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Changes in Structure, Composition, and Nutrients During 15 Years of Hurricane-induced Succession in a Subtropical Wet Forest in Puerto Rico

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ABSTRACT

The trajectory of hurricane-induced succession was evaluated in a network of forest plots measured immediately before and 3 mo, 5, 10, and 15 yr after the direct impact of a Category 4 hurricane. Comparisons of forest structure, composition, and aboveground nutrients pools were made through time, and between species, life-history groups and geomorphic settings. The hurricane reduced aboveground biomass by 50 percent, causing an immediate decrease in stem density and diversity indices among all geomorphic settings. After 15 yr, basal area and aboveground biomass returned to pre-hurricane levels, while species richness, diversity indices, and stem densities exceeded pre-hurricane levels. Differences in species composition among geomorphic settings had not returned after 15 yr but differences in stem densities and structure were beginning to emerge. Significant differences were observed in the nutrient concentration of the three species that comprised the most aboveground biomass, and between species categorized as secondary high-light species and primary, low-light species. Species whose abundance was negatively correlated with the mature forest dominant also had distinct nutrient concentrations. When total aboveground nutrient pools were compared over time, differences in leaf nutrients among species were hidden by similarities in wood nutrient concentrations and the biomass dominance of a few species. The observed successional trajectory indicates that changes in species composition contributed to fast recovery of aboveground biomass and nutrient pools, while the influence of geomorphic setting on species composition occurs at time scales > 15 yr of succession.

Abstract in Spanish is available at http://www.blackwell-synergy.com/loi/btp

Key words: aboveground biomass; Bisley Experimental Watersheds; *Cecropia schreberiana*; leaf chemistry; magnesium; secondary succession; species composition.

Hurricanes are large infrequent disturbances that can have severe and long-lasting effects on forests within 500 km of most oceans (Dale *et al.* 2001). Recent studies indicate that plant species richness and diversity typically increase during hurricane-induced forest succession and that local geomorphic and environmental conditions can influence the rate and direction of these compositional changes (Weaver 1989, Bellingham *et al.* 1995, Scatena & Lugo 1995, Imbert *et al.* 1996, Vandermeer *et al.* 2000, Mascaro *et al.* 2005, Tanner & Bellingham 2006, Chazdon *et al.* 2007, Lugo 2008). Relationships between the successional status of species and wind damage, wood density, and foliar nutrient chemistry have also been identified for some tropical trees (Bloomfield *et al.* 1993, Reich *et al.* 1995, Schowalter & Ganio 1999, Han *et al.* 2005, Townsend *et al.* 2007). Although broad, global scale relationships are complicated by environmental heterogeneity and within species differences; fast growing species with low-density woods are more susceptible to wind damage than high-density, late successional species (Putz 1983, Zimmerman *et al.* 1995b). The amount of wind damage also related to the morphology, age, size, and health of the individual stem and its topographic position, drainage, soil and rooting conditions (Scatena *et al.* 2005). At all scales, hurricanes create patches of survivors and new regeneration that change in structure and composition over decades (Crow 1980, Weaver 1989). Past land use or past disturbances also have successional legacies that play out along with successional changes following hurricanes (Zimmerman *et al.* 1995a, Thompson *et al.* 2002).

Defoliation and the transfer of biomass and nutrients from the canopy to the forest floor can also cause major shifts in nutrient cycling pathways (Brokaw & Walker 1991, Scatena *et al.* 1993, Lodge *et al.* 1991, Walker *et al.* 2003, Erickson & Ayala 2004, Ostertag *et al.* 2005, Teh *et al.* 2009). In the current study area, hurricane Hugo caused a 50 percent reduction in aboveground biomass (Scatena *et al.* 1993). However, stream flow returned to pre-storm conditions within 1 yr, rates of canopy throughfall returned to pre-hurricane conditions within 2 yr, and the rate of forest litterfall recovered in *ca* 5 yr. Solutes in shallow ground water and stream flow increased after the storm but typically returned to background levels within 1–2 yr (McDowell *et al.* 1996, Schaefer *et al.* 2000). Nevertheless, the increased nutrient exports in the first 2 yr were equivalent to only one to four of the nutrients in the hurricane-derived litter, indicating that most of the nutrients transferred by the hurricane were recycled into biomass and soils and not exported from the watersheds. It has also been suggested that geomorphic stability, edaphic conditions, and biotic adaptations eventually override the importance of spatial variations in total soil nutrients in the accumulation of aboveground biomass at this site (Scatena & Lugo 1995). How and when aboveground nutrient pools change in response to hurricane-induced changes in forest structure and composition at the landform and watershed scale have not been documented.

This study evaluates changes in forest composition and structure during 15 yr of hurricane-induced succession in a mature secondary forest and in its varied geomorphic settings to: (1) evaluate changes in

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forest composition, structure, and aboveground nutrient pools over 15 yr of hurricane-induced succession; and (2) evaluate the influence of species, life histories, and geomorphology on forest nutrient accumulation. The study uses data from a network of forest plots that were measured immediately before, and after 3 mo, 5, 10, and 15 yr of the direct impact of hurricane Hugo on 18 September 1989 and companion studies of rainfall and throughfall (Heartsill Scalley *et al.* 2007), litterfall and biomass accrual (Scatena *et al.* 1993), and belowground and soil dynamics (Silver *et al.* 1996, Teh *et al.* 2009).

METHODS

STUDY AREA.—This study was conducted in the subtropical wet forest of the Bisley Experimental Watersheds (BEW; 18°20′ N 65°50′ W) of the Luquillo Experimental Forest (LEF) in northeast Puerto Rico. Annual rainfall averages 3482 mm/yr and is influenced by hurricanes, tropical storms, and particulates from Saharan dust and Caribbean volcanic activity (Heartsill Scalley *et al.* 2007). The watersheds are covered by a mature, secondary Tabonuco, or *Dacryodes–Sloanea* type forest (Ewel & Whitmore 1973.) This forest type is also found in other Caribbean islands and is named for Tabonuco (*Dacryodes excelsa*), the dominant tree that grows in high abundance on ridges (Beard 1949, Smith 1970, Alvarez Ruiz 2002). The flora at BEW includes *ca* 336 plant species in 255 genera and 102 families (Chinea *et al.* 1993). In the steep and highly dissected landscape of the BEW, biomass and structure, species composition, soil properties, and the frequency of disturbance and forest turnover have been related to four distinct geomorphic settings; ridges, slopes, upland valleys, and riparian valleys (Scatena 1989, Scatena & Lugo 1995). In general, valleys have poorly drained soils and the lowest soil oxygen values (Silver *et al.* 1999), the least biomass, younger aged stands, lower species richness, soils with more exchangeable bases, and the highest frequency of treefalls and landslide (Scatena & Lugo 1995). Ridges are well drained and have relatively acidic soils with high organic matter but lower base cations than adjacent valleys. The oldest and largest trees are found along ridges, where Tabonuco trees form dense stands of connected roots whose grafting indicates that over time noncompetitive forces are important in shaping the Tabonuco forest community (Basnet *et al.* 1993).

Although the BEW have always been forested, they were selectively harvested for timber and charcoal and supported small-scale plantings of coffee and subsistence crops before their purchase by the United States Forest Service in the 1930s (Scatena 1989, García-Montiel & Scatena 1994). In 1987, the watersheds were designated as a research area and since then vegetation, climate, water, and nutrients have been monitored (http://luq.lternet.edu/data.html). Hurricane Hugo, the largest storm to affect the area since the 1930s, passed over the site on 18 September 1989. The hurricane defoliated the entire area, and reduced the aboveground biomass by 50 percent (Scatena *et al.* 1993). After Hugo, the forest was also affected by eight smaller hurricanes that passed near the area (Beard *et al.* 2005, Heartsill Scalley *et al.* 2007). Hurricane Georges, in 1998, was the largest of these and resulted in localized defoliation and uprooting (Ostertag *et al.* 2005). Six meteorological droughts of varying intensity were also recorded during the 15-yr study period (Larsen 2000, Heartsill Scalley *et al.* 2007).

A decade of monitoring belowground reorganization following Hugo indicates that the belowground nutrient and carbon pools of Bisley were less affected than aboveground pools (Silver *et al.* 1996). Effective soil cation exchange capacity did increase immediately after hurricanes Hugo and Georges, but soil base cations remained close to pre-hurricane values (Teh *et al.* 2009). Soil P did fluctuate over time and declined during periods of rapid plant recovery and growth.

VEGETATION CENSUSES.—Tree characteristics were measured in a network of permanent plots that were geographically referenced to a 1:500 scale topographic map of the area. These plots consist of 10 m diam circles located at the nodes of a 40 × 40 m grid that covers the two watersheds (Scatena *et al.* 1993, 1996; Scatena & Lugo 1995). All stems $\geq$2.5 cm diam at 1.3 m height diameter at breast height (dbh) were measured and identified to species following Liogier (1985). Each plot was classified by geomorphic setting and placed into the categories of ridge, slope, upland valley, or riparian valley. Because the area occupied by each of these categories was unequal, (Scatena & Lugo 1995) the number of sample plots in each category also varied.

The establishment of 85 plots and the first census was started in late 1988, and was completed in the summer of 1989. Hurricane Hugo passed over the study site on 18 September 1989. To assess hurricane effects, the second census was started 3 mo after (December 1989). Landslides and extensive uprooting completely eliminated seven plots (Table 1). The third census was done between April and July of 1994 and reestablished the 7 destroyed plots and added four additional plots to expand the grid to a total of 89 plots. The fourth and fifth census were also started in April and finished in July of their respective census year. During the fifth census, in 2004, one plot was added. When calculating watershed scale vegetation structure and community characteristics all plots per census were included in the calculations (Table 1). To consistently compare species composition through time (among censuses), multivariate ordinations included only data from 75 plots that were consistently measured in all five censuses. To give more weight to species presences in each census than to species absences, only species that had at least four stems in each census were included in the analysis of species composition through time. The cumulative species vs. cumulative number of plots suggests that sample size used may slightly underestimate total species richness, but does provide a representative estimate of the study area (Fig. 1).

BIOMASS AND NUTRIENT CALCULATIONS.—Leaf and wood samples from 18 tree species were collected from the BEW before (1988) and after hurricane Hugo (1989). The leaf and wood samples were analyzed for C, N, P, K, Ca, and Mg concentrations in the International Institute of Tropical Forestry (IITF) Plant and Soils Analytical Laboratory (Scatena *et al.* 1993, 1996; Sánchez *et al.* 1997). Aboveground biomass was calculated using a general allometric equation and species-specific equations that were developed for the Bisley vegetation and have been previously used to quantify nutrients pools (Scatena *et al.* 1993) as well as initial hurricane effects and re-growth (Scatena *et al.* 1996). The general biomass equation is similar to other equations developed for the Tabonuco forest

TABLE 1 *Forest structure and community parameters per census of the Bisley Experimental Watersheds. Mean (stems/ha), basal area (m^2), and biomass (Mg/ha) of all measured plots (SD). Biomass is aboveground biomass of stems > 2.5 cm diameter at breast height (dbh), excluding understory palms with stems < 1.5 m tall. Plot (78.5 m^2) mean number of species and diversity value, exponent of Shannon's (H'), were calculated using 75 plots per census. Letters next to mean values indicate groupings of* post-hoc *analyses.*

	Census number and year				
	1	2	3	4	5
	1989 (Pre-Hugo)	1989 (Post-Hugo)	1994	1999	2004
Stems/ha	1480b	660d	1215c	2436a	2662a
	(760)	(408)	(565)	(1021)	(1117)
Basal area (m^2)	36a	22b	28ab	35a	36a
	(31)	(27)	(26)	(25)	(26)
Biomass (Mg/ha)	221a	111b	192a	225a	231a
	(237)	(160)	(219)	(220)	(238)
Total species	56	49	47	63	60
Species/plot	6b	3d	5c	8a	8a
Diversity/plot	4.7b	3.0c	3.7c	6.1a	6.6a
Total census plots	85	78	89	89	90

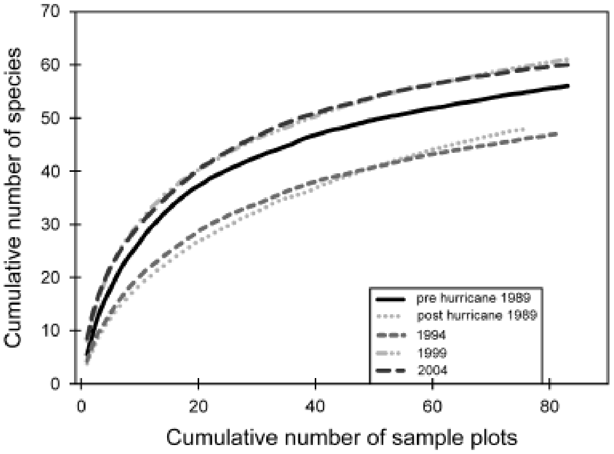

FIGURE 1. Cumulative sampled plots and number of species in each census of the Bisley Experimental Watersheds, Luquillo, Puerto Rico.

(Weaver & Gillespie 1992) and wet tropical forests (Brown *et al.* 1989). To calculate total aboveground nutrient pools and mass-weighted concentrations (MWC) of different pools (*i.e.*, total nutrient/total mass), we used pre- and post-Hugo nutrient concentrations (Scatena *et al.* 1993) and additional leaf and wood nutrient data collected over the 15-yr study period (Lugo 1992, Bloomfield *et al.* 1993, Frangi & Lugo 1998, Schowalter & Ganio 1999, Vogt *et al.* 2002, Fonte & Schowalter 2004; E. Medina & E. Cuevas, unpubl. data). These studies indicate that there were no significant differences in species-specific nutrient concentrations of plant organs (*i.e.*, leaves, wood) through time in this forest.

Leaf and wood chemistry were compared between selected dominant species and species that were grouped into: (1) primary forest or low-light species (*Cordia borinquensis*, *D. excelsa*, *Eugenia eggersii*, *Ocotea leucoxylon*, *Ormosia krugii*, *Sloanea berteriana*, *Tetragastris balsamifera*, *Inga laurina*); and (2) secondary forest or high light species (*Sapium laurocerasus*, *Andira inermis*, *Casearea arborea*, *Cecropia schreberiana*, *Palicourea riparia*, *Schefflera morototoni*, *Psychotria berteriana*, and *Alchornea latifolia*). These groups use the primary forest species definition from Smith (1970), and additional studies that combine the species-specific characteristics of seed size, seedling regeneration under different light conditions, and relative densities of various life-history stages in this forest type (Devoe 1989, Lugo & Zimmerman 2002). We also compared nutrients of species whose abundance was negatively correlated with *D. excelsa*, the dominant tree species.

STATISTICAL ANALYSIS.—Tree species community dynamics through time were explored using non-metric multidimensional scaling (NMS). A single NMS ordination was made using species abundance data from the five censuses and was based on a dissimilarity matrix that was generated using Bray–Curtis distance (PC-ORD, Gleneden Beach, Oregon, U.S.A., McCune & Mefford 2006). We chose NMS because it is an ordination method that efficiently reduces high dimensional multivariate species space to two dimensions, has minimal assumptions about relationships among the variables, and is robust against noise in the data set (Johnson 1998, McCune & Grace 2002, Urban *et al.* 2002). Differences in community composition among census year (*i.e.*, census year as the grouping variable) were tested using a one-way analysis of similarities (ANOSIM) on the matrix of species abundance. This way, we were able to compare community composition between consecutive time periods (census year), and with the initial pre-hurricane census. The ANOSIM statistic, Clarke's *R*, is based on the difference of mean ranks between and within any number of groups or samples. A value of 0 indicates completely random grouping while a value close to 1 indicates complete difference among groups (Vegan package, Oksanen *et al.* 2007, R version 2.4, 2006, R Core Development Team, Vienna, Austria). When used to assess differences in communities within the same landscape, ANOSIM is a relative measure of within and between group similarities (Clarke 1993, Cao *et al.* 2005). In addition, we used ANOSIM to test for differences in species composition among geomorphic setting (*i.e.*, geomorphic category as the group). The exponent of Shannon–Weaver's H', $\exp(H')$, was used as a diversity index. Repeated measures analysis of variance (ANOVA) and generalized linear models (GLM) were conducted using SAS software (SAS Version 9.1, SAS Institute 2003, Cary, North Carolina, U.S.A.). *Post-hoc* Ryan–Einot–Gabriel–Welsch multiple range (REGWQ) analyses were used to evaluate mean differences within test categories. All statistics were considered significant at an α level of 0.05.

RESULTS

FOREST STRUCTURE AND COMMUNITY CHARACTERISTICS.—Comparison of the same size classes over time indicates that the 20–40 cm dbh category had a relatively large decrease in the number of stems following the hurricane (Fig. 2). Immediately after the hurricane (second census), biomass and stem density were significantly less than at any other time ($F_{4,371} = 4.42$, $P = 0.0017$; Table 1). Ten years after the hurricane, the forest had attained a basal area and biomass that was similar to the pre-Hugo forest and after 10 and 15 yr stem density was higher than pre-hurricane levels ($F_{4,371} = 84.8$, $P < 0.0001$; Table 1). After 15 yr the number of stems with diameters > 20 cm dbh was still below pre-hurricane Hugo levels (Fig. 2).

Throughout the study period 86–91 percent of the aboveground biomass was comprised by only ten species (Table S1). Consistently, *D. excelsa* was the species that contributed most aboveground biomass in every census. In the first two censuses, (pre- and posthurricane), 55 percent of the aboveground biomass was contributed by *D. excelsa* and *Guarea guidonia*. Five years later *G. guidonia* was replaced by *C. schreberiana* as the second most important species in terms of biomass. Along with *D. excelsa*, these three species represented > 63 percent of the biomass in the 1994, 1999, and 2004 censuses.

After 10 yr the number of species and the diversity indices were greater than pre-hurricane values (Table 1). Composition was also different among the five censuses ($R = 0.208$, $P < 0.001$). In general, primary forest species *C. borinquensis* and *G. guidonia* decreased in density, while the secondary forest species *C. schreberiana* and *S. laurocerasus* increased (Table S1). Five years after the hurricane, the secondary species *S. laurocerasus* became one of the most abundant stems. Before hurricane Hugo, *S. laurocerasus* was a relatively rare species represented by a few large individuals. Ten years after hurricane Hugo, secondary forest species *C. schreberiana* and *P. berteriana* (a tall shrub) were the two most abundant stems (Table S1). Nevertheless, during the entire 15-yr period, three primary forest species, *S. berteriana*, *Prestoea montana*, and *D. excelsa*, remained among the most abundant species in terms of density (Table S1).

Before hurricane Hugo, species composition was similar among plots, as represented by plots clustered in a small area of NMS species space (Fig. S1B). Although species composition immediately after the hurricane was statistically different from the composition before the hurricane ($R = 0.037$, $P = 0.004$), these differences were small compared with those observed between later censuses (Fig. S1). In subsequent censuses, there was more variation in species composition among plots, as evidenced by the scatter of the plots in ordination space. The largest difference in species composition between consecutive censuses was between the 1989 posthurricane and 1994 census ($R = 0.241$, $P < 0.001$; Fig. S1C). In the subsequent 10 and 15 yr censuses, plot composition tended to converge in ordination space (Fig. S1D, E). Species composition of plots in the 2004 census was still different from that observed before hurricane Hugo, as the plots in the ordination are clustered in a space that was not occupied in the first census (Fig. S1F). Moreover, pair-wise comparisons indicate that species composition of the 2004 plots had greater differences with the pre-hurricane ($R = 0.235$, $P < 0.001$; Fig. S1F), and the posthurricane (1989) censuses ($R = 0.363$, $P < 0.001$; Fig. S1G) than with any of the other censuses.

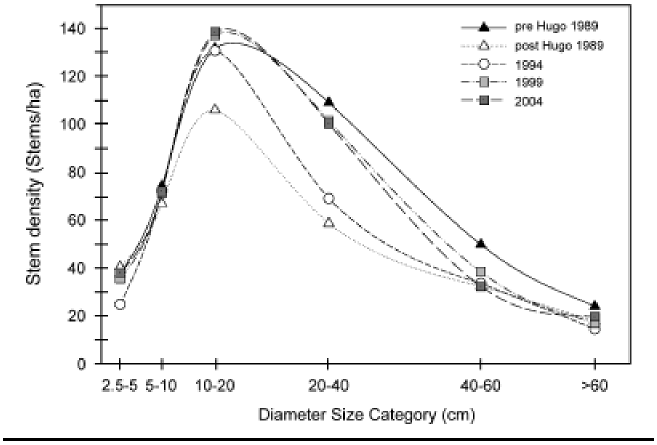

FIGURE 2. Distribution of stems by diameter size class (diameter at breast height) per census of the Bisley Experimental Watersheds, Puerto Rico.

COMPARING FOREST CHARACTERISTICS AMONG GEOMORPHIC SETTINGS.—Within each of the geomorphic settings, there were increases in stem density, species richness, and diversity indices following hurricane Hugo ($F > 8.76$, $P < 0.001$; Fig. 3). Both species richness ($F_{3,79} = 4.0$, $P = 0.010$) and stem density ($F_{3,79} = 4.54$, $P = 0.005$) were lowest in riparian valleys before and immediately after (species richness $F_{3,79} = 4.09$, $P = 0.009$; stem density $F_{3,79} = 3.57$, $P = 0.017$) hurricane Hugo; however, by 1994 there was no difference in stem density or species richness among geomorphic settings. This similarity of species richness among these settings remained during all the following censuses. The diversity index was significantly different among geomorphic settings before and immediately after hurricane Hugo ($F_{3,79} > 3.22$, $P < 0.027$). Differences in the diversity index among geomorphic settings were not observed during the following 10 yr. By the 2004 census, however, the diversity indices in the different geomorphic settings had returned to their pre-hurricane levels ($F_{3,79} = 4.20$, $P = 0.008$). Ridge and riparian valleys plots had different stem densities in the pre-Hugo ($F_{3,79} = 4.00$, $P = 0.010$) and post-Hugo census ($F_{3,79} = 3.57$, $P = 0.017$). Five years later those differences were not observed ($F_{3,79} = 1.84$, $P = 0.146$), and it was not until the 2004 census that differences in stem density between geomorphic settings were re-established ($F_{3,79} = 4.01$, $P = 0.010$).

In the pre-hurricane census, there were differences in species composition between geomorphic settings ($R = 0.121$, $P = 0.006$). These differences diminished in the posthurricane census ($R = 0.097$, $P = 0.018$). Furthermore, differences in species composition based on geomorphic setting were not observed 5, 10, or 15 yr after the hurricane. Within geomorphic settings, however, there were relative changes in species composition among the five censuses. In general, species composition on ridges ($R = 0.194$, $P = 0.001$) and riparian valleys ($R = 0.182$, $P < 0.001$) had less change throughout these 15 yr when compared with slopes ($R = 0.245$, $P < 0.001$) and upland valleys ($R = 0.324$, $P < 0.001$). This was due to the constant presence of *D. excelsa*, *S. berteriana*, *C. borinquensis*, *O. leucoxylon*, and *P. montana* on ridges and of *C.*

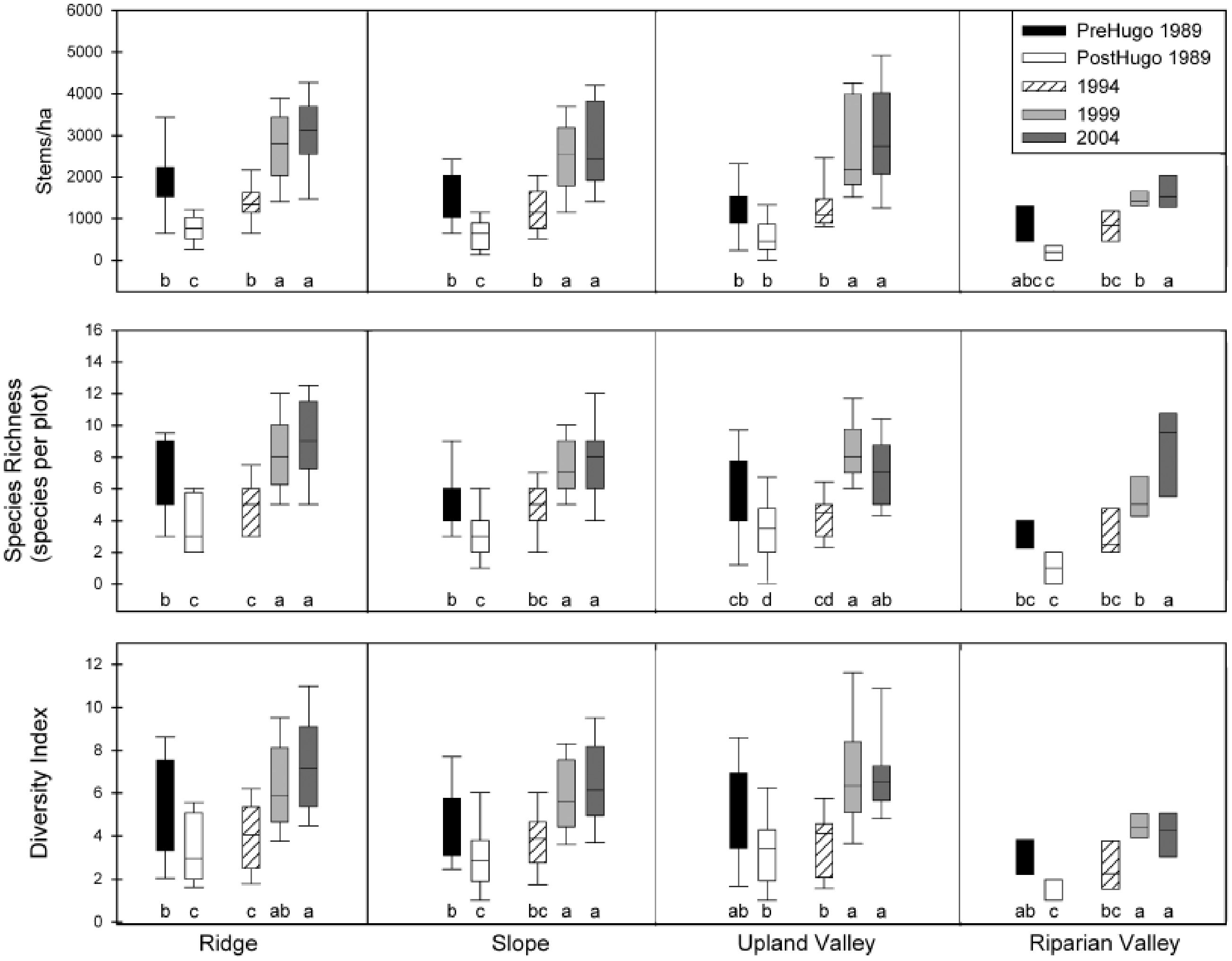

FIGURE 3. Stems/ha, species richness, and diversity index (H′) values for each of the geomorphic settings per census of the Bisley Experimental Watersheds, Puerto Rico. Each box encompasses the 25th through 75th percentile, and the horizontal lines mark the median, 10th and 90th percentiles. Letters on box plots represent groupings of *post-hoc* means analyses.

schreberiana, *P. montana*, *C. arborea*, *P. berteriana*, and *I. laurina* in riparian valleys. In slopes and upland valleys, there were greater changes in species composition through time. Among the most abundant species on slopes and in upland valleys in the first two censuses were *Manilkara bidentata*, a primary forest tree, and *Dendropanax arboreus*, a secondary forest tree. These two species were absent from slope plots in all later censuses. In the 2004 census, there was higher stem density on slopes and upland valleys relative to ridges and riparian valleys. Most of these stems were *C. schreberiana* which became very abundant on slopes 5 yr after hurricane Hugo and was still abundant in the following censuses. In upland valleys the density of *D. excelsa* gradually decreased while that of *S. laurocerasus* increased over the 15-yr study period.

Comparing nutrients among species.—The species that contributed the most aboveground biomass, *D. excelsa*, *C. schreberiana*, and *G. guidonia*, had differences in their leaf and wood nutrient concentrations (Fig. 4). Leaf nutrient concentrations for all five constituents (N, P, K, Ca, Mg) were different ($F_{2,3} > 16.6$, $P < 0.023$) among *D. excelsa*, *G. guidonia*, and *C. schreberiana*. In *post-hoc* analyses, leaf N, P, and K was highest in *G. guidonia*, compared with *D. excelsa* and *C. schreberiana*. *Cecropia schreberiana* had the highest values for Ca and Mg, compared with *D. excelsa* and *G. guidonia*. Nutrient concentrations in wood were highest for N and P in *G. guidonia*, and Ca lowest in *D. excelsa* (Fig. 4B). Wood K values were not different between these three species. The highest concentrations of Mg in wood were from *C. schreberiana* followed by *G. guidonia*, and *D. excelsa*. The carbon content of leaves was highest in *G. guidonia* and lowest in *C. schreberiana* (Fig. 4A).

The dominant species that define the *Dacryodes–Sloanea* forest type also had some differences in their chemistry. *Sloanea berteriana* had higher leaf concentrations of Mg ($F_{1,4} = 25.4$, $P = 0.007$) compared with *D. excelsa*, but there were no differences in foliar N, P, K, or Ca between these species. In wood, *S. berteriana* had higher N

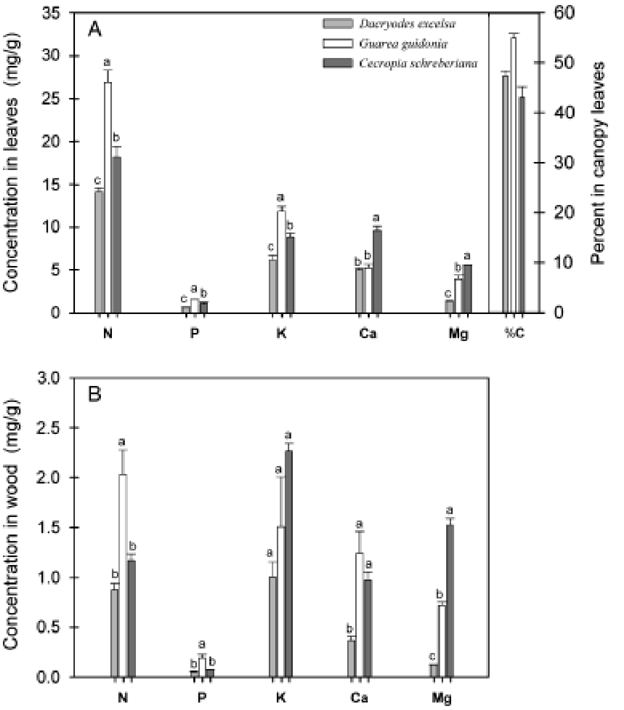

FIGURE 4. (A) Leaf and (B) wood tissue nutrient concentrations of three species dominant by aboveground biomass. For box plot description see Fig. 3 legend.

($F_{1,4} = 12.7$, $P = 0.023$), K ($F_{1,4} = 14.3$, $P = 0.019$), Ca ($F_{1,4} = 29.1$, $P = 0.005$), and Mg ($F_{1,4} = 132$, $P < 0.0001$) that *D. excelsa*. Wood P was not different between *D. excelsa* and *S. berteriana*.

There were six species whose abundances were negatively correlated with the abundance of the dominant tree, *D. excelsa*: *C. schreberiana* ($r^2 = -0.16$, $P < 0.0001$), *Cyathea portorricensis* ($r^2 = -0.17$, $P < 0.0001$), *S. laurocerasus* ($r^2 = -0.14$, $P = 0.002$), *G. guidonia* ($r^2 = -0.13$, $P = 0.002$), *I. laurina* ($r^2 = -0.10$, $P = 0.017$), and *P. berteriana* ($r^2 = -0.09$, $P = 0.031$). Of these species *D. excelsa* had the lowest leaf N ($F_{5,12} = 39.2$, $P < 0.001$), and leaf P concentrations ($F_{5,12} = 22.4$, $P < 0.0001$). For leaf K ($F_{5,12} = 13.6$, $P < 0.0001$) and leaf Ca ($F_{5,12} = 12.8$, $P < 0.0001$), *D. excelsa*, *I. laurina*, and *G. guidonia* had the lowest concentrations. For leaf Mg ($F_{5,12} = 57.0$, $P < 0.0001$), *D. excelsa*, and *I. laurina* had the lowest values. The lowest concentrations of N in wood were found in *D. excelsa* and *C. schreberiana* ($F_{3,8} = 6.68$, $P = 0.014$), while the lowest concentrations of P in wood were found in *D. excelsa*, *I. laurina* and *C. schreberiana* ($F_{3,8} = 12.7$, $P = 0.002$). The wood of *D. excelsa* also had the lowest concentrations of Ca ($F_{3,8} = 8.02$, $P = 0.009$) and K ($F_{3,8} = 6.68$, $P = 0.014$), while the lowest Mg was observed in *D. excelsa* and *I. laurina* wood ($F_{3,8} = 280$, $P < 0.0001$). Compared with *D. excelsa*, the tree fern, *C. portorricensis*, had higher K ($F_{1,7} = 8.25$, $P = 0.024$) and Mg ($F_{1,7} = 12.2$, $P = 0.010$), but had no differences in N, P, and Ca.

The two secondary forest species with the highest stem density 10 yr after hurricane Hugo, *C. schreberiana* and *P. berteriana* (Table S1), also had differences in their leaf nutrient concentrations. *Cecropia schreberiana* had higher leaf Ca ($F_{1,4} = 21.4$, $P < 0.009$) and leaf Mg ($F_{1,4} = 120.8$, $P < 0.0001$) than *P. berteriana*. In contrast, *P. berteriana* had higher foliar N ($F_{1,43} = 40.6$, $P = 0.003$) and K ($F_{1,4} = 119$, $P = 0.012$) concentrations. Leaf P was not different between *C. schreberiana* and *P. berteriana*.

Comparing between species grouped by life history, species categorized as primary forest or low light tended to have lower leaf nutrient concentrations than species of the high light group (Fig. 5). The species included in the low-light group were *C. borinquensis*, *D. excelsa*, *E. eggersii*, *O. leucoxylon*, *O. krugii*, *S. berteriana*, *T. balsamifera*, and *I. laurina*. Species in the high light group included *S. laurocerasus*, *A. inermis*, *C. arborea*, *C. schreberiana*, *P. riparia*, *S. morototoni*, *P. berteriana*, and *A. latifolia*. Although mean leaf concentrations tended to be higher for the high light group, there were no significant differences between the groups for leaf P, K, and Ca. The high light group did have higher foliar concentrations of N ($F_{2,25} = 4.67$, $P = 0.019$) and Mg ($F_{2,25} = 11.2$, $P < 0.0001$). Concentrations of N, P, K, and Ca were not different in the wood of these two groups; however, the high light species did have higher concentrations of Mg in their wood ($F_{1,19} = 6.54$, $P = 0.019$).

NUTRIENTS TOTALS AND MASS WEIGHED CONCENTRATIONS IN THE WATERSHED.—At the watershed scale, aboveground total nutrient pools were at their lowest levels immediately after hurricane Hugo; N ($F_{4,371} = 6.53$, $P < 0.001$), P ($F_{4,371} = 5.86$, $P < 0.001$), K ($F_{4,371} = 6.17$, $P < 0.001$), Ca ($F_{4,371} = 3.36$, $P < 0.001$), and Mg ($F_{4,371} = 11.0$, $P < 0.001$). In contrast, the MWC of nutrients remained relatively constant over the 15 yr for all nutrients except Mg ($F_{4,371} = 9.13$, $P < 0.0001$) (Table 2; Fig. S2), which was lowest in the first two censuses.

NUTRIENTS WITHIN GEOMORPHIC SETTINGS.—Comparing total nutrients among census year within each geomorphic setting, ridge sites had different Mg stocks over time ($F_{4,104} = 3.41$, $P = 0.011$), while slopes had differences in N, P, K, and Mg over time

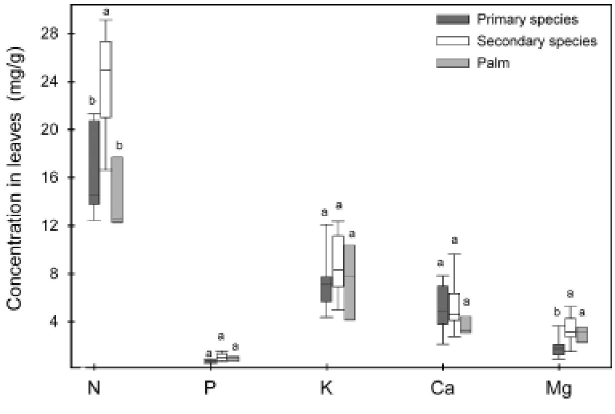

FIGURE 5. Leaf nutrients of life-history based species groups. Primary species $N = 12$, secondary species $N = 13$ (list of species per group in methods and results section). Palm, $N = 5$, is *Prestoea montana*. For box plot description see Fig. 3 legend. Letters on box plots represent groupings of *post-hoc* means analyses.

TABLE 2 *Total storage (kg/ha ± SE) and mass weighted concentration (MWC; mg/ha ± SE) of nutrients in aboveground biomass per census, Bisley Experimental Watersheds. Letters next to mean plot (78.5* m^2*) values indicate groupings of* post-hoc *analyses per nutrient column.*

	N	P	K	Ca	Mg
Total storage					
1989 pre-Hugo	687 ± 72.9a	39 ± 4.4a	580 ± 66.7a	568 ± 67.4ab	141 ± 14.7a
1989 post-Hugo	326 ± 55.9b	19 ± 3.0b	287 ± 47.4b	287 ± 49.7b	67 ± 10.8b
1994	651 ± 74.7a	37 ± 4.3a	558 ± 62.4a	505 ± 65.5ab	154 ± 14.5a
1999	758 ± 68.3a	43 ± 4.0a	657 ± 61.9a	603 ± 64.3a	183 ± 13.1a
2004	746 ± 72.1a	43 ± 4.7a	647 ± 63.3a	702 ± 137.0a	188 ± 17.4a
MWC					
1989 pre-Hugo	3.9 ± 0.2a	0.21 ± 0.0a	3.1 ± 0.1a	2.9 ± 0.1a	0.8 ± 0.0b
1989 post-Hugo	4.0 ± 0.3a	0.22 ± 0.0a	3.5 ± 0.2a	3.0 ± 0.1a	0.9 ± 0.1b
1994	4.0 ± 0.2a	0.22 ± 0.0a	3.5 ± 0.1a	2.6 ± 0.1a	1.2 ± 0.1a
1999	3.8 ± 0.1a	0.21 ± 0.0a	3.3 ± 0.1a	2.7 ± 0.1a	1.1 ± 0.0a
2004	3.7 ± 0.1a	0.20 ± 0.0a	3.2 ± 0.1a	2.8 ± 0.1a	1.0 ± 0.0a

($F_{4,164} > 3.71$, $P < 0.007$). Upland valleys varied through time in total N, K, and Mg ($F_{4,50} > 2.46$, $P < 0.057$). Riparian valleys had no differences in total storage of nutrients among years. In terms of MWC, the only difference observed among years was for Mg in both ridge ($F_{4,109} = 3.62$, $P = 0.008$) and slope ($F_{4,165} = 5.30$, $P < 0.001$) plots, and this was highest 5 yr after hurricane Hugo and lowest in the pre- and immediately posthurricane censuses. Upland and riparian valleys had no differences in MWC of N, P, K, Ca, and Mg among census year.

DISCUSSION

STRUCTURE AND COMPOSITION DURING HURRICANE-INDUCED SUCCESSION.—Evaluation ofchanges in forest composition and structure over time indicates that hurricane Hugo caused an immediate decrease in stem density and diversity indices and a reduction in the differences in species composition between geomorphic settings. After 15 yr, watershed-level basal area and aboveground biomass returned to their pre-hurricane values, but total species richness, diversity indices, and stem densities exceeded pre-hurricane levels (Table 1). During this time period, smaller scale storms and droughts may have slowed the recovery of forest structure, but they did not modify the overall direction of re-organization and regrowth (*sensu* Clements 1936, Lugo *et al.* 2000). The changes in species composition, in particular in slopes and upland valley areas, were drastic enough that after 15 yr, the pre-hurricane differences in species composition among geomorphic settings had not re-established and differences in stem density and structure were just beginning to emerge.

SPECIES AND NUTRIENTS DURING HURRICANE-INDUCED SUCCESSION.—Following the hurricane two secondary forest species, *C. schreberiana* and *P. berteriana* became the most common species in the forest. *Dacryodes excelsa* remained the species with highest biomass in every census, followed by *G. guidonia* and *C. schreberiana*. These species represent a combination of different strategies that allow them to dominate; *D. excelsa* grows on ridges in unions that are resistant to hurricane winds (Basnet *et al.* 1993, Scatena & Lugo 1995) and has long lasting (Mercado 1970), low-nutrient leaves (Fig. 4) that contain many secondary compounds (Bloomfield *et al.* 1993); *G. guidonia* is a generalist that has life-history traits of both secondary and primary forest species (García-Montiel & Scatena 1994, Aide *et al.* 1995) and relatively high foliar P concentrations; *C. schreberiana* is a fast growing pioneer with relatively high concentrations of Mg in both its leaves and wood.

Even though differences were observed in the biomass and nutrient concentrations of individual species, forest scale average MWC were fairly constant through time. The only nutrient with significant differences in MWC was Mg, a key nutrient for photosynthesis (Fig. S2). We related this to the 100-fold increase in stem density of the Mg-rich *C. schreberiana*. Previous studies also indicated that Mg increased in litterfall following hurricane Hugo, coinciding with the period during which *C. schreberiana* stem density increased (Scatena *et al.* 1996).

The measured changes in forest structure, biomass, and composition over the 15-yr period are evidence of the different roles species contribute to the recovery and succession of this forest. For individual species there are clear differences in the concentrations of their nutrients that can be related to their life history strategies and influence ecosystem properties and processes. When comparing nutrient pools or the MWC of the entire study area over time, however, between species nutrient differences were hidden by similarities in wood nutrient concentrations and the biomass dominance of a few species. Thus, while it is temping to suggest that consistency in aboveground MWC over successional time reflects internal biogeochemical controls, in this forest these consistencies are linked to the biomass dominance and resilience of a few species.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

TABLE S1. *Stem density and biomass for the top ten species per census of the Bisley Experimental Watersheds.*

FIGURE S1. Non-metric multidimensional scaling of abundance-based species composition and associated ANOSIM *R* statistics.

FIGURE S2. Distribution of values per census plot for stem density, diversity index, NMS axis 1, aboveground biomass, mass-weighted concentration N, Mg, and N/P ratio.

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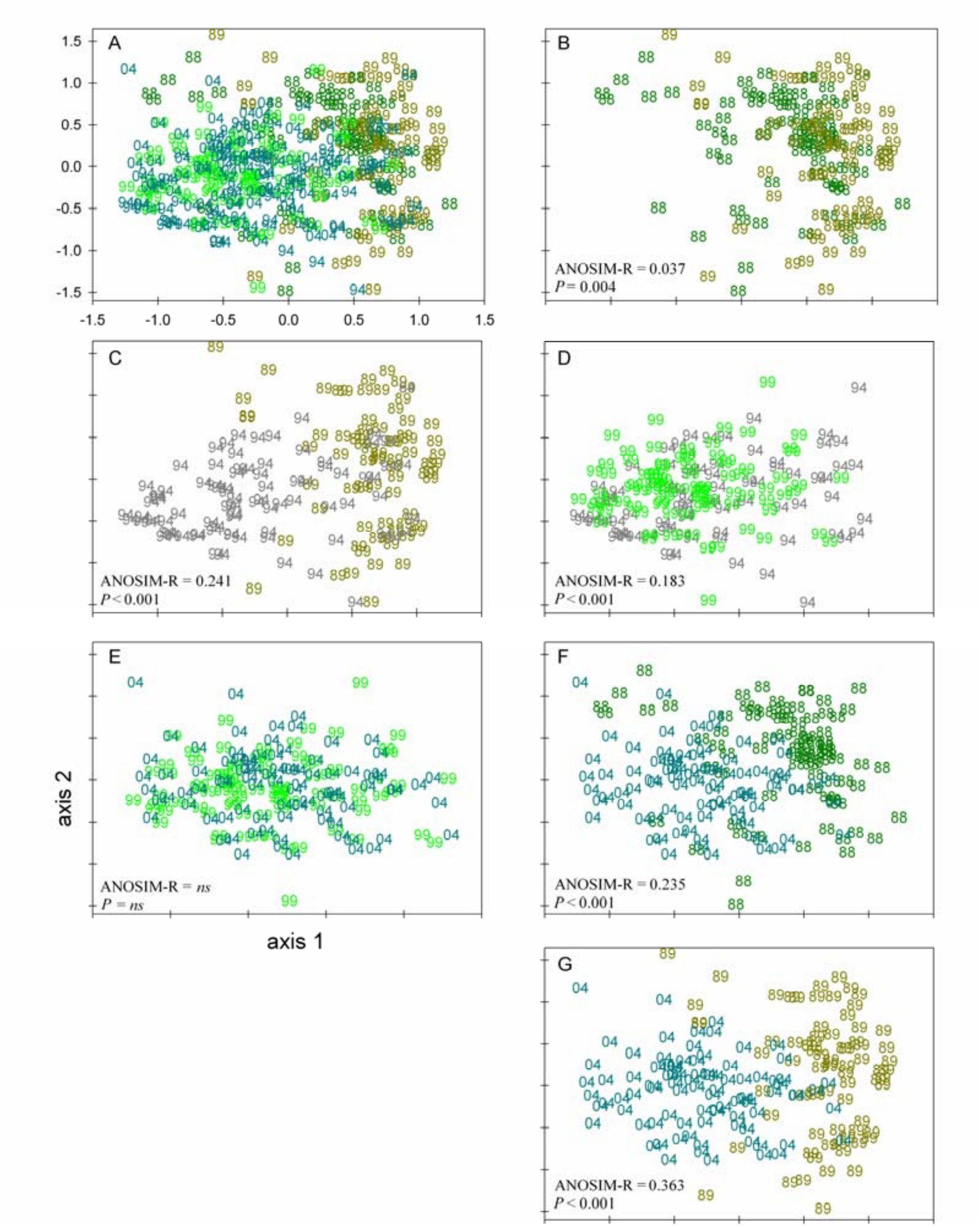

FIGURE S1. Non-metric multidimensional scaling (NMS) of abundance-based species composition and associated ANOSIM R statistics. The panels present the output of one NMS ordination, using data from all five censuses, as shown in panel A. Panels B–G present the same ordination, but for clarity only show two censuses at a time. Panels illustrate the following censuses: (B) 1988 pre-Hugo and 1989 post-Hugo; (C) 1989 post-Hugo and 1994; (D) 1994 and 1999; (E) 1999 and 2004; (F) 1988 pre-Hugo and 2004; and (G) 1989 post-Hugo and 2004.

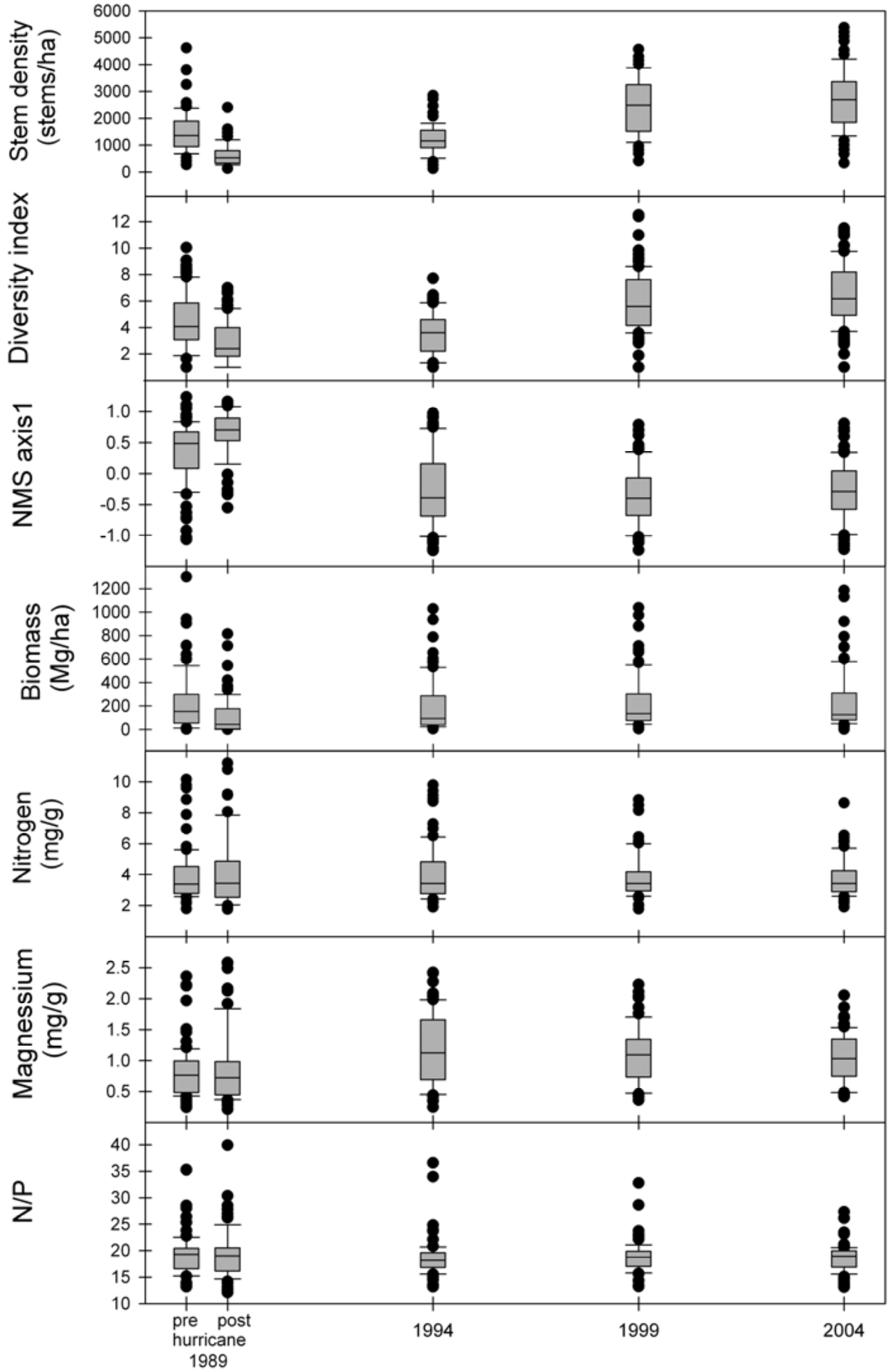

FIGURE S2. Distribution of values per census plot (78.5 m^2) for stem density, diversity index, NMS axis1, aboveground biomass, mass weighted concentration (MWC) N, Mg, and N/P (mg/g) ratio. For box plot description see Fig. 3 legend.

TABLE S1. *Stem density and biomass for the top ten species per census of the Bisley Experimental Watersheds. In* **bold** *low light/ primary forest species, underlined high light/ secondary forest species, other species are intermediary in their successional status and light requirements.*

Pre Hugo	1989	Post Hugo	1989		1994		1999		2004
a. Stems/ha									
Sloanea berteriana	92.9	***Sloanea berteriana***	76.7	*Cecropia schreberiana*	104.4	*Cecropia schreberiana*	107.3	*Cecropia schreberiana*	103.3
Prestoea montana	71.9	***Prestoea montana***	55.5	***Prestoea montana***	61.5	*Psychotria berteriana*	95.9	***Prestoea montana***	100.4
Dacryodes excelsa	61.4	***Dacryodes excelsa***	45.7	***Sloanea berteriana***	60.1	***Prestoea montana***	94.4	***Sloanea berteriana***	76.4
Inga laurina	40.4	*Inga laurina*	26.1	***Dacryodes excelsa***	37.2	***Sloanea berteriana***	84.4	*Psychotria berteriana*	76.4
Ocotea leucoxylon	38.9	*Casearea arborea*	19.6	*Inga laurina*	27.2	***Dacryodes excelsa***	48.6	***Dacryodes excelsa***	52.3
Cyathea portoricensis	35.9	***Cyathea portorricensis***	18.0	*Casearea arborea*	24.3	*Sapium laurocerasus*	41.5	***Cyathea portorricensis***	42.4
Guarea glabra	28.5	*Guarea guidonia*	16.3	*Guarea guidonia*	18.6	***Cyathea portorricensis***	37.2	***Ocotea leucoxylon***	38.2
Guarea guidonia	25.5	*Cordia borinquensis*	14.7	*Sapium laurocerasus*	18.6	*Inga laurina*	34.3	*Sapium laurocerasus*	35.4
Casearea arborea	25.5	***Ocotea leucoxylon***	14.7	***Cyathea portorricensis***	17.2	***Ocotea leucoxylon***	34.3	*Inga laurina*	32.5
Psychotria berteriana	25.5	*Guarea glabra*	13.1	*Cordia borinquensis*	12.9	*Casearea arborea*	32.9	*Casearea arborea*	32.5

b. % Biomass

Dacryodes excelsa	39.8	***Dacryodes excelsa***	43.9	***Dacryodes excelsa***	39.4	***Dacryodes excelsa***	35.0	***Dacryodes excelsa***	33.0
Guarea Guidonia	16.4	*Guarea guidonia*	11.4	*Cecropia schreberiana*	14.1	*Cecropia schreberiana*	18.7	*Cecropia schreberiana*	18.8
Sloanea berteriana	8.9	*Alchorneopsis floribunda*	8.3	*Guarea guidonia*	12.5	*Guarea guidonia*	9.2	*Guarea guidonia*	13.9
Alchorneopsis floribunda	4.3	***Buchenavia capitata***	7.0	***Sloanea berteriana***	5.5	***Prestoea montana***	7.8	***Prestoea montana***	8.1
Ormosia krugii	3.77	*Ormosia krugii*	4.21	***Prestoea montana***	4.7	***Sloanea berteriana***	5.6	***Sloanea berteriana***	3.6
Buchenavia capitata	3.5	*Inga laurina*	3.9	*Inga laurina*	4.6	*Inga laurina*	4.0	*Alchornea latifolia*	2.6
Schefflera morototoni	2.6	***Prestoea montana***	2.8	*Alchorneopsis floribunda*	3.1	***Buchenavia capitata***	2.6	***Buchenavia capitata***	2.2
Cecropia schreberiana	2.5	***Sloanea berteriana***	2.7	***Buchenavia capitata***	2.7	*Alchorneopsis floribunda*	2.1	***Manilkara bidentata***	1.8
Prestoea Montana	2.44	*Alchornea latifolia*	2.61	*Ormosia krugii*	2.3	*Laetia procera*	1.8	*Laetia procera*	1.7
Sapium laurocerasus	2.1	*Laetia procera*	1.9	*Alchornea latifolia*	2.0	*Alchornea latifolia*	1.7	*Inga laurina*	1.5