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Non-arborescent vegetation trajectories following repeated hurricane disturbance: ephemeral versus enduring responses

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Abstract. Hurricanes strongly influence short-term patterns of plant community structure, composition, and abundance and are a major contributor to the maintenance of plant diversity in many forests. Although much research has focused on the immediate and long-term effects of hurricane disturbance on tree diversity, far less attention has been devoted to the non-arborescent understory community that often account for the vast majority of the vascular species. Using a unique 20 year dataset, we tracked changes in richness, cover, biomass, and diversity (H') of non-arborescent species following Hurricane Hugo (1989) and Hurricane Georges (1998) in a mature secondary subtropical wet forest of Puerto Rico. Hurricanes caused an immediate, albeit transient, increase in overall species richness, cover, and diversity. Over a twenty year period, the non-arborescent community exhibited pronounced and persistent changes in composition, including a dramatic increase in abundance and richness of ferns and vines and a concomitant decrease in forbs and shrubs. By 2010, understory composition and relative abundance hierarchies were significantly altered; ferns and vines combined comprised 75 and 90% of total understory cover and biomass, respectively. Our results for this community contrast sharply with prior studies on similar temporal and spatial scales that demonstrate hurricanes rarely alter dominant tree species composition over the long-term. These results suggest that the role of hurricane disturbance in structuring plant diversity may be even more important than previously thought.

Key words: Bisley Experimental Watersheds; ferns; hurricane disturbance; Luquillo; understory; vines.

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INTRODUCTION

Ecologists have long recognized the central role of disturbance in structuring natural communities (Clements 1916, White 1979, Sousa 1984, Whitmore and Burslem 1998). In a wide-range of forest types, experimental and observational studies consistently find that disturbances that open up the canopy are often the primary mechanism determining species recruitment, growth, survival, and turnover in the understory (Pickett and White 1985, Denslow 1987). This widely accepted generalization is based predominantly on evidence from relatively small, recurrent disturbances (e.g., treefall gaps). In contrast, the effects of much larger, infrequent disturbances (e.g., hurricanes) remains less certain (Romme et al. 1998). Nevertheless, a growing body of knowledge has shed light on the impact of large-scale wind events on forest vegetation (reviewed by Tanner et al. 1991, Everham and Brokaw 1996, Chazdon 2003, Laurance and Curran 2008, Lugo 2008). These studies suggest that although the effects of most wind events on plant community diversity are strongly determined by storm changes to the canopy and by plant species' life-history traits, storms with high speed winds such as those associated with hurricanes may cross a disturbance severity threshold yielding successional dynamics that differ qualitatively from those of less severe storms (Everham and Brokaw 1996, Romme et al. 1998).

With a few notable exceptions, our understanding of hurricane effects on vegetation is limited to tree species (but see, Rodríguez-Robles et al. 1990, Migenis and Ackerman 1993, Pascarella 1998, Chinea 1999, Meléndez-Ackerman et al. 2003, Halleck et al. 2004). This focus on trees creates a critical knowledge gap as responses of non-arborescent species (i.e., ferns, forbs, grasses, shrubs, vines) to disturbance often differs from those of trees on an individual-, population-, and community-level basis (Roberts 2004). For example, although storms may severely defoliate ramets of non-arborescent species, survival is typically high and recovery is rapid relative to tree species due to the prevalence of clonality, carbohydrate reserves in below-ground storage organs, and lower investment in secondary tissue (Meléndez-Ackerman et al. 2003, Bruna and Ribeiro 2005). Additionally, increased understory light availability following canopy disturbance is known to enhance fruiting of resident non-tree species (Levey 1988, Dirzo et al. 1992, Pascarella 1998), whereas the severe tissue loss associated with storms often suppresses tree fruit production for months (e.g., Wunderle 1999). This reproductive benefit to understory plants relative to trees is often accompanied by increased recruitment from dispersed or dormant propagules and aggressive vegetative spread (Guariguata 1990, Meléndez-Ackerman et al. 2003, Shiels et al. 2010). Further, the prevalence of clonality in many non-arborescent species allows for the rapid exploitation and colonization of previously unoccupied patches, whereas tree resprouting is typically restricted to the immediate area of the affected stem. Finally, given the broad variation in life-history strategies exhibited by non-arborescent species, hurricanes may disproportionately affect certain life-forms over others. For instance, high-intensity winds may cause greater mortality in arboreal epiphytic and semi-epiphytic species than on terrestrial species (Rodríguez-Robles et al. 1990, Migenis and Ackerman 1993, Weaver 1999).

Differences in traits determining susceptibility and recovery to hurricanes for non-arborescent and tree species may result in post-disturbance successional trajectories that contrast markedly between these two communities. Indeed, while post-hurricane disturbance vegetation is often characterized by a high abundance of surviving resident species (e.g., Everham and Brokaw 1996, Chazdon 2003), succession in tree communities often incorporates many shade-intolerant, pioneer recruits (but see, Vandermeer et al. 2000) and shifts in tree community composition accrue over decades as shade-tolerant species progressively recruit into sites and pioneers slowly senesce (Lugo 2008, Heartsill Scalley et al. 2010). In sharp contrast, shifts in non-arborescent species communities may occur almost instantly (e.g., vines falling to forest floor during canopy disturbance; Putz 1984, Schnitzer and Bongers 2011) or relatively quickly (e.g., recruitment of seed-banking species or expansion of clonal ferns; Guariguata 1990, Horvitz and Schemske 1994). These rapid changes in understory plant dominance patterns may delay subsequent vegetation development and ultimately reduce diversity in disturbed sites (Royo and Carson 2006, Walker et al. 2010). Finally, non-arborescent species typically represent the most diverse plant forms in Neotropical forests constituting as much as two-thirds of the vascular flora (Gentry and Dodson 1990, Chinea et al. 1993, Royo and Carson 2005). Thus, given the range of responses to disturbance and the sheer diversity exhibited by non-arborescent species relative to tree species, the role of wind disturbance in the maintenance of overall forest plant diversity may currently be underestimated (see Schnitzer and Carson 2000).

In this study we examine non-arborescent plant species responses and successional trajectories over 20 years in a mature secondary forest impacted by multiple hurricanes. This unique record allows an examination of non-arborescent vegetational response that followed two severe ($\geq$3 Saffir-Simpson index) hurricanes. This dataset extends previously reported short-term ($\leq$5 yr) results (Chinea 1999) and complements data published on the arborescent community on these same permanent plots (Scatena et al. 1993, Heartsill Scalley et al. 2010).

METHODS

Study area and hurricane history

We conducted our study within the Bisley Experimental Watersheds (18°20′ N 65° 50′ W) of the Luquillo Experimental Forest (LEF) in Puerto Rico. The forests are subtropical wet forests receiving a mean annual rainfall of 3.5 m/yr (Heartsill Scalley et al. 2007). The watersheds are characterized by a mature, secondary tabonuco (*Dacryodes excelsa*) forest canopy. Light levels under intact canopies are generally low (median: 23.0 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$; Walker et al. 1992). Further detailed description of the geomorphology and vegetation can be found in Scatena and Lugo (1995) and Chinea et al. (1993).

The study area faces northeast and is therefore exposed to a dominant weather pattern characterized by north-easterly trade winds. Hurricanes directly pass over the study area an average of every 50–60 years (Scatena and Larsen 1991). Over the past two decades, however, the LEF has been affected by at least five hurricanes (Heartsill Scalley et al. 2007). The most significant were Hurricane Hugo (Category 4; September 18, 1989) and Hurricane Georges (Category 3; September 22, 1998). The area also experienced moderate, localized damage from hurricanes Bertha, Hortense, and Marilyn (July–September 1996). Hurricane Hugo resulted in a near complete defoliation of the forest canopy and caused a 50% reduction in aboveground biomass while Georges defoliated approximately 77% of the trees in the tabonuco forest type (Scatena and Larsen 1991, Ostertag et al. 2003). Canopy damage from these two storms increased understory light availability by as much as an order of magnitude, although these changes were relatively short-lived (10–36 months; Walker et al. 1992, Comita et al. 2009). Additionally, the storms generated large-scale deposition of green litter and debris to the forest floor and increased soil disturbance through erosion, landslides, and treefalls (Scatena and Lugo 1995, Lenart et al. 2010). These disturbances may alter nutrient availability and nutrient cycling pathways as well as creating favorable establishment microsites for some plant species (Lodge and McDowell 1991, Scatena et al. 1993, Teh et al. 2009, Walker et al. 2010).

Vegetation sampling

Within the 13 ha area encompassing the Bisley watersheds in the LEF, a network of 85 permanent woody vegetation monitoring plots was established at the nodes of a 40 × 40 meter grid in 1988–89. In the months following Hurricane Hugo, we randomly selected 25 points for intensified sampling of non-arborescent vegetation. At each selected point, we established five 1 m^2 permanent quadrats at randomly selected azimuth and distance ($\leq$5 m) radiating from the center point. Within each quadrat, we visually estimated the percent cover, by species, of all non-arborescent vegetation located within the space defined by vertically projecting the perimeter of the quadrat to $\leq$1.5 m in height, regardless of whether vegetation was rooted in the plot or not. Censusing began in September 1990 (one year post-Hugo) and ran through 2010. Aboveground biomass was determined for each sample period by destructively sampling an additional 25 1 m^2 quadrats that were interspersed with the permanent monitoring quadrats. Samples were collected at the same time as the 125 quadrats. Biomass of all non-arborescent vegetation in each of these destructively sampled plots was sorted by species, dried at 65°C to a constant weight, and weighted to the nearest 0.1 g. All censuses were conducted annually for the first decade and in 2001, 2003, 2005, 2007, and 2010.

Analyses

For each of the 25 points, we calculated richness, species diversity (Shannon, H'), and percent cover at each census period based on the combined species across all five replicate quadrats per point. We also calculated richness and percent cover on five species groups: ferns, forbs, vines (herbaceous and woody), graminoids, and shrubs (i.e., multi-stemmed woody plant with mature height $\leq$5 m; USDA Plants Database). We calculated richness as species density (i.e., species/m^2) in order to correct for the unequal sampling at some points due to loss of a total of five quadrats to landslides over time. Additionally, we compared overall richness between census intervals using species richness accumulation curves with 95% confidence intervals. Species accumulation curves were derived using EstimateS v. 8.2 software (Colwell 2009).

Our primary interest was to examine changes in species richness, abundance, and diversity over time. Thus, we used a repeated-measures analysis of variance treating each sample as a random subject ($N = 25$ points × 15 census periods $= 375$). Analyses of biomass cover were similar with the exception that the analyses did not include a random subject component because biomass plots could not be repeatedly sampled. The analyses used the restricted maximum likelihood estimation method, a spatial power covariance structure, and the Kenward-Rogers adjustment for denominator degrees of freedom calculation (Littell et al. 2006). We performed six a priori comparisons to further examine differences between response variables among census periods that immediately precede a hurricane (1998), two that immediately followed hurricanes (1990 and 1999) and our final census (2010). This approach is preferable over multiple, unplanned comparisons when the hypotheses allow examination of specific pair-wise contrasts as opposed to the 105 possible comparisons among the 15 (14 for biomass) census intervals (Day and Quinn 1989). Percent cover and biomass data were strongly right-skewed, contained a high number of zero values, and were over-dispersed. Therefore, we employed a general linear mixed model (PROC GLIMMIX) using a gamma distribution with a log-link function on cover after adding a constant of 0.1 to adjust for zero values (Bolker 2008). All other analyses were modeled using a normal distribution. The inverse link (ilink) option was used to back-transform least squares means and standard errors to the original units of measure; these back-transformed means rather than means from the transformed data are presented.

Changes in species composition were examined using non-parametric analysis of similarity (ANOSIM) on the species abundance (% cover) matrix using Bray-Curtis distance. The analysis calculates an *R*-statistic based on the difference of mean ranks between and within groups. This value varies between 1 and -1: values near zero indicate groups are homogenous and values approaching 1 indicate progressively more distinct groups (Clarke 1993). Prior to analyses, the species abundance matrix was relativized by species maximum to equalize the effect of common and rare species (McCune and Grace 2002). Finally, we identified the individual species most responsible for the separation between the initial and final census using the similarity percentage (SIMPER) routine. The SIMPER procedure determines each species contribution to the average dissimilarity coefficient. ANOSIM and SIMPER analyses were run using the PAST software (Version 1.94; Hammer and Ryan 2001).

RESULTS

Community metrics

Species richness (no. species/m^2) was greatest in the year following Hurricane Hugo, declined, and then significantly increased in the year following Hurricane Georges (Fig. 1A, Table 1). The species accumulation curves yielded a similar pattern; however, the differences among years were not significant at a 0.05 level (Fig. 2). Overall cover, biomass, and diversity (H') all increased significantly following Hurricane Georges (Fig. 1B, C; Table 1).

The non-arborescent community at the Bisley watersheds grew increasingly different over time with pronounced shifts in the relative abundance of species groups (Fig. 3). In the nine years following Hugo, ferns expanded from approximately 18% to nearly 60% of the understory cover and biomass. Further shifts occurred following Georges when vines captured an additional 16% of the total cover and 29% of the total biomass. By 2010, these two groups dominated the understory community (Fig. 3). The ANOSIM results confirm the shift as species composition grew increasingly different (Global *R*: 0.053, $P < 0.0001$). Examination of pair-wise differences (partial *R* values) in ANOSIM results between census intervals reveal the majority of changes in composition occur when comparing the first two years post-Hugo (i.e., 1990 or 1991) to any subsequent year, suggesting compositional changes accrue rapidly. Furthermore, although the passage of Hurricane Georges generated a pulse in overall diversity (Fig. 1, Table 1), pair-wise differences (partial *R* values) in ANOSIM detected no significant changes in species composition between 1998 and any subsequent year.

Species groups and dominant species

Over time, the abundance and richness of the five species groups all varied, yet these groups sorted out into three patterns according to whether their abundance or richness consistently increased, had bimodal fluctuations, or consistently decreased (Figs. 4 and 5, Table 2).

Ferns consistently increased over time. In the decade following Hurricane Hugo, fern cover and biomass both increased over 200% and remained at high levels during the next 12 years (Fig. 4A, Table 2). Fern richness briefly increased following Hugo then significantly increased again after Hurricane Georges (Fig. 5A). By 2010, ferns dominated the understory of the Bisley watersheds in terms of cover, biomass, and richness. The SIMPER results reveal three fern species (*Bolbitis nicontanifolia*, *Danaea nodosa*, and *Thelypteris deltoidea*) constitute nearly 30% of the difference in the understory community across census dates (Table 3). Several other fern species also increased in abundance over time (Appendix).

Vines and graminoids displayed bimodal peaks in abundance and richness following hurricanes (Figs. 4B, C and 5B, C; Table 2). Vine cover, biomass, and richness significantly declined following Hugo only to significantly increase again after Georges. Following Georges, vine cover more than doubled and biomass quadrupled reaching levels comparable to those following Hugo and, unlike in the decade following Hugo, remained highly abundant over the next 12 years (Fig. 4B, Table 2). Vine richness also significantly increased following Georges and remained at comparable levels over the following years, although richness was still below that measured in the year after Hugo (Fig. 5B). Similarly, graminoid cover and biomass declined in the decade following Hugo (Figs. 4C and 5C). Graminoid cover increased ephemerally after Georges and both cover and biomass significantly declined over the 12 years following Georges (Table 2). Fluctuations in graminoid richness over time tended to exhibit a similar bimodal pattern (P = 0.051). The SIMPER results identified two vines, one woody (*Marcgravia rectiflora*) and one non-woody (*Philodendron scandens*), along with a graminoid (*Ichnanthus pallens*) as significant contributors to community differences over time (Table 3). These two vines increased four-fold, in the decade following Georges, whereas the graminoid experienced distinct peaks of high abundance in the year following both hurricanes.

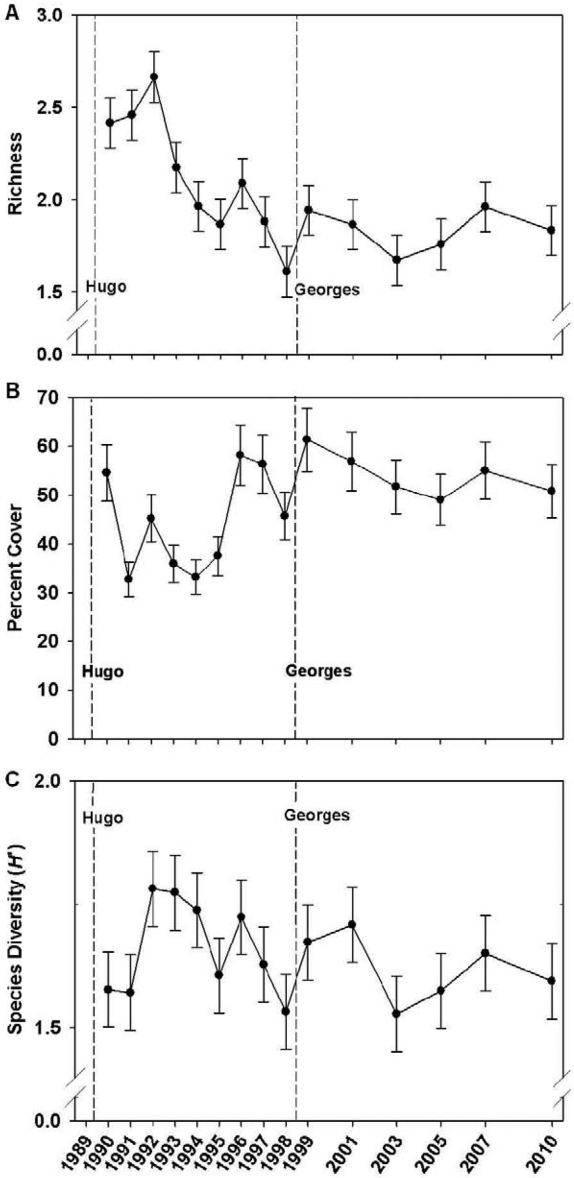

Fig. 1. Changes in mean overall (a) species richness, (b) percent cover, and (c) species diversity (H') at the Bisley Experimental Watersheds (LEF) in each census period (mean ± 1 SE). Recording began in September 1990, 12 months after Hurricane Hugo.

Finally, forb and shrub richness and abundance decreased steadily over the two decades following Hugo and this trajectory was unaltered by Hurricane Georges (Figs. 4D, E and 5D, E). Initially, forbs were the second most abundant group, yet, over 21 years, this group declined in

Table 1. Overall repeated-measures ANOVA results and specific a priori contrasts of community-level response variables among years immediately preceding Hurricane Georges (1998), the years following both Hurricane Hugo (1990) and Georges (1999) and our final census at the Bisley Experimental Watersheds (LEF). Different letters among time periods denote significant ($P < 0.05$) differences. Richness is species density (no. species/m^2), cover is mean percent (%) cover, biomass is dry weight biomass (g/m^2), and diversity is Shannon (H') value.

					Overall model		
Variable	Post-Hugo (1990)	Pre-Georges (1998)	Post-Georges (1999)	Final (2010)	Df†	*F*	*P*
Richness	2.42 ± 0.14^{a}	1.61 ± 0.14^{b}	1.94 ± 0.14^{c}	1.83 ± 0.14^{bc}	14, 289	7.29	<0.0001
Cover	54.52 ± 5.79^{ab}	45.70 ± 4.86^{a}	61.36 ± 6.52^{b}	50.79 ± 5.40^{ab}	14, 322.6	9.15	<0.0001
Biomass (g/m^2)	82.82 ± 16.08^{ab}	54.27 ± 11.55^{a}	115.03 ± 24.47^{b}	87.29 ± 18.95^{ab}	13, 347	2.35	0.0051
Shannon (H')	1.58 ± 0.08^{ab}	1.53 ± 0.08^{a}	1.67 ± 0.08^{b}	1.59 ± 0.08^{ab}	14, 290.1	2.65	0.0012

† Denominator degrees of freedom can be fractional in REML analyses with Kenward Roger adjustment.

cover, biomass, and richness by 57, 53, and 35%, respectively (Table 2). Shrubs had the lowest abundance and richness of all groups at the Bisley watersheds, and their cover and richness declined by 83 and 75%, respectively (Table 2). Shrubs were absent in most biomass quadrats in several years, thus precluding a rigorous analysis on shrub biomass trajectory. Although several forbs and shrubs found in earlier censuses were absent from sample plots by 2010 (Appendix), the SIMPER results indicate only *Pilaea inaequalis* (a forb) contributed to compositional differences over time and remained an important component of the understory community.

DISCUSSION

Ephemeral versus enduring hurricane effects on non-arborescent communities

Our unique long-term dataset of non-arborescent plant communities across adjacent watersheds subjected to two severe and several minor hurricanes facilitates a greater understanding of the rate and direction of vegetation response to

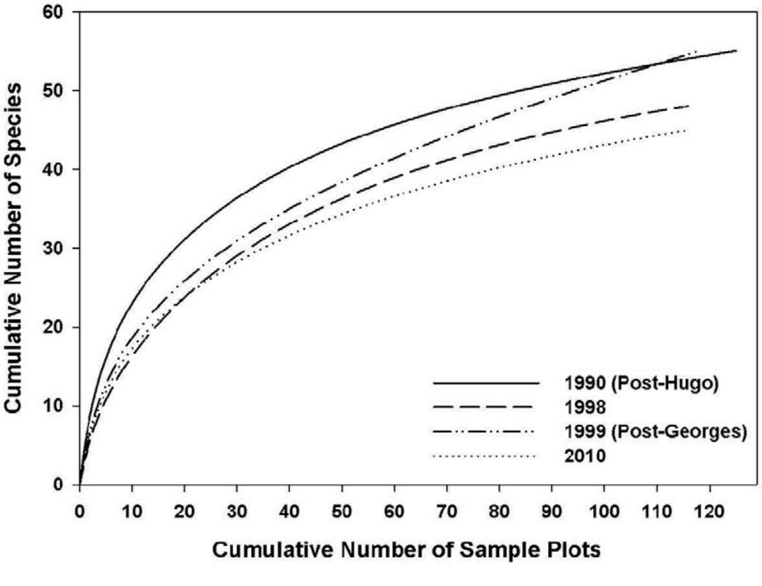

Fig. 2. Species richness accumulation curves in the Bisley Experimental Watersheds (LEF) for the year immediately preceding Hurricane Georges (1998), the years following Hurricane Hugo (1990) and Georges (1999) and the final census (2010). For ease of interpretation, we did not plot 95% confidence intervals because these broadly overlap among all curves.

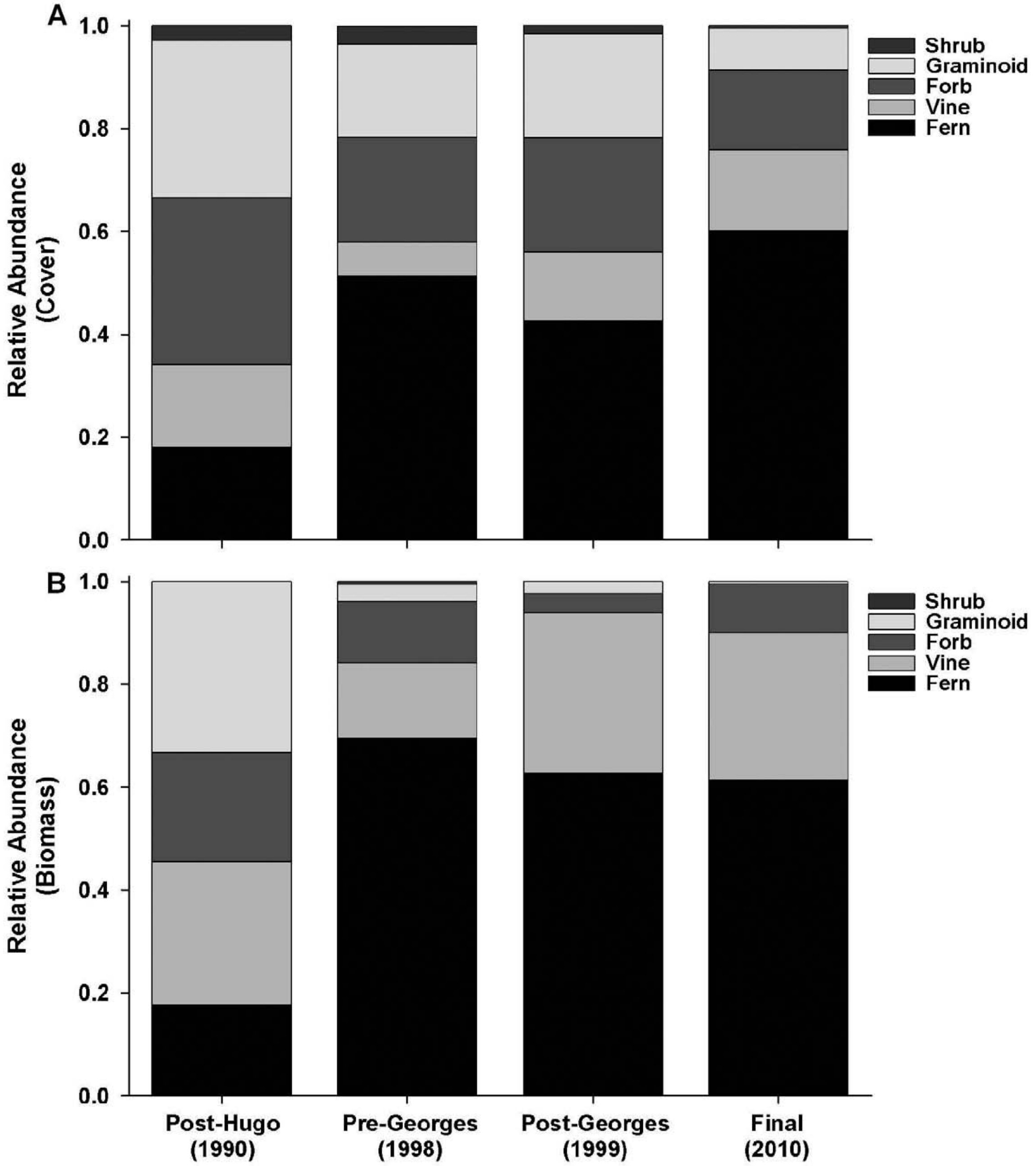

Fig. 3. Changes in non-arborescent species group patterns of relative abundance in the Bisley Experimental Watersheds (LEF) in terms of percent cover (A) and biomass (B) for the year immediately preceding Hurricane Georges (1998), the years following Hurricane Hugo (1990) and Georges (1999) and the final census (2010). Relative abundance measures calculated from actual means rather than back-transformed least squares means.

disturbance. Although some facets of the non-arborescent community response to hurricanes manifested themselves rapidly following Hugo (Chinea 1999), other changes accrued over a longer term and in response to subsequent storms and, consequently, were not predicted by the early data.

In a manner consistent with the observed

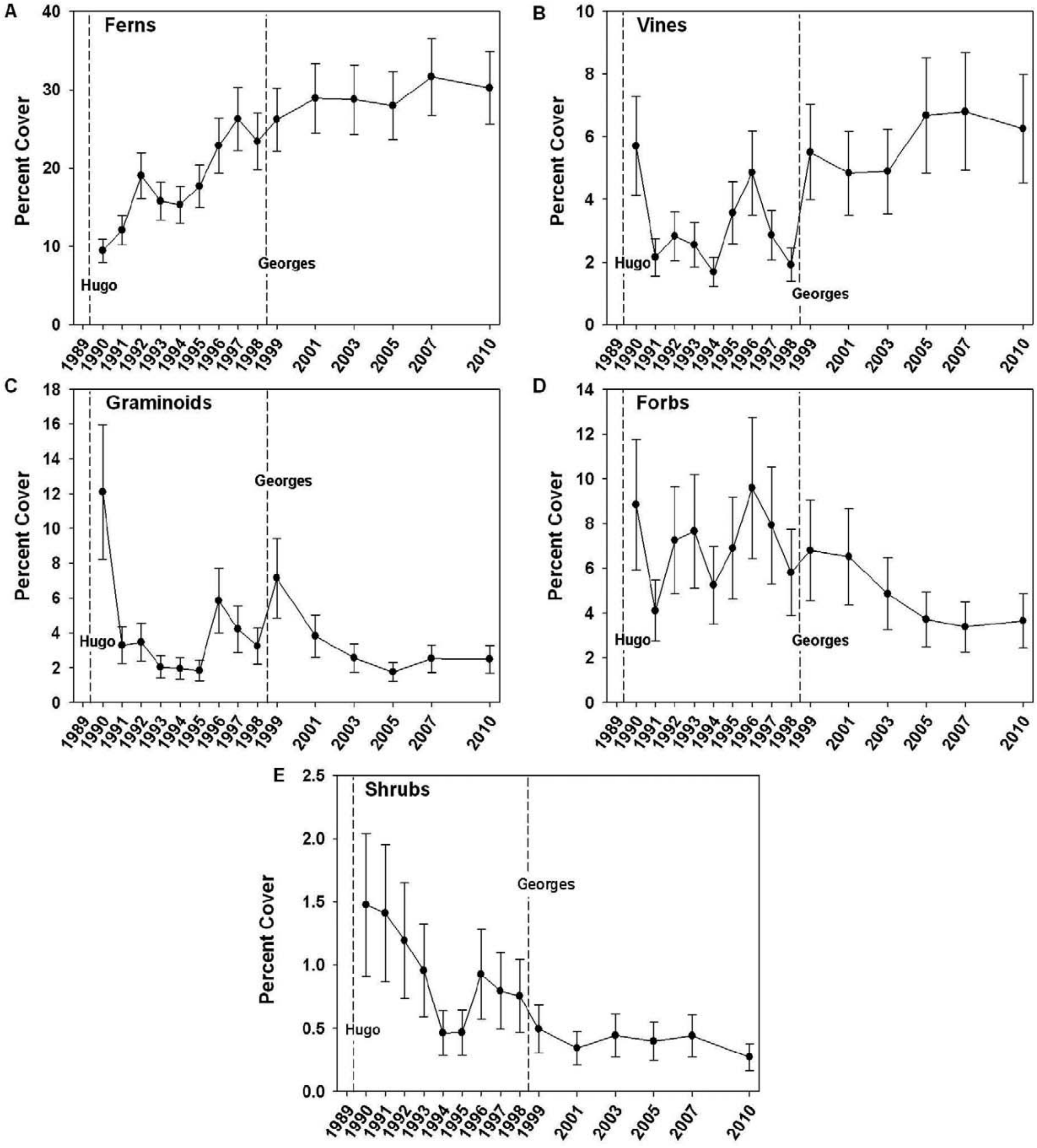

Fig. 4. Changes in mean percent cover for ferns (A), vines (B), graminoids (C), forbs (D), and shrubs (E) in the Bisley Experimental Watersheds (LEF) at each census period (mean ± 1 SE). Recording began in September 1990, 12 months after Hurricane Hugo.

response from tree seedling communities (Battaglia et al. 1999, Walker et al. 2003, Tanner and Bellingham 2006), we documented recruitment pulses that led to short-term increases in plot-level species richness, diversity, cover, and biomass in response to the passing of Georges. As predicted by Lugo (2008) for trees, changes in diversity observed as species entered or exited at a plot scale (i.e., Fig. 1, Table 1) were not observed at the watershed scale (Fig. 2; see also

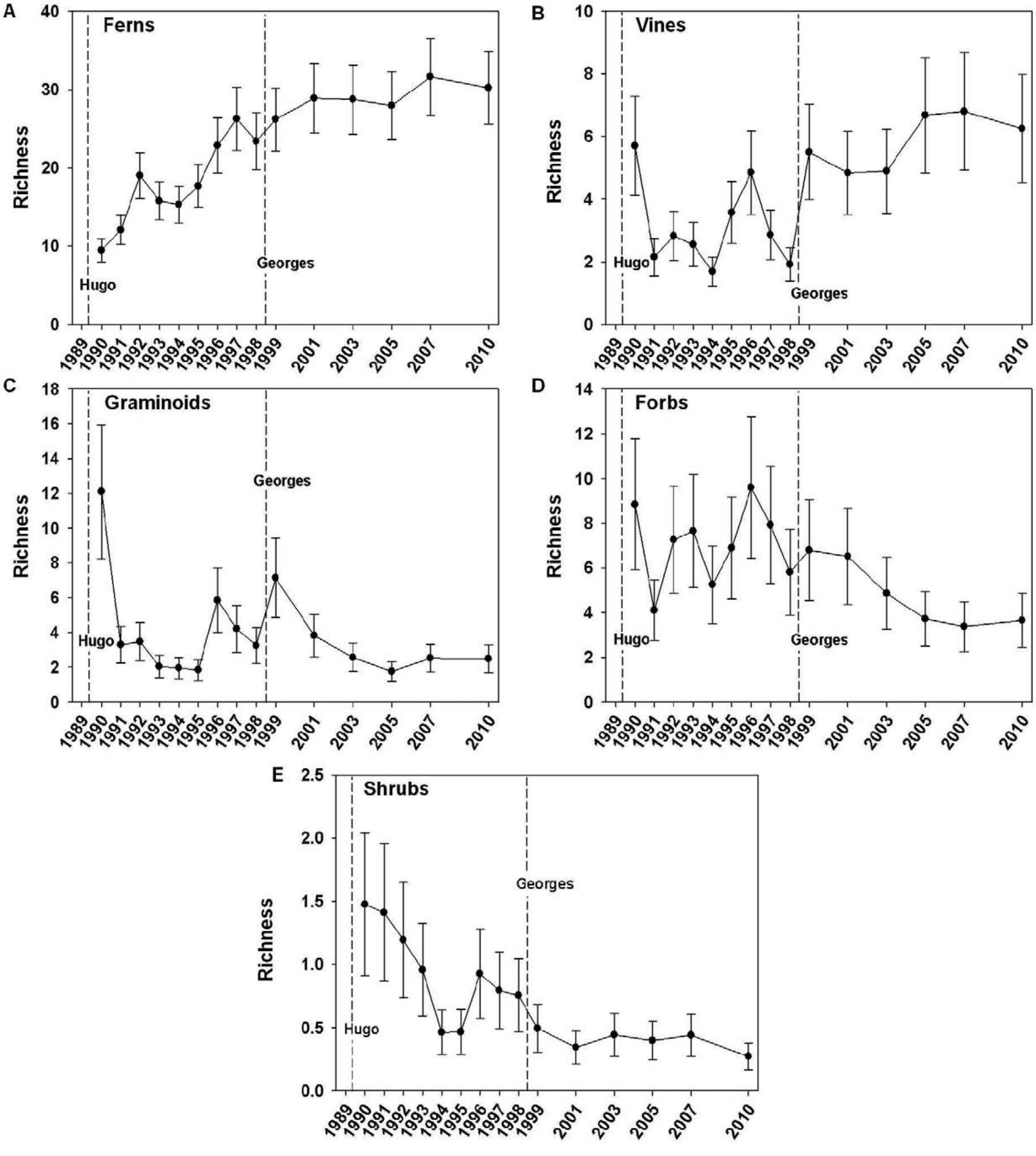

Fig. 5. Changes in mean richness (species/m^2) for ferns (A), vines (B), graminoids (C), forbs (D), and shrubs (E) in the Bisley Experimental Watersheds (LEF) at each census period (mean ± 1 SE). Recording began in September 1990, 12 months after Hurricane Hugo.

Heartsill Scalley et al. 2010). This suggests that while interactions among landscape history and vegetation structure, species pools and life histories, and hurricane severity can structure local species composition (e.g., Comita et al. 2009), at larger scales the net effect is the maintenance of diversity across a heterogeneously disturbed landscape (e.g., Burslem et al. 2000, Vandermeer et al. 2000).

We found several non-arborescent species

Table 2. Overall repeated-measures ANOVA results and specific a priori contrasts of species group response variables among years immediately preceding Hurricane Georges (1998), the years following both Hurricane Hugo (1990) and Georges (1999) and our final census at the Bisley Experimental Watersheds (LEF). Different letters among time periods denote significant ($P < 0.05$) differences. Richness is species density (no. species/m^2), cover is mean percent (%) cover, and biomass is dry weight biomass (g/m^2).

					Overall model		
Variable	Post-Hugo (1990)	Pre-Georges (1998)	Post-Georges (1999)	Final (2010)	Df†	*F*	*P*
Ferns							
Richness	0.59 ± 0.08^{a}	0.63 ± 0.08^{ab}	0.77 ± 0.08^{c}	0.73 ± 0.08^{bc}	14, 256.3	2.89	0.0005
Cover	9.44 ± 1.45^{a}	23.38 ± 3.60^{b}	26.18 ± 4.03^{b}	30.21 ± 4.65^{b}	14, 322.9	4.49	<0.0001
Biomass	14.75 ± 4.05^{a}	37.72 ± 11.34^{b}	72.25 ± 21.72^{b}	52.63 ± 16.46^{b}	13, 347	2.91	0.0005
Vines							
Richness	0.74 ±0.07^{a}	0.29 ± 0.07^{b}	0.44 ± 0.07^{c}	0.44 ± 0.07^{c}	14, 323.2	6.20	<0.0001
Cover	5.69 ± 1.57^{a}	1.91 ± 0.53^{b}	5.50 ± 1.52^{a}	6.24 ± 1.73^{a}	14, 295.2	5.28	<0.0001
Biomass	23.07 ± 8.06^{a}	8.02 ± 3.07^{b}	35.86 ± 13.72^{a}	25.21 ± 9.85^{a}	13, 347	3.45	<0.0001
Forbs							
Richness	0.50 ± 0.05	0.33 ±0.05	0.38 ±0.05	0.30 ±0.05	14, 321.2	1.39	0.1577
Cover	8.83 ± 2.92^{a}	5.81 ± 1.92^{ab}	6.80 ± 2.25^{a}	3.65 ± 1.21^{b}	14, 296.5	3.80	<0.0001
Biomass	17.75 ± 5.66^{a}	6.63 ± 2.32^{b}	4.40 ± 1.54^{b}	8.25 ± 2.94^{ab}	13, 347	5.32	<0.0001
Graminoids							
Richness	0.29 ± 0.04	0.23 ± 0.04	0.25 ± 0.04	0.22 ± 0.04	14, 325.2	1.72	0.0508
Cover	12.09 ± 3.85^{a}	3.24 ± 1.34^{b}	7.14 ± 2.27^{a}	2.48 ± 0.79^{b}	14, 287.8	9.88	<0.0001
Biomass	27.56 ± 8.14^{a}	1.90 ± 0.62^{b}	2.81 ± 0.91^{b}	0.39 ± 0.15^{c}	13, 347	19.31	<0.0001
Shrubs							
Richness	0.16 ± 0.03^{a}	0.10 ± 0.03^{b}	0.09 ± 0.03^{b}	0.05 ± 0.03^{b}	14, 317.3	2.15	0.0095
Cover	1.48 ± 0.56^{a}	0.75 ± 0.29^{ab}	0.49 ± 0.19^{bc}	0.27 ± 0.10^{c}	14, 286.1	2.28	0.0057
Biomass‡	-	-	-	-	-	-	-

† Denominator degrees of freedom can be fractional in REML analyses with Kenward Roger adjustment.
‡ No analyses on shrub biomass due to zero values in multiple years.

recruited into the understory or increased dramatically in abundance only after hurricanes (Appendix). Many were epiphytic or semi-epiphytic species (e.g., *Asplenium serratum, Microgramma lycopodioides*) or climbing vines (e.g., *Mikania cordifolia*). Hurricane force winds and associated canopy disturbance often displaces many of these arboreal species from the tree canopy and deposits them onto the forest floor (Putz 1984, Rodríguez-Robles et al. 1990, Weaver 1999). Although this displacement produces an instantaneous 'recruitment' into the understory, the ephemeral pulse in diversity suggests many individuals do not persist in the understory either through high mortality (Hietz 1997, Winkler et al. 2007) or by ascending back into the canopy after finding suitable trellises (Putz 1984). Recruitment of seed-banking, shade-intolerant species (e.g., *Clibadium erosum, Phytolacca rivinoides, Scleria scindens*) and short-term increases in growth and reproduction by resident shade-tolerant species (e.g., *Begonia decandra, Ichnanthus pallens*) also likely contributed to the ephemeral diversity peak after canopy disturbance (Lawton

Table 3. Mean cover of important non-arborescent species discriminating among all census periods in the 20 years following Hurricane Hugo within the Bisley Experimental Watersheds (LEF). Species are listed in order of their contribution (Cumulative %) to the mean dissimilarity. Overall average dissimilarity was 75.64%.

Taxon	Life-form	Cumulative (%)	Post-Hugo (1990)	Pre-Georges (1998)	Post-Georges (1999)	Final (2010)
Danaea nodosa	Fern	15.28	3.47 ± 1.14	11.66 ± 2.75	10.32 ± 2.20	14.82 ± 3.21
Pilea inaequalis	Forb	24.82	7.16 ± 1.85	5.32 ± 1.26	6.75 ± 1.57	5.37 ± 1.20
Ichnanthus pallens	Graminoid	34.18	11.76 ± 3.10	6.42 ± 2.23	11.10 ± 3.29	2.32 ± 0.57
Thelypteris deltoidea	Fern	43.03	1.54 ± 0.61	3.50 ± 1.05	4.04 ± 1.14	3.60 ± 1.18
Bolbitis nicotianifolia	Fern	48.33	1.05 ± 0.48	3.09 ± 1.16	4.24 ± 1.49	2.69 ± 0.82
Marcgravia rectiflora	Vine	53.12	0.20 ± 0.12	0.73 ± 0.41	1.99 ± 0.76	3.48 ± 0.94
Philodendron scandens	Vine	57.06	1.07 ± 0.30	0.61 ± 0.41	3.02 ± 0.98	2.77 ± 0.70

and Putz 1988, Guariguata 1990, Arnold 1996, Cordero 2000, Shiels et al. 2010).

We further observed that while the pattern and magnitude of many responses measured post-Georges are comparable to those found immediately post-Hugo (Appendix), the recruitment pulse for some seed banking species was more restrained (e.g., *P. rivinoides, C. erosum*; see also Fig. 4C). Uriarte et al. (2009) similarly found a seed banking tree, *Cecropia schreberiana*, had a lower recruitment response following Georges than after Hugo. These diminished recruitment pulses following Georges may be attributable to at least three mechanisms. First, Georges caused less canopy damage than Hugo and thus, potentially restricted the expected increases in light quantity, quality and temperature at the soil surface which are important germination cues for seed-banking species (Odum and Pigeon 1970). Second, sapling ingrowth and fern expansion in the decade following Hugo may have further moderated potential abiotic germination cues created by Georges (Horsley 1993). Finally, outbreaking lepidopteran populations severely defoliated populations of many early-successional plants (e.g., *P. rivinoides* and *C. erosum*) in the months following Hugo, thus potentially limiting seed bank replenishment (Torres 1992). These results underscore the importance disturbance return interval timing and suggest successive hurricanes may act synergistically in influencing recovery trajectories (Ostertag et al. 2005, Lugo 2008, Uriarte et al. 2009).

In contrast to the transient effects on diversity, more pronounced and persistent changes to the understory community were directly associated with select fern and vine species that capitalized on the opportunities created by hurricane disturbance (Table 3, Appendix). Some ferns (e.g., *B. nicotianifolia, D. nodosa,* and *Dennstaedtia obtusifolia*) and vines (e.g., *M. rectiflora* and *P. scandens*) flourished in the understory following canopy disturbance. We suggest traits including high genet survival, vigorous resprouting, and rapid vegetative expansion facilitate this process in the resource-rich (e.g., light, nutrient) environment created by disturbance (Kelly 1985, Everham and Brokaw 1996, reviewed by Royo and Carson 2006, Schnitzer and Bongers 2011). Additionally, hurricane disturbance may increase fern abundance through enhancing spore production (e.g., *T. deltoidea*; J. Sharpe, *personal communication*) and recruitment microsite creation (e.g., landslides, uprooted trees; Guariguata 1990, Walker et al. 2010).

Shifts in relative abundance hierarchies and recalcitrant understory layers

Despite the considerable short-term effects on established tree structure and biomass caused by hurricanes, long-term observations find the pre-disturbance relative abundance hierarchies of tree communities are generally unaltered due to high survival and rapid resprouting of residual vegetation (Burslem et al. 2000, Tanner and Bellingham 2006, Imbert and Portecop 2008). In fact, Lugo (2008) conjectured that hurricanes often reinforce the pre-disturbance hierarchies of established dominant tree species. We suggest non-arborescent plant communities may follow a different trajectory. We found that while dominance patterns in the understory of the Bisley watersheds did converge towards a few species, this process was driven, not by species that were initially dominant, but rather by a restricted set of ferns and vines that were far less dominant at the onset of monitoring. Although we lack detailed non-arborescent community data prior to Hurricane Hugo, Scatena et al. (1993) report biomass estimates within the our existing Bisley plot network both pre- and post-Hugo. Their results document Hugo caused biomass reductions from 31g/m^2 to 21 g/m^2 and 13g/m^2 to 9 g/m^2 in herbs (forbs + graminoids) and ferns, respectively. These results demonstrate that in relatively undisturbed mature forest stands within the LEF, fern and vine abundance is equal to or even subordinate to forbs. More importantly, these results show that, pre-Hugo, ferns were only one-fourth as abundant as the levels they ultimately attained. By 2010, ferns dominated 60% of the non-arborescent plant cover and biomass and ferns and vines collectively captured 75% and 90% of the cover and biomass, respectively.

We suggest the combined effect of repeated hurricanes has promoted the development of a recalcitrant understory layer (sensu Royo and Carson 2006) at the Bisley watersheds over the past 10–15 years. These novel vegetation layers are found in forests worldwide where changes in historic disturbance regimes (e.g., increased frequency or severity) alter understory succession towards pathways where previously suppressed non-arborescent clonal plant species expand and monopolize the understory. Once established, these dense thickets of non-arborescent vegetation can inhibit the establishment of late successional woody species and stall or alter expected successional trajectories (Slocum et al. 2004; reviewed by Royo and Carson 2006 and Paul and Yavitt 2010). As many of these species are shade-tolerant and possess long-lived genets, their dominance and effect on community assembly and succession often persists for decades (Walker et al. 2010, Young and Peffer 2010).

Our results from the non-arborescent plant community complement the growing number of studies examining tree seedling communities that document marked shifts in composition and dynamics following hurricanes relative to the generally modest response of the established tree community (Walker et al. 2003, Uriarte et al. 2005, Comita et al. 2009, Shiels et al. 2010). Whether the changes in the non-arborescent understory community we observed over 20 years will persist over a longer term remains untested (but see Uriarte et al. 2009 for simulation on tree communities). Nevertheless, as most tropical plant diversity is comprised of non-arborescent species and this layer can shape future forest succession, it is clear that hurricanes play an even larger role in structuring plant communities than previously thought.

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APPENDIX

Table A1. Total plant cover of each non-arborescent plant species found in the year immediately preceding Hurricane Georges (1998), the years following Hurricane Hugo (1990) and Georges (1999) and the final census (2010) based on the 125 permanent 1-m^2 sample quadrats. Asterisks (*) denote species found in other census periods, but not in any of these four focal dates. Nomenclature follows USDA PLANTS Database (2010).

Species	1990	1998	1999	2010
Forbs				
Anthurium crenatum	0.00	20.00	0.00	0.00
Anthurium spp.	0.00	0.00	10.00	0.00
Begonia decandra	1.20	0.00	68.00	32.00
Canna glauca	5.00	0.00	0.00	0.00
Canna indica	*	*	*	*
Commelina diffusa	177.40	158.00	230.00	53.00
Desmodium adscendens	*	*	*	*
Desmodium wydlerianum	*	*	*	*
Erythrodes plantaginea	0.00	2.00	7.50	0.00
Guzmania berteriana	0.00	12.00	2.00	35.00
Heliconia caribaea	0.00	40.00	30.00	130.00
Heliconia spp.	0.00	0.00	7.00	0.00
Musa paradisiaca	640.00	100.00	380.00	30.00
Oeceoclades maculata	0.00	8.00	5.00	12.00
Phytolacca rivinoides	235.30	0.00	0.00	0.00
Pilea inaequalis	895.60	661.00	821.00	654.00
Pilea krugii	0.00	27.00	0.00	0.00
Pseudelephantopus spicatus	*	*	*	*
Xanthosoma atrovirens	129.10	120.00	0.00	0.00
Xanthosoma spp.	0.00	0.00	80.00	0.00
Zingiber zerumbet	3.00	0.00	0.00	0.00
Ferns				
Adiantum deltoideum	*	*	*	*
Adiantum latifolium	*	*	*	*
Adiantum obliquum	*	*	*	*
Adiantum pyramidale	146.70	208.00	217.00	330.00
Adiantum tetraphyllum	*	*	*	*
Anetium citrifolium	0.00	0.00	19.00	45.00
Arachniodes chaerophylloides	*	*	*	*
Asplenium auritum	0.00	0.00	3.00	2.00
Asplenium serratum	0.00	0.00	8.00	23.00
Blechnum occidentale	15.00	30.00	45.00	0.00
Bolbitis aliena	*	*	*	*
Bolbitis nicotianifolia	131.50	378.00	517.00	333.00
Ctenitis hirta	0.00	14.00	3.00	0.00
Cyathea borinquena	0.00	0.00	0.00	332.00
Danaea elliptica	0.00	0.00	30.00	41.00
Danaea nodosa	433.30	1443.00	1278.00	1836.00
Dennstaedtia bipinnata	135.00	115.00	12.00	11.00
Dennstaedtia obtusifolia	40.00	128.00	345.00	105.00
Dieffenbachia seguine	16.00	8.00	26.00	0.00
Diplazium cristatum	*	*	*	*
Diplazium plantaginifolium	*	*	*	*
Elaphoglossum spp.	4.00	0.00	19.00	19.00
Grammitis aspleniifolia	*	*	*	*
Grammitis taxifolia	*	*	*	*
Hemidictyum marginatum	20.10	0.00	20.00	0.00
Hypolepis repens	0.00	0.00	10.00	0.00
Lellingeria suspensa	*	*	*	*

Table A1. Continued.

Species	1990	1998	1999	2010
Lonchitis hirsuta	0.10	0.00	8.00	15.00
Megalastrum subincisa	*	*	*	*
Microgramma lycopodioides	*	*	*	*
Microgramma piloselloides	*	*	*	*
Nephrolepis biserrata	0.00	0.00	0.00	16.00
Nephrolepis rivularis	10.00	0.00	42.00	0.00
Nephrolepis spp.	*	*	*	*
Niphidium crassifolium	0.00	20.00	0.00	0.00
Odontosoria aculeata	0.20	8.00	0.00	0.00
Oleandra articulata	*	*	*	*
Olfersia cervina	0.00	10.00	26.00	46.00
Pityrogramma calomelanos	10.00	0.00	0.00	0.00
Polypodium dissimile	*	*	*	*
Polypodium spp.	0.10	6.00	0.00	7.00
Pteris altissima	0.00	10.00	0.00	0.00
Sauvagesia erecta	8.30	0.00	0.00	0.00
Tectaria trifoliata	28.20	73.00	89.00	93.00
Thelypteris deltoidea	193.40	411.00	480.00	420.00
Thelypteris spp.	*	*	*	*
Trichomanes membranaceum	*	*	*	*
Trichomanes rigidum	*	*	*	*
Vines				
Cayaponia racemosa	10.00	0.00	0.00	0.00
Centrosema pubescens	0.00	20.00	0.00	3.00
Centrosema spp.	0.00	0.00	11.00	0.00
Cissampelos pareira	*	*	*	*
Cissus erosa	56.10	0.00	0.00	23.00
Cissus obovata	*	*	*	*
Cissus spp.	*	*	*	*
Cissus verticillata	0.00	10.00	81.00	0.00
Dioscorea polygonoides	175.10	14.00	121.00	2.00
Heteropterys wydleriana	*	*	*	*
Hippocratea volubilis	0.00	20.00	10.00	6.00
Ipomoea batatas	*	*	*	*
Ipomoea repanda	*	*	*	*
Ipomoea setifera	*	*	*	*
Ipomoea spp.	9.20	0.00	0.00	0.00
Marcgravia rectiflora	24.70	91.00	242.00	416.00
Mikania cordifolia	558.20	0.00	69.50	0.00
Mikania fragilis	14.00	22.00	0.00	0.00
Neorudolphia volubilis	1.00	12.00	0.00	0.00
Paullinia pinnata	3.00	22.00	0.00	0.00
Peperomia rotundifolia	5.30	18.00	12.00	7.00
Philodendron scandens	133.90	76.00	350.00	334.00
Pinzona coriacea	29.00	0.00	0.00	0.00
Pueraria phaseoloides	*	*	*	*
Rajania cordata	5.00	0.00	0.00	0.00
Rourea surinamensis	6.40	34.00	69.00	139.00
Sabicea villosa	3.10	10.00	0.00	0.00
Schlegelia brachyantha	0.00	0.00	0.00	7.00
Securidaca virgata	0.60	10.00	8.00	9.00
Smilax smallii	1.00	0.00	0.00	1.00
Vigna vexillata	*	*	*	*
Graminoids				
Bamabusa tulda	0.00	0.00	10.00	50.00
Bambusa vulgaris	*	*	*	*
Cynodon nlemfuensis	*	*	*	*
Ichnanthus pallens	1471.10	689.00	1233.00	275.00
Ichnanthus spp.	0.00	0.00	10.00	0.00
Olyra latifolia	30.20	111.00	74.00	64.00
Paspalum conjugatum	0.00	0.00	5.00	0.00
Pharus latifolius	7.10	35.00	23.00	106.00
Scleria pterota	*	*	*	*
Scleria scindens	470.00	75.00	22.00	1.00
Shrubs†				
Clibadium erosum	75.00	0.00	0.00	0.00
Columnea ambigua	0.00	0.00	3.00	0.00

Table A1. Continued.

Species	1990	1998	1999	2010
Gonzalagunia hirsuta	29.20	86.00	33.00	0.00
Heteropterys laurifolia	0.00	70.00	32.00	15.00
Nepsera aquatica	50.30	13.00	15.00	0.00
Palicourea crocea	6.00	0.00	0.00	0.00
Piper glabrescens	*	*	*	*
Piper hispidum	*	*	*	*
Pothomorphe spp.	*	*	*	*
Psychotria uliginosa	0.00	0.00	0.00	2.00
Ruellia coccinea	2.70	7.00	5.00	7.00
Solanum torvum	*	*	*	*
Tournefortia spp.	10.00	0.00	0.00	0.00

† Shrub category follows USDA PLANTS Database growth habit definition and includes species that may attain 4–5 m in height.