata* (A. DC.) Chev., *Prestoea montana* (R. Graham) Nichols, *Schefflera morototoni* (Aubl.) Maguire, Steyerm. & Frodin, *Sloanea berteriana* Choisy), have been dominant on EV-3 since measurements began or have well known successional roles and are highlighted in the ongoing plot dynamics.

Plot assessment

Since the assessment by Tom Crow in 1976 (Crow, 1980), EV-3 was assessed by Mark Johnston in 1988 (Johnston, 1990), Salvador Alemañy in 1993, by Yinghao Zhao in summer, 1998 just prior to the passage of Hurricane Georges over Puerto Rico and by Jeremy Boley in 2005. In all censuses, all individuals of all tree species >4.0cm diameter at breast height (dbh) were measured at 1.37m from the ground. Palms were not measured for dbh unless their most current internode had reached 1.37m. Ingrowth trees and palms that entered the smallest diameter class since the previous measurement were numbered and marked with aluminum tags nailed at 10cm below breast height.

Stand parameters used to characterize changes in EV-3 since 1943 were absolute and relative distribution of stems by diameter class, basal area, species richness, evenness and overall diversity, stand biomass (aboveground woody and total aboveground), palm biomass (total aboveground), importance value, and number of species gained and lost per sampling interval. Importance value (IV) was calculated as the sum of relative dominance (basal area), relative frequency (over 18 sub-plots, each 20×20m), and relative density on a scale of 0 to 300.

Diversity was assessed using the Shannon-Weiner diversity index (Shannon and Weaver, 1949) $H= -\Sigma p_i \log_e p_i$, where p_i is the proportion of trees in species i. Overall evenness of species abundances was expressed by Pielou's J (Pielou, 1966; Peet, 1974) where $J= H/H_{max}$. H_{max} is the maximum possible value of H for the observed number of species which would occur with all p_i equal.

Stand biomass was determined using equations developed by Weaver and Gillespie (1992) for tabonuco forest on the LEF. Total aboveground dry weight (Y, leaves + wood) in kg per tree, independent of species, was estimated using tree dbh (D) in cm as the sole predictor. For D<5cm, $Y= 0.3210D^{1.3925}$, and for D>5cm, $Y= 4.7306-2.8566D+0.5832D^2$.

Aboveground woody dry weight (Y) in kg per tree was similarly estimated using tree dbh (D) in cm as the sole predictor. In this case, for D<5cm, $Y= 0.2634D^{1.4539}$, and for D>5cm, $Y= 5.7266-3.0469D+0.5659D^2$.

The dry weights of individual stems were summed using both equations to yield the total aboveground and aboveground woody biomass for the stand exclusive of palms. Crow's (1980) biomass figures, based on equations of Ovington and Olson (1970), were recalculated using Weaver and Gillespie's (1992) improved equations and presented for the plot from its inception.

Palm stand biomass was determined using the linear regression equation developed by Frangi and Lugo (1985). Total aboveground dry weight (Y) in kg per palm was estimated using stem height (X) in m as the sole predictor, as $Y= 7.7X+4.5$. Palm biomass was only calculated for 1998 because of differences in height growth assessment methods in earlier years or the absence of height measurements.

Results

Community Development

Following the major hurricanes of 1928, 1931 and 1932, an increase in total stem number was recorded between 1943 and 1946. Part of this increase in stem numbers may be attributed to disturbance and canopy opening by the 1937 selection harvest. Stem numbers appeared to stabilize between 1946 and 1951 then steadily declined until 1988. The 1993 census showed an increase after Hurricane Hugo in 1989 which has continued through Hurricane Georges to date (Figure 1a). Increases in diversity occurred simultaneously with the addition of new stems

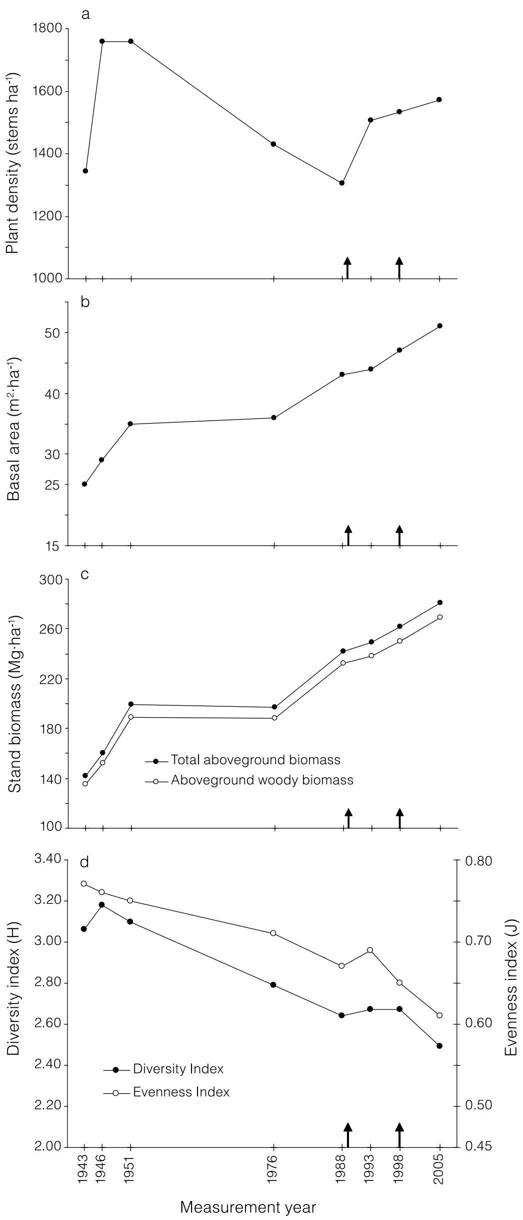

Figure 1. a: plant density, b: total basal area, c: total aboveground biomass (leaves and wood) and aboveground woody biomass, and d: Shannon-Weiner diversity index (H) and overall evenness index (Pielou's J) for trees on El Verde plot EV-3 for measurement years between 1943 and 2005. Arrows indicate years of Hurricanes Hugo (1989) and Georges (1998).

to the plot, but in between, i.e., 1946-88, and after 1998, diversity declined (Figure 1d). Evenness was highest at 0.76 in 1943 and has since declined to 0.61 following the trend in diversity through 2005.

Basal area and stand biomass increased between 1943 and 1951 after which there was little change until the 1976-2005 period when both increased again, basal area by ~50% and biomass by 40%. In the four years post-Hugo, basal area and biomass increased, but at a slower rate than before the storm, then resumed a more rapid rate to 2005 (Figures 1b, c). In 1998, total aboveground biomass, exclusive of palms, was 262.3Mg/ha. Palm biomass in 1998 was estimated as 16.4Mg/ha for a total aboveground plot biomass of 278.7Mg/ha.

Tree species gained on the plot were in excess of species lost in the years 1943-51 following the hurricanes of the 1930's. There was a net gain of 12 species between 1943-46. The same trend appeared again following Hurricane Hugo, when the plot gained a net total of 11 species between 1993-98. Between those events, however, such as the 42 years from 1951-93 the plot experienced a net loss of 13 species. In the seven years following Hurricane Georges there was neither net gain nor net loss of species (Table I).

Overall, *D. excelsa* was the most abundant and dominant species on the plot through 1998, a position it had held since 1943 (Figure 2; Crow, 1980). By 2005, *P. montana* had overtaken it in abundance, having risen steadily since shortly after plot establishment. No other species has shown such steady increases in abundance over the past 50 years. *M. bidentata* and *C. schreberiana* increased sharply in numbers following changes in stand conditions created by Hurricane Hugo, although *C. schreberiana* had nearly disappeared from the plot prior to the Hurricane. Similarly, *S. morototoni* responded favorably to Hurricane Hugo although its increase was recent, reversing a long term decline. Two species, *C. poecilanthus* and *S. berteriana*, are in marked decline.

The absolute numbers of stems on EV-3 peaked at 1244 in 1946 during the years immediately following the hurricanes of 1928 to 1932 (Crow, 1980) then dropped to 940 stems in 1988 before rising to a peak of 1132 in 2005 after disturbance created by Hurricanes Hugo and Georges. These figures reflect large numbers of recruitment to smaller size classes that occur following hurricanes. Today, there are more trees >24cm in diameter on EV-3 than at any time over the past 62 years even allowing for damage done by Hugo. The total number of trees >32cm was 115 in 2005, up from 103 in 1988. Most of the large trees are *D. excelsa*, and secondarily *M. bidentata* with only a few large *S. berteriana* in the overstory. The intermediate size classes, 8-20cm in diameter, have been dominated by *P. montana* since 1976 and the trend is toward increasing dominance with 144 palms in 1976, 173 in 1988, 173 in 1993, 215 in 1998 and 290 in 2005. The smallest diameter class, >4 to 8cm, has been dominated by *M. bidentata* since 1993.

Heights measured in 1993 corroborate the existence of taller trees than when heights were last assessed in 1976. There were at least four trees in the ≥27m class in 1976; in 1993 there were at least 15 trees in the same height class.

Species dynamics

The most striking feature of species dynamics on EV-3 over the past 62 years has been the transition in most dominant ingrowth species from *S. berteriana* between 1943-51 to *P. montana* in all periods since, 1951-76 (Crow, 1980), 1976-88, 1988-93, 1993-98, and 1998-2005 (Table II). Between 1988-93, 97 stems of sierra palm were added to the plot in the >4cm dbh class. At ~23 stems per year over the latter four years of this five year period, more palms were added as ingrowth in the years immediately following Hugo than at any other period between measurements since the plot was established. The comparative rate for *S. berteriana* in the 1988-93 period was 5 stems per year.

Other species also seemed to be stimulated by Hurricane Hugo as evidenced by large numbers of ingrowth of *C. schreberiana* (89), *D. excelsa* (31), *M. bidentata* (31), and *S. berteriana* (21) during the 1988-93 period. *D. excelsa* has shown high numbers of ingrowth on the plot for all censuses. During the periods reported by Crow (1980), it ranked second in numbers of stems added (42) from 1943-51 and second (55) from 1951-76. From 1976-88, ingrowth of *D. excelsa* was third highest of any species on the plot (4); from 1988-93, *D. excelsa* ingrowth was third (31); from 1993-98, *D. excelsa* was fourth (10); and from 1998-2005 it ranked third (13). Of these periods, the least *D. excelsa* ingrowth (~0.3 stems/year) occurred during 1976-88 just prior to Hurricane Hugo, the latest in a continuous decrease since the hurricanes of the 1930's (Crow,

TABLE I
NUMBER OF SPECIES GAINED AND LOST PER YEAR, AND TOTAL SPECIES AT PERIOD END, DURING SEVEN TIME PERIODS ON THE 0.72ha EL VERDE PLOT*

Time period	Species gained per year	Species lost per year	Total Species
1943-46	12 (4)	0 (0)	65
1946-51	6 (1.2)	9 (1.8)	62
1951-76	4 (0.2)	16 (0.6)	50
1976-88	10 (0.8)	8 (0.7)	52
1988-93	7 (1.4)	10 (2)	49
1993-98	13 (2.6)	2 (0.4)	60
1998-2005	3 (0.4)	3 (0.4)	60

* Determined by comparing the species lists from 1943 to those for 1946, and so on. Inventories were restricted to trees >4cm dbh.

1980). Following Hurricane Hugo the rate of addition of *D. excelsa* ingrowth to the plot rose to ~6 stems/year. *C. schreberiana* ingrowth between 1943-46 amounted to 13 stems (Crow, 1980). The species does not appear again as significant ingrowth until 1988-93 then drops from 89 stems during this period to 5 stems during 1993-98 and 1998-2005. Overall, in the 1988-93 period including and following Hugo 35 total species were added to EV-3 as ingrowth (Table II). The only other period of record with higher numbers of ingrowth species was 1943-46.

C. poecilanthus, never a major species on the plot, nevertheless showed moderate ingrowth from 1943 to 1976 (Crow, 1980). However, the only ingrowth since then has been three stems added during 1988-93. Likewise, *Tetragastris balsamifera* showed moderate ingrowth between 1943-76, but with no stems added during 1976-88. Since then, however, only six stems were added during 1988-93, none between 1993-98, and 3 from 1998-2005. *Psychotria berteriana*, a small evergreen shrub or understory tree, responded with a surge in ingrowth during the years 1943-46, 1993-98 and 1998-2005, years closely following major hurricane disturbance; the species was absent from ingrowth lists in intervening years.

The increased ingrowth across all species in the years immediately following Hurricane Hugo (91 stems/ha/year) was not maintained in subsequent periods of 1993-98 (33) and 1998-2005 (33). Hurricane Georges, although it appeared to produce significant effects to EV-3, did not have the immediate effect on the plot that Hugo did 9 years earlier. Total ingrowth is still higher than in the 12 years prior to 1988 when it averaged 11 stems/ha/year.

There are indications that many of the important ingrowth species responded following Hurricane Hugo (1988-93) with increased total numbers of stems and basal area (Figure 2). *D. excelsa* and *M. bidentata* reached plateaus in the total number of stems between 1951 and 1988 while basal area continued to increase, but then accrued a net number of new stems between 1988-2005. Basal area of both species has continued to increase since 1988 (Figures 2a, b). *S. berteriana* showed a sharp decrease in basal area in response to Hugo, but the net long-term trend has been a slow decline in basal area and density (Figure 2c). According to Crow (1980), in the 1958 timber stand improvement *D. excelsa*, *M. bidentata* and *S. berteriana* were among the most prevalent species removed and thus may have affected overall trends. In the case of *C. schreberiana* however, the response to Hurricane Hugo was dramatic (Figure 2d). After increasing in number and basal area on the plot following the hurricanes of the 1930's *C. schreberiana* had decreased to near zero numbers by 1988. In the four years following Hurricane Hugo large

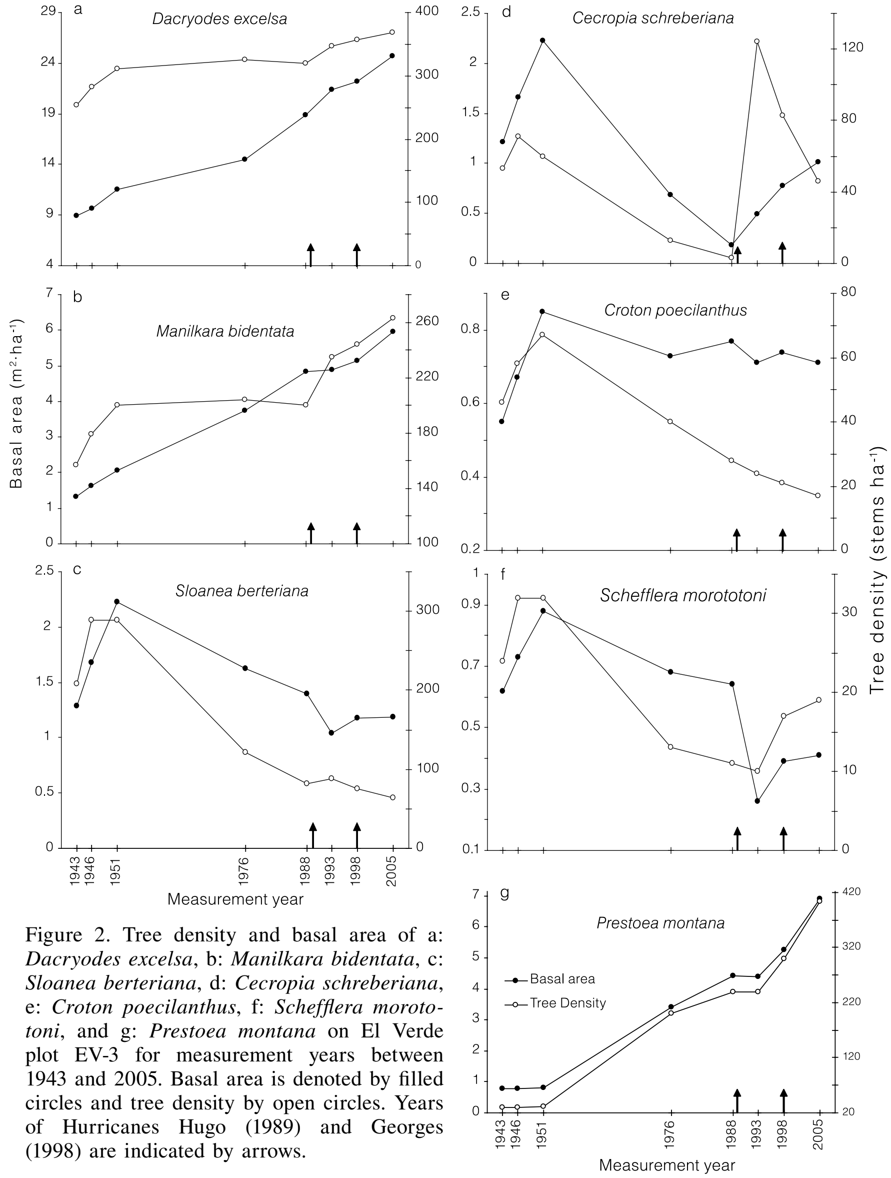

Figure 2. Tree density and basal area of a: *Dacryodes excelsa*, b: *Manilkara bidentata*, c: *Sloanea berteriana*, d: *Cecropia schreberiana*, e: *Croton poecilanthus*, f: *Schefflera morototoni*, and g: *Prestoea montana* on El Verde plot EV-3 for measurement years between 1943 and 2005. Basal area is denoted by filled circles and tree density by open circles. Years of Hurricanes Hugo (1989) and Georges (1998) are indicated by arrows.

TABLE II
SPECIES AND NUMBER OF TREE STEMS OF THE 10 MOST ABUNDANT INGROWTH SPECIES THAT ENTERED THE >4.0cm DBH CLASS BETWEEN CENSUS INTERVALS

1976-1988		1988-1993		1993-1998		1998-2005	
Species	Stems	Species	Stems	Species	Stems	Species	Stems
Prestoea montana	79	*Prestoea montana*	97	*Prestoea montana*	48	*Prestoea montana*	89
Sloanea berteriana	7	*Cecropia schreberiana*	89	*Psychotria berteriana*	14	*Manilkara bidentata*	19
Dacryodes excelsa	4	*Dacryodes excelsa*	31	*Manilkara bidentata*	11	*Dacryodes excelsa*	13
Miconia prasina	2	*Manilkara bidentata*	31	*Dacryodes excelsa*	10	*Psychotria berteriana*	10
Drypetes glauca	1	*Sloanea berteriana*	21	*Sloanea berteriana*	5	*Cecropia schreberiana*	5
Guarea guidonia	1	*Tetragastris balsamifera*	6	*Cecropia schreberiana*	5	*Schefflera morototoni*	5
		Micropholis chrysophylloides	5	*Schefflera morototoni*	4	*Sloanea berteriana*	4
		Miconia tetrandra	5	*Guarea glabra*	3	*Guatteria caribaea*	3
		Guarea glabra	4	*Myrcia leptoclada*	2	*Tetragastris balsamifera*	3
		Croton poecilanthus	3	*Palicourea riparia*	2	*Miconia prasina*	2
		25 other species	37	14 other species	14	11 other species	11
Stand total	94 (131)		329 (457)		118 (164)		164 (228)

Stand totals for the 0.72 ha plot are shown on a per hectare basis in parentheses.

numbers of new stems were added to EV-3 and the basal area was increasing.

C. poecilanthus, like *S. berteriana*, exhibited a declining trend in number of stems between 1951 and 2005 with fluctuations in basal area related to the loss of large trees from recent hurricanes (Figure 2e). Similarly, *S. morototoni* decreased in numbers on the plot from 1951 to 1993 then increased again in 1998 and 2005 presumably a response to Hurricanes Hugo and Georges. Basal area of *S. morototoni* continues to decrease overall on the plot with a noted drop in 1993 followed by an increase as a result of stems added later (Figure 2f).

P. montana has increased on EV-3 since 1951 both in terms of number of stems and basal area, shows no signs of diminishing in either absolute density or dominance, and has increased further by both measures following recent hurricanes. Because of its lack of secondary growth the two trend lines are nearly identical in shape with basal area proportional to number of stems (Figure 2g). Sierra palm along with *S. morototoni* appear to exhibit delayed responses to hurricane disturbance over other woody species, which may be merely a consequence of a longer period of initial growth before reaching measurement size.

Importance values for 2005 (Table III) confirm that *D. excelsa* outranks all other species on EV-3 followed in order by *P. montana*, *M. bidentata*, and *S. berteriana*. The first three species are nearly ubiquitous on the plot and the high basal area of *D. excelsa* confers upon it the highest ranking. The high density of *P. montana* contributes to its exceptional ranking, but its lack of woody tissue limits its ultimate basal area and so relegates it to lower importance.

TABLE III
RELATIVE DOMINANCE, FREQUENCY, DENSITY, AND IMPORTANCE VALUES FOR THE TOP FIFTEEN SPECIES

Species	Rank [a]	Relative dominance	Relative frequency [b]	Relative density	Importance value
2005					
Dacryodes excelsa	1	48.10	100.0	23.41	171.51
Prestoea montana	2	13.41	94.4	25.62	133.43
Manilkara bidentata	3	11.57	100.0	16.70	128.27
Sloanea berteriana	4	2.32	88.9	4.06	95.28
Tetragastris balsamifera	5	5.71	77.8	6.01	89.52
Cecropia schreberiana	6	1.97	61.1	2.92	65.99
Andira inermis	7	0.91	55.6	1.33	57.84
Drypetes glauca	8	0.37	50.0	1.15	51.52
Micropholis chrysophylloides	9	0.38	44.4	1.15	45.93
Tabebuia heterophylla	10	0.15	44.4	0.97	45.52
Myrcia leptoclada	11	0.14	44.4	0.88	45.42
Schefflera morototoni	12	0.80	38.9	1.24	40.94
Croton poecilanthus	13	1.37	33.3	1.06	35.73
Guarea glabra	14	0.27	33.3	0.71	34.28
Ixora ferrea	15	0.07	33.3	0.71	34.08

[a] Ranking of importance value of 15 out of 60 species.
[b] Frequency based on presence in 18 subplots.

Discussion

After 62 years of plot evaluation EV-3 clearly shows some of the effects of hurricanes which occurred in the years prior to 1943 and those due to Hurricane Hugo in 1989 and to a lesser extent, Hurricane Georges in 1998. Since the two hurricanes were so close together in time it is difficult to determine whether forest community changes from 1998-2005 were a long-term response to Hugo or a shorter term response to Georges. Widespread windthrow created new openings where woody regeneration established, increasing total numbers of stems as well as adding new species. Some decline in aboveground biomass following Hugo was noted, but that was superimposed upon an accreting trend. These changes are similar to those shown by Frangi and Lugo (1985) for a 0.25ha flood plain palm forest at 750m between 1980-95, where new species were added and tree density and biomass increased following Hurricane Hugo.

The most commonly regenerating species following hurricanes has been the shade intolerant *C. schreberiana*, whose numbers rose markedly following episodes of hurricane force winds and associated plot damage. The 16ha LFDP showed an eight-fold increase in the number of stems of *C. schreberiana* >10cm following Hurricane Hugo (Thompson, 2002). The intensity of disturbance to plot EV-3 was such that the dominant species, *D. excelsa*, only lost a few stems and its basal area has continued to increase both in absolute magnitude and as a proportion of the total plot basal area. *D. excelsa* responded to Hugo with significant ingrowth as did *M. bidentata* and to a lesser degree, *S. berteriana*. As well, the understory tree *P. berteriana* appears to be an indicator of disturbance with large amounts of ingrowth following Hurricane Hugo and after earlier hurricanes as reported by Crow (1980).

Losses of tall *P. montana* as a result of Hurricane Hugo were significant as the 1943 population lost 11 of 21 individuals, but large amounts of ingrowth accrued so that the net result was increased numbers. Zimmerman *et al*. (1994) noted that *P. montana*, the most common species on the LFDP, had 8.8% mortality from Hurricane Hugo, mostly due to broken stems presumably occurring as surrounding trees fell on the palms. Their plot had 9.0% mortality, overall, for palms plus trees >10cm dbh. Species richness, density and basal area on plot EV-3 are similar to those reported for the LFDP. However, species richness is low relative to other humid tropical forests at low to middle elevations (Thompson *et al*., 2004).

The interim between hurricanes on plot EV-3 was marked by long-term basal area and biomass accretion and an increase in the dominance of *D. excelsa*. Similarly, Frangi and Lugo (1985) noted that Hugo's effects on palm forest composition were such that the dominant species in that forest, *P. montana*, became even more dominant after the hurricane. During the period 1946-88, the total number of woody stems on EV-3 declined due to self-thinning (termed the "thinning phase" by Vandermeer *et al*., 1998, and "transition period" by Lugo *et al*., 2000) and timber stand improvement and the diversity fell due to a decline in evenness.

In the aftermath of Hurricane Joan at Bluefields, Nicaragua, the forest underwent an initial "building phase" followed by a "thinning phase" (Vandermeer *et al*., 1998; 2001; Vandermeer and Granzow de la Cerda, 2004). The building phase was characterized by the presence of fast growing pioneers, surviving saplings and seedlings and resprouting of damaged trees to form a dense secondary canopy whereas in the thinning phase, intense competition drove the development of the upper primary canopy with significant mortality of remnant species and disadvantaged individuals. Both phases are evident in the 62 year record of community change on plot EV-3; the periods 1943-46 and 1988-2005 were building phases following major hurricanes when the stem density increased, heliophytic pioneers regenerated on the plot and the total number of species increased; and the period 1951-88 was a phase in which thinning of both natural and man-made origins reduced stem density and species richness declined. Hurricane Joan produced 70% tree mortality, Hurricane Hugo 9% (LFDP), and Hurricane Georges, 4% (EV-3), yet the same phases of post-disturbance succession are apparent in the forest at El Verde as at Bluefields.

The "intermediate disturbance hypothesis" (Connell, 1978; Huston, 1979) proposes that both small and large disturbances result in the loss of species whereas disturbances of intermediate size have the effect of preserving species richness. At El Verde, hurricane disturbance has stimulated the addition of new species to the forest yet maintained species richness without its declining in the years between major hurricanes. If competitive exclusion processes were predominant then the long-term disappearance of species should be evident. The level of disturbance and its effect on the forest has been greater than that of treefall gaps allowing pioneer species like *Cecropia* to return to the forest after declining to negligible abundance just prior to Hurricane Hugo. As Brokaw (1998) has pointed out, *C. schreberiana* does not colonize well in the normally fewer and smaller ($50m^2$) treefall gaps formed in the Luquillo Mountains, but typically requires the larger gaps associated with hurricanes. In this sense, Hugo has produced a level of disturbance "intermediate" in scope and species richness has been maintained over time. Vandermeer *et al.* (2000) concluded that hurricane disturbance produces a more species rich forest as at Bluefields from Hurricane Joan because pioneers do not suppress other species to the degree that they do in smaller treefall gaps. Molino and Sabatier (2001) have shown that intermediate levels of silvicultural disturbance to Guianan tropical forests analyzed relative to percent of heliophytes produced a more species rich forest, "validating the intermediate disturbance hypothesis."

In the recent census years following 1976 there was a decline in evenness that reflects the increased abundance, dominance and, hence, importance of the major canopy species, *D. excelsa* and *M. bidentata*, and the precipitous rise in numbers of the understory palm, *P. montana*. *S. berteriana*, *C. schreberiana*, *S. morototoni*, and *C. poecilanthus* declined in abundance between 1976-88, and aside from *C. schreberiana* and to a lesser degree, *S. morototoni*, do not appear to have recovered from the disturbance created by Hurricane Hugo. *S. berteriana* and *C. poecilanthus*, in particular, may be inferior competitors with *P. montana* on similar sites.

S. berteriana and *P. montana* both occur on steep slopes, moist ravines and on lower slope positions where soils may be unstable, although Johnston (1992) showed that *P. montana* tended to occur on the Coloso soil series, a poorly-drained gleyed clay, whereas *S. berteriana* was associated with Cristal soils, a somewhat poorly-drained clay soil adjacent and higher on the toposequence. *S. berteriana* was once (1946) the most abundant woody species on EV-3, but since then has been in continuous decline. *C. poecilanthus* occupies similar sites to *P. montana*, poorly drained swampy areas and along stream courses, and has also declined with negligible ingrowth in recent years. Both *S. berteriana* and *C. poecilanthus* have decreased in numbers on the plot during the same time that *P. montana* has increased and these changes may be the outcome of interspecific competition for similar site resources.

Plot EV-3 does not appear to have been very disturbed by timber harvesting prior to 1943, as indicated by the present abundance and dominance of *D. excelsa* and the scarcity of the secondary species, *Casearia arborea*, which was the second most abundant species after *P. montana* on the 16ha LFDP at the time of Hurricane Hugo (Zimmerman, 1994). Zimmerman *et al.* (1994) report the relatively high proportion of *C. arborea* in a portion of the LFDP associated with marked human disturbance as shown on 1936 air photos. However, the slight decrease in stand biomass from 1951 to 1976 on EV-3 and the near plateau in basal area during this period were possibly related to the 1958 silvicultural treatment. Crow (1980) felt that the effects of the timber stand improvement and Hurricane Santa Clara in 1956 on stand composition and structure of EV-3 were minor. The strong dominance of *D. excelsa* observed on the plot today is more probably a consequence of its hurricane resistance, i.e., in spite of the abundance of hurricanes throughout the Caribbean, it is the most abundant species in the regional *Dacryodes-Sloanea* rain forest association.

Trees ≥27m high on EV-3 continue to grow in height and diameter and there are greater numbers of them than at any time since plot establishment, suggesting that long-term accretion of biomass is continuing and that the forest community on EV-3 is probably in an intermediate stage of recovery from the heavy disturbance of the early 1930's. Hurricane Hugo did not appreciably disturb the plot in the sense of damaging the largest trees even though large openings were created that quickly became filled with shade intolerant species. Zimmerman *et al.* (1994) found that shade tolerant "non-pioneer" species suffered less stem breakage, which was related to their having higher wood density than pioneer trees which have less dense wood and more stem breakage. The present results are consistent with this finding.

Overall, the plot EV-3 has had a net gain of seven species since 1943 yet diversity has dropped 19%. Species richness has not changed as much as evenness, due to the increased dominance of a few species. Indeed, species richness of this subtropical wet forest has been bolstered by hurricanes and maintained in years between hurricanes. Hurricane Hugo seems only to have affected the general trend of increasing woody biomass in a temporary way and has introduced a perturbation in which the regeneration and long term promotion of dominant species in the stand has been enhanced.

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SESENTA Y DOS AÑOS DE CAMBIO DE ESTRUCTURA Y COMPOSICIÓN FORESTAL HÚMEDA SUBTROPICAL EN EL VERDE, PUERTO RICO

Allan P. Drew, Jeremy D. Boley, Yinghao Zhao, Mark H. Johnston y Frank H. Wadsworth

RESUMEN

Una parcela de crecimiento establecida en 1943 en un bosque subtropical húmedo en Puerto Rico ha sido evaluada periódicamente en relación a cambios en las especies y tamaño de los árboles con diámetro >4cm. La dinámica forestal en una parcela de 0,72ha (EV-3, situada en El Verde a 400msnm) muestra principalmente la recuperación de los huracanes de 1928 y 1932, de aclareos para el mejoramiento de rodales madereros en 1958 y de los huracanes Hugo y Georges en 1989 y 1998. Los daños de Hugo disminuyeron solo temporalmente la acumulación de biomasa arbórea del bosque en desarrollo. Se siguieron registrando aumentos de área basal y biomasa del rodal, principalmente por crecimiento de las especies dominantes Dacryodes excelsa y Manilkara bidentata, cuya renovación fue estimulada. La pionera Cecropia schreberiana *se estableció abundantemente en espacios abiertos por el huracán y en el sotobosque proliferó* Psychotria berteriana. *El crecimiento de la regeneración de* Prestoea montana *ha sido el mayor registrado desde 1976 y fue estimulado por Hugo y George, así como por huracanes anteriores, siendo la especie más abundante en 2005. Hugo causó poca mortalidad de árboles grandes. En la medida en que pocas especies han llegado a ser dominantes, la uniformidad de las parcelas ha declinado. La riqueza de especies es ligeramente mayor que en 1943. Los resultados se discuten en términos de fases de "construcción" y "aclareo" asociadas con el paso de huracanes. Éstos han estimulado la adición de especies en "años de construcción", pero han mantenido la riqueza en "años de aclareo", añadiendo credibilidad a la hipótesis de perturbaciones intermedias.*

SESSENTA E DOIS ANOS DE MUDANÇA DE ESTRUTURA E COMPOSIÇÃO FLORESTAL ÚMIDA SUBTROPICAL EM EL VERDE, PUERTO RICO

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RESUMO

Uma parcela de crescimento estabelecida em 1943 em um bosque subtropical úmido em Puerto Rico tem sido avaliada periodicamente em relação às mudanças nas espécies e tamanho das árvores com diâmetro >4 cm. A dinâmica florestal em uma parcela de 0,72ha (EV-3, situada em El Verde a 400msnm) mostra principalmente a recuperação dos furacões de 1928 e 1932, de clareiras para o melhoramento de lotes madeireiros em 1958 e dos furacões Hugo e Georges em 1989 e 1998. Os danos de Hugo diminuíram somente temporalmente a acumulação de biomassa arbórea do bosque em desenvolvimento. Seguiram-se registrando aumentos de área basal e biomassa do lote, principalmente por crescimento das espécies dominantes Dacryodes excelsa e Manilkara bidentata, cuja renovação foi estimulada. A pioneira Cecropia schreberiana *se estabeleceu abundantemente em espaços abertos pelo furacão e no sotobosque proliferou* Psychotria berteriana. *O crescimento da regeneração de Prestoea montana tem sido o maior registrado desde 1976 e foi estimulado por Hugo e George, assim como por furacões anteriores, sendo a espécie mais abundante em 2005. Hugo causou pouca mortalidade de árvores grandes. Na medida em que poucas espécies têm chegado a ser dominantes, a uniformidade das parcelas tem declinado. A riqueza de espécies é ligeiramente maior que em 1943. Os resultados se discutem em termos de fases de "construção" e "clareiras" associadas com a passagem de furacões. Estes têm estimulado a adição de espécies em "anos de construção", mas tem mantido a riqueza em "anos de clareiras", acrescentando credibilidade à hipótese de perturbações intermediarias.*