The interaction of land-use legacies and hurricane disturbance in subtropical wet forest: twenty-one years of change

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Abstract. Disturbance shapes plant communities over a wide variety of spatial and temporal scales. How natural and anthropogenic disturbance interact to shape ecological communities is highly variable and begs a greater understanding. We used five censuses spanning the years 1990–2011 from the 16-ha Luquillo Forest Dynamics Plot (LFDP) in northeast Puerto Rico to investigate the interplay of human land-use legacies dating to the early 20th century and two recent hurricanes (Hugo, 1989 and Georges, 1998). The LFDP is a landscape mosaic comprised of an area of mature subtropical wet forest and three areas of secondary forest with differing past land-use intensities. We examined the degree to which hurricane disturbance–effect and subsequent community recovery varied across past land-use classes. We expected areas with greater intensity of human land use to be more affected by hurricane disturbance therefore exhibiting greater initial damage and longer successional recovery times. Structurally, areas of secondary forest contained smaller trees than old-growth areas; hurricanes caused widespread recruitment of shrubs and saplings that thinned with time since the first hurricane. Species richness of the plot declined over time, mostly due to the loss of rare species, but also due to the loss of some heliophilic, pioneer species that became abundant after the first hurricane. Species composition differed strongly between areas of secondary and mature forest, and these differences were largely constant over time, except for an increase in compositional differences following the second hurricane. An indicator species analysis attributed this pattern to the longer persistence of pioneer species in areas of greater past land-use intensity, likely due to the more open canopy in secondary forest. When secondary forest areas of differing past land-use intensity were considered separately, few species of low community rank were found as indicators. When these areas were combined, more and higher-ranked species emerged as indicators, creating ecologically meaningful indicator species combinations that better captured the broad-scale plant community response to past land use. Our findings support the idea that effects of past land use can persist for decades to centuries following land-use abandonment, illustrating the importance of land-use legacies in shaping regenerating tropical secondary forests.

Key words: hurricanes; indicator species; land-use legacies; Luquillo; multiresponse permutation procedures; Puerto Rico; tropical secondary forest dynamics.

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INTRODUCTION

Understanding disturbances and their effects on forest communities is a critical aspect of forest ecology and provides important insights into the ecological interpretation of current landscape states (Turner 1989, Burslem and Whitmore 1999). Disturbances produce spatial and temporal heterogeneity in biological communities by facilitating individual and species turnover (Pickett and White 1986). Typically, anthropogenic disturbances are thought to be of decreased magnitude relative to large, infrequent natural disturbances (e.g., hurricanes), but affect communities over longer time scales than most natural disturbances, frequently resulting in unique ecosystem responses and novel communities (Pickett 1985, Chazdon 2003, 2014, Lugo 2009). Differential effects of human land use and natural disturbances are commonly generalized as short-term pulse vs. longer-term press disturbance regimes, respectively (Bender et al. 1984), emphasizing the idea of the enduring effects of land-use practices on ecosystem function and community composition (Lugo et al. 1981, Brokaw 2012). The compound effects of natural and anthropogenic disturbances can potentially lead to nonlinear ecosystem responses that result in non-analog communities and alternative stable states (Collins and Smith 2006, Buma and Wessman 2012, Kulakowski et al. 2013).

Studies in New England have documented long-term broad-scale effects of past agricultural activity on temperate forests (Foster 1992, Foster et al. 1998). These studies found that at the local scale, variability in community composition (i.e., β-diversity) was consistently influenced by the last crop prior to abandonment. At regional scales, however, land-use history was the primary driver of forest community composition and structure, creating regional homogeneity in forest composition, which exceeded the effects of regional climate (Foster et al. 1999, 2003) that governed forest species composition prior to European colonization. These findings indicate that there are suites of species that respond to human land-use effects, and the broad-scale homogeneity of modern forests is the result of human disturbance over an entire region.

In the Caribbean, regional-scale land-use alterations to the forest community composition exhibit patterns similar to the case of New England (Grau et al. 2003). Puerto Rico has an extensive history of human land uses dating back to the sugarcane industry of the 18th and 19th centuries and to precolonial indigenous cultures (Dietz 1986, Thomlinson et al. 1996, Zimmerman et al. 2007). Beginning in the 1950s, agriculture abandonment, facilitated by industrialization and urban development in Puerto Rico, resulted in rapid forest recovery (i.e., the forest transition). Forest cover reached a low of < 5% in 1940 and subsequently recovered to > 50% at the turn of the 21st century (Lugo and Helmer 2004, Brandeis et al. 2007, Parés-Ramos et al. 2008). These regenerated forests are dominated by secondary forest species whose composition differs locally due to the effect of the last crop (Grau et al. 2003), but whose resistance and resilience to natural disturbances, such as hurricanes, have not been well studied (Zimmerman et al. 1994, Pascarella et al. 2004, Comita et al. 2010).

Secondary tropical forests should be more susceptible to large-scale wind disturbances due to the abundance of early-successional species with low wood densities (Chazdon 2003, Foster et al. 2003), which incur more damage and mortality when affected by hurricanes (Walker 1991, Lugo and Zimmerman 2003, Uriarte et al. 2012). For example, in recent studies in Puerto Rico comparing forest communities across a land-use gradient from secondary forests regenerating in tobacco fields and shade coffee to undisturbed forest, the importance of introduced species decreased, and the abundance of native forest and endemic species increased with decreasing land-use intensity (Flynn et al. 2010, Ruiz and Lugo 2012). A trade-off between forest resilience (i.e., the capacity of a forest community to recover to its original state) and forest resistance (i.e., the ability of a forest community to remain unchanged when subject to disturbance) is commonly hypothesized to govern natural ecosystem response to disturbance (Halpern 1988, MacGillivray et al. 1995). Therefore, due to compositional difference related to past land use, it is reasonable to infer that areas with greater levels of past land use harbor less resistant forest that are more susceptible to natural disturbances than areas with little or no history of human land use.

Understanding how currently regenerating forests function as they mature is of interest to the

scientific, conservation, and global communities, especially considering the role of tropical forests in mitigating climate change effects and conserving natural resources (Laurance 1998, Dale et al. 2000, DeFries et al. 2004). Furthermore, understanding the role of recovering secondary tropical forests is crucial to filling in gaps in global carbon cycle dynamics, as tropical forests are considered to be substantial carbon sinks, although the magnitude of their ability to sequester carbon is still being debated (Lugo and Brown 1992, Phillips et al. 1998, Pan et al. 2011). Thus, exploring interactions of past land use and forest dynamics provides the following: (1) a historical explanation for observed species compositions of today's forests (Foster et al. 1999); (2) information on successional dynamics following disturbances; that is, anthropogenic disturbances can be compared to the compounded and/or separate effects of natural disturbance trajectories to gauge community resistance and resilience (Uriarte et al. 2009); and (3) management and restoration perspectives with regard to anthropogenically altered secondary forest communities (Martínez-Garza et al. 2005, Lugo 2009).

In this study, we investigated the interaction of human land use and hurricane disturbances in the Luquillo Forest Dynamics Plot (LFDP), situated within the subtropical wet forest of northeastern Puerto Rico (Ewel and Whitmore 1973). Based on the initial census of trees ≥10 cm diameter at 1.3 m height (diameter at breast height, hereafter dbh), Thompson et al. (2002) found that land-use history had significantly stronger influence on species composition than background environmental variation (soil types and topography). We expanded on the initial discoveries about land use within the LFDP to address two objectives:

1. Examine changes in forest structure and diversity of the LFDP over time, evaluating the effects of land-use legacies on these attributes. We expected areas of secondary forest to have, on average, smaller diameter stems and greater variability in community composition than the portion of the plot with more mature forest.
2. Explore the impact of land-use history on forest community composition over time, considering the impact of two hurricanes that

occurred subsequent to land-use abandonment. We hypothesized that strong land-use legacies decrease the ability of secondary forests to recover from severe hurricane disturbances, as increased successional lag time can indicate less community resistance to disturbance.

METHODS

Plot design and tree census methods

The LFDP (18°20′ N, 62°49′ W) is a 16-ha (320 × 500 m) permanent forest plot situated on the northwestern flank of El Yunque National Forest in Puerto Rico (Thompson et al. 2002). The plot has elevations ranging from 332 to 427 masl, with steep topographies and deeply dissected drainages running to the northwest. Southwest facing grades dominate the terrain with slopes averaging 17% and ranging from 3% to 60% (Thompson et al. 2002). Since 1975, annual rainfall has averaged 3685 mm (Ramírez and Melendez-Colóm 2003). The soils in the plot originate from uplifted volcanic parent material and are classified as deeply weathered kaolinitic Oxisols (Cristal) and Ultisols (Zarzal) and less-developed Entisols and Inceptisols in stream channels (Soil Survey Staff 1995). In the absence of human disturbance, the area is dominated by *Dacryodes excelsa* (tabonuco), *Manilkara bidentata* (asubo), and *Sloanea berteriana* (motillo) (Waide and Lugo 1992). Few trees in the LFDP exceed 100 cm dbh, and community structure and canopy height are variable and both subject to hurricane damage with canopy height and presence of large trees both decreasing immediately following hurricane disturbances (Zimmerman et al. 1994, 1995, 2014).

The LFDP is part of the Luquillo Long-Term Ecological Research (LTER) Program and is a member of the Center for Tropical Forest Science (CTFS) (Losos and Leigh 2004) Forest Global Earth Observatory (Forest-GEO) Network (see Anderson-Teixeira et al. 2015). The plot was established in 1990, and within the study area, all free-standing woody stems were mapped and measured at breast height and identified to species. Beginning in June 1990, all tree stems in the LFDP ≥10 cm dbh (hereafter referred to as large stems) were identified, assessed for hurricane damage, mapped, measured, and tagged. Starting

in 1992, the LFDP was surveyed for all stems ≥1 but <10 cm dbh (hereafter referred to as small stems), completing the first census. These stems were also identified, tagged, and measured. Starting in 1995, the second census was carried out, with all stems ≥1 cm dbh being measured in a single survey. Subsequent third, fourth, and fifth censuses of all stems ≥1 cm dbh were conducted beginning in 2000, 2005, and 2011, respectively.

Land-use legacies and hurricane disturbances

The LFDP has a mosaic of land-use histories closely linked to the economic history and past hurricanes of Puerto Rico (Thompson et al. 2002). Previous land uses included cutting timber for a small sawmill, coffee plantations, small garden plots associated with human settlements, and silvicultural experimentation. Settlers inhabited the northern part of the plot during the late nineteenth and early twentieth centuries (Gerhart 1934). Between 1924 and 1934, the land on which the LFDP is located was owned by the Bliss Plywood and Keystone plywood Corporations where they operated a small sawmill (Thompson et al. 2002). United States Forest Service (USFS) assessment transect records indicate the northern portion of the plot was clearcut in 1934 (Gerhart 1934, see figure 4 in Thompson et al. 2002).

Two large hurricanes, San Felipe in 1928 and San Ciprian in 1932, passed through the area causing heavy damage to the forest and forcing many people to emigrate from the area (Scantena 1989, Drew et al. 2009). Following these two hurricanes, no large hurricanes passed over the area until Hurricane Hugo in 1989. This is consistent with the historical records for hurricane occurrence for the Luquillo Mountains, with damaging hurricanes occurring on average every 50–60 yr, despite frequent tropical storm and hurricane occurrence in the region (Scantena 1989, Brokaw et al. 2012). The emigration of residents in the Luquillo Mountains following Hurricane San Ciprian preceded a more widespread movement of people from rural to urban areas throughout Puerto Rico following World War II (Rudel et al. 2000), setting the stage for a forest transition to take place (Grau et al. 2003, Lugo 2004). By the 1940s, the USFS would more than double the size of El Yunque National Forest with the purchase of adjacent private

lands and the majority of human land use is believed to have ceased at that time (Miller and Lugo 2008).

Past land use within the LFDP was categorized into four cover classes (Thompson et al. 2002) based on the appearance of the forest canopy in aerial photographs taken in 1936 (Foster et al. 1999). Land-use intensity was derived from the aerial photographs based on the amount of canopy cover present. Approximately 5.3 ha (33.1%) of the plot was classified as having >80% forest cover and were never clearcut, but rather only subject to selective tree harvest by the USFS in the 1940s (Wadsworth 1970). This area of relatively primary forest was designated as cover class 4. The remaining three cover classes had 0–10% (cover class 1–7.1% of the plot), 20–50% (cover class 2–24.7% of the plot), and 50–80% (cover class 3–35.1% of the plot) forest cover, respectively, in the 1936 aerial photographs (Fig. 1).

Additionally, Thompson et al. (2007) documented the presence of anthropogenically associated and introduced species within the LFDP, showing key species related to past land-use practices (shown in Fig. 8 in blue) to be more abundant in cover classes 1–3. Species representing agricultural crops are represented in various locations in cover classes 1–3, but never reach high levels of dominance. *Calophyllum antillanum*, found in cover class 1, was planted under the USFS efforts to explore the silvicultural capabilities (Weaver 2012); the ornamental *Thespesia pernambucina* is also abundant there. In addition, *Swietenia macrophylla* (broad-leafed mahogany) has become naturalized in the area after its silvicultural introduction and can be found sporadically throughout the LFDP.

Since 1932, there have been two intense (category 2 or greater on the Saffir–Simpson hurricane wind scale) hurricanes in eastern Puerto Rico. In September 1989, Hurricane Hugo severely damaged forests in the area where the LFDP was established (Zimmerman et al. 1994, Thompson et al. 2002). A second hurricane, Georges, passed over Puerto Rico in 1998; however, damages to El Yunque National Forest were less severe than those created by Hugo (Canham et al. 2010). The effect of the second disturbance on the forest was less because forest structure had yet to recover from the damage 9 yr earlier, as well as inherent meteorological
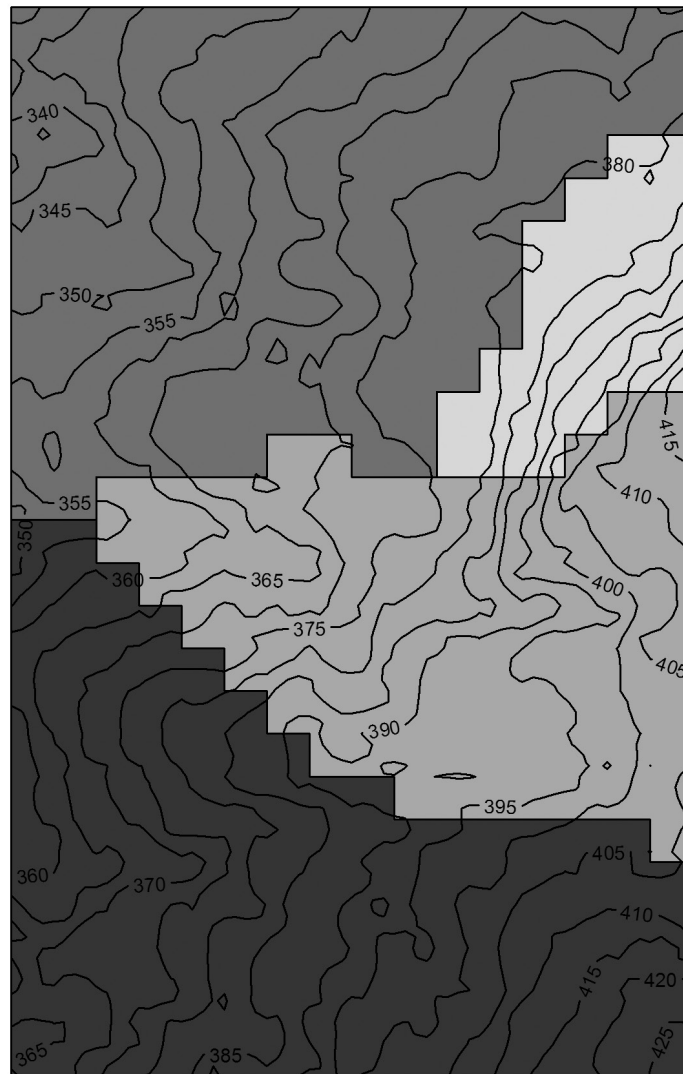
Fig. 1. Luquillo Forest Dynamics Plot (LFDP) by cover classes based on forest cover from 1936 aerial photographs (Foster et al. 1999). In order from lightest to darkest: 1 (0–10%), 2 (20–50%), 3 (50–80%), and 4 (80–100%).

differences between the two hurricanes, such as storm trajectory or wind speed (Canham et al. 2010).

Land-use effects over time

To investigate changes in forest structure, stem diameter distributions were grouped according to size into one of six stem size classes (1–2.5, 2.51–5, 5.01–10, 10.01–25, 25.01–50, and > 50 cm). Diversity patterns were examined using raw species richness from each of the full tree censuses, beginning with the first census (1990–1992, which lasted two full years, because of the establishment of the plot), with respect to large and small stems. Due to high levels of mortality and a decreasing trend in species richness over the 21-yr study period, we were particularly interested in species turnover. Using all of the stem data (i.e., both large and small stems), we identified the species lost and gained between each census interval. We also quantified the number of rare, endemic, and common species for each land-use type by census. Lastly, we calculated

Simpson's diversity, Shannon diversity, and Evenness, and dominance–diversity curves for each of the five censuses at the plot level.

Multiresponse permutation procedures (MRPP) was employed to investigate community compositional differences by land use for all stems within the LFDP over time. MRPP is a nonparametric method that tests the hypothesis of no difference between two or more site groupings (McCune et al. 2002). One advantage of MRPP is that it allows for the comparison of multiple groups regardless of group size (number of sites in each group) (Biondini et al. 1985). We compared diversity metrics for groups in all four cover classes and by combining cover classes 1–3 and comparing them to cover class 4. The MRPP was implemented using the "vegan" package for community ecology in the R statistical environment (Oksanen et al. 2008, R Development Core Team 2014).

MRPP was carried out using natural weighting, where group means were corrected by the number of sample units in the group (Mielke 1984, Mielke and Berry 2001). The observed difference between groups was compared to the difference between groups when permuted to obtain the within-group chance-correlated agreement, A, the agreement statistic. A describes the within-group homogeneity, or dissimilarity, compared to the random expectation. Values range from 0 to 1, with a value of 1 occurring when species composition is completely different between groups, and with a value of 0 signifying that compositional differences between groups are equal to the expectation given random chance alone (McCune et al. 2002).

We used indicator species analyses (ISA) (Dufrêne and Legendre 1997) to examine species-specific responses to land use within and between groups. For groupings, we used land-use intensity in the LFDP represented by the a priori cover class delineations. The purpose of an ISA is to determine which species can be considered as representative species, or indicators, for particular site-groups. Our analysis included site-group combinations (De Cáceres and Legendre 2009) of cover classes 1 and 2 and cover classes 1, 2, and 3.

The indicator value is defined as the positive measure of the association between a species and the site-group (De Cáceres and Legendre 2009). The method incorporates two parameters:

the species fidelity, or the probability that the sampled site belongs to the target site-group, given that the species is present, and the species specificity, or the probability that the species is found in sites belonging to the same site-group. The logic is that good indicator species ought to be both highly abundant and constrained within their indicating site-group. Indicator values range from 0 (no indication) to 100 (perfect indication). Perfect indication translates to the presence of a species corresponding to a particular site-group without error, given the data.

In addition to identifying indicator species for each cover class and combination of cover classes, we calculated the number of sites (20 × 20 m quadrats) within each cover class that contained the identified indicator species for that cover class. This quantity is defined as the coverage of the site-group (De Cáceres and Legendre 2009). Understanding the coverage of indicator species is useful when beta diversity or habitat variation between site-groups is large (Legendre et al. 2005). Assessing the coverage of indicator species can detect areas where none of the identified indicators were present and can be interpreted as the percent to which valid indicator species accurately indicate site-group classifications (De Cáceres and Legendre 2009). The ISA was implemented via the "indicspecies" package in the R statistical environment (R Development Core Team 2014) using the "multipatt()" function, with the function parameter set to "indval" (De Cáceres and Legendre 2009).

Results

Changes in forest structure of the LFDP over time

Stem density and number of individuals have declined steadily over time since the first census in the LFDP (1990–1992), with the greatest decreases occurring in the smallest diameter size-class (1–2.5 cm) (Fig. 2). Over 103,000 stems (including individual stems on multistemmed trees) were recorded in the first census (combined small and large stems, from 1990 to 1992), consisting of nearly 85,000 individuals. The number of stems exceeds the number of individuals due to the widespread growth of tree sprouts after hurricane damage in 1989, and the number of multiple stemmed shrubs in the population. In the most recent census (2011), just over 41,000
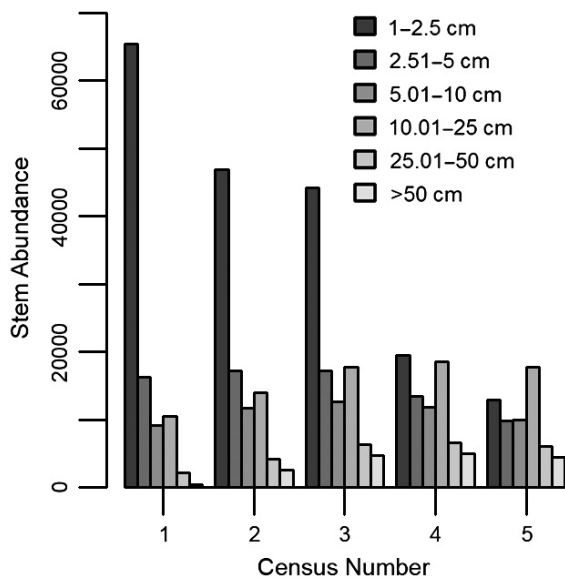
Fig. 2. Stem diameter distributions for the entire LFDP for all tree censuses (1 – 1990, 2 – 1995, 3 – 2000, 4 – 2005, and 5 – 2011). Abundance of all stems in the LFDP (regardless of species) was divided into six size classes (1–2.5, 2.51–5, 5.01–10, 10.01–25, 25.01–50, and >50 cm).

living stems were observed on approximately 36,000 individuals. Over the entire study period, the ratio of stems to individuals has decreased from 1.21 to 1.14. Over time, stem decline occurred mainly in the small size-class. The densities of small stems (stems ≥1 cm dbh but <10 cm dbh) were recorded at over 5700 stems/ha at the initial census and declined sharply to just under 1400 stems/ha in the most recent census. In the first census, small stems comprised 89% of stems and declined steadily to 83% in 1995, 80% in 2000, 68% in 2005, and most recently 60% in 2011.

Stand structure, visible in stem diameter distributions, was variable with respect to land-use cover class (Fig. 3). Forest structural differences were greatest in censuses following hurricane disturbance. The occurrence of Hurricane Hugo (September 1989) and Georges (September 1998) relative to the census periods means that the each census took place around 2 yr after the respective hurricane disturbance. Therefore, the difference in stem numbers resulted from differences in hurricane damage on the forest structure present at each time, rather than artifacts of the census

interval. At the initiation of the LFDP, secondary areas with forest cover ≤80% (cover classes 1–3) had disproportionately greater numbers of stems in the smallest diameter size-class. The number of stems in this size-class steadily declined over time for all cover classes. However, cover class 3 exhibited two recruitment pulses in the smallest diameter stems over time, whereas the smallest diameter stems of the other three cover classes responded with only one recruitment event, despite the occurrence of two distinct hurricane disturbances roughly a decade apart. In all cover classes, the abundance of stems in the largest diameter class increased over time. Despite large changes in stem diameter distribution over time, total basal area of all stems remained relatively stable, increasing steadily from 38 to 41 m²/ha over the 21-yr period.

Similar to the changes in stem densities, species richness in the LFDP has also decreased over time (Table 1). There were 154 species recorded at the establishment of the plot, soon after Hurricane Hugo, and by 2011, the number had declined by 30 species (a decrease of 24.8%). The second census, in 1995, is the only census to record a net species increase, gaining one species from the 1990 to 1992 establishment stem inventories. Although four species were gained in 2000, nine were lost, and net species losses of five, nine, and twelve were recorded for the 2000, 2005, and 2011 censuses, respectively.

Species losses have occurred primarily in small stems. Some of the species losses occurred in rare species represented by one or a few individuals that died and were never recruited back in the plot, such as *Ternstroemia luquillensis* (DC.) Britton (Bignoniaceae) and *Solanum torvum* Sw. (Solanaceae). Other instances represent species losses at the upper elevation boundaries of the LFDP, such as *Clusia clusioides* (Giseb.) D'Arcy (Clusiaceae) and *Phytolacca rivinoides* Knuth & D. C. Bouché (Phytolaccaceae). Additional cases represent the loss of shade-intolerant pioneer species as the forest canopy recovered from hurricane damage, for example *Clibadium erosum* (Sw.) DC (Asteraceae) and *Clidemia eggersii* (Cogn.) F. S. Axlerod (Melastomataceae).

The loss of heliophilic species, such as *Piper aduncum*, *Piper amalago*, *Piper peltatum*, and *Piper hispidum*, was notable in the overall trend of declining species richness. Beginning with
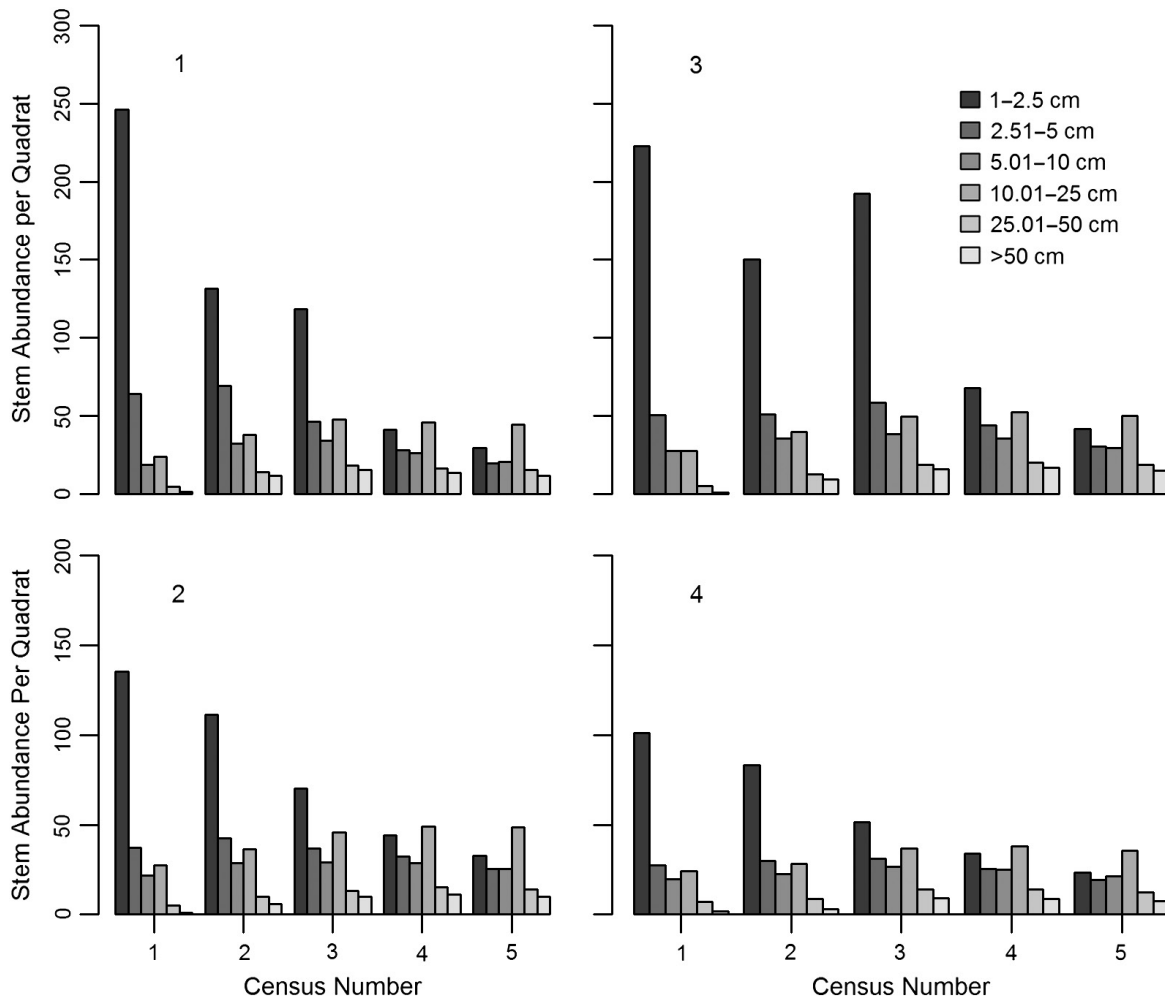
Fig. 3. Stem diameter distributions for the LFDP by cover class. The cover classes correspond to land-use intensity (see Fig. 1), and the same six stem diameter size classes that were used in Fig. 2 are used (1–2.5, 2.51–5, 5.01–10, 10.01–25, 25.01–50, and >50 cm).

species with a recorded density of at least 1 stem/ha at any point in time, of the seven species that have been lost from the plot, six of the seven were pioneer species, and five of those six pioneer species were species in the Piperaceae family (Fig. 4). Despite decreases in species richness, Simpson's and Shannon diversity indices show little change over time (Table 1). Dominance–diversity curves (Fig. 5) were generally stable over the five censuses, the decline in species richness reflected in the right-hand tail of the distributions. This emphasizes the low rank of the species lost from the community. There is a visible minor trend toward a decreasing slope in the rank-abundance curves, illustrating increasing evenness in the

community, which is also supported by changes in calculated evenness (Table 1).

Changes in community composition of the LFDP over time

Compositional differences among (or between) land uses were significant for all censuses and when both two and four land-use classes were compared. Differences in plant community composition, as shown by the *A* statistic, initially increased over time, peaking at the intermediate census (2000, 2 yr after Hurricane Georges) before decreasing once again (Table 2, Fig. 6). Both the four cover class comparison and the high vs. low land-use classification show similar

Table 1. Species richness for two size classes, ≥ 1 to < 10 cm dbh (small stems) and ≥ 10 cm dbh (large stems), and measures of diversity for the LFDP by census.

	Species richness			Diversity indices		
Census	≥ 1 to < 10 cm dbh	≥ 10 cm dbh	Total	Simpson (λ)	Shannon (H')	Evenness ($E_{H'}$)
1	143	94	154	0.917	3.16	0.628
2	137	90	145	0.914	3.20	0.644
3	130	89	141	0.934	3.34	0.675
4	121	87	130	0.934	3.38	0.695
5	113	90	123	0.908	3.22	0.668
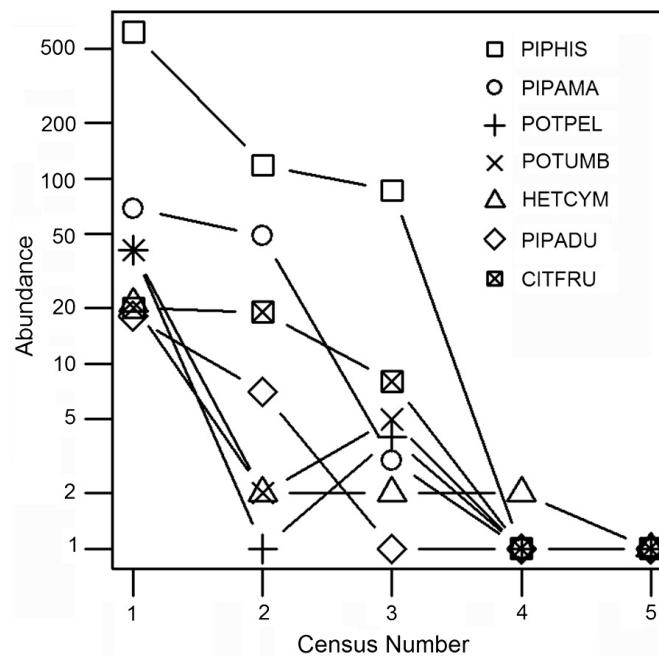
Fig. 4. Decline of heliophilic species in the LFDP. Seven heliophilic species were lost in the LFDP since its establishment. We show their declining abundances over time. Five Piper species: PIPHIS, *Piper hispidum* Sw.; PIPAMA, *Piper amalago* L.; POTPEL, *Piper peltatum* L.; POTUMB, *Piper umbellatum* L.; and PIPADU, *Piper aduncum* L., one Melatsome: HETCYM, *Clidemia eggersii* (Cogn.) F.S. Axelrod, and one Verbenaceae: CITFRU, *Cithrarxelyum spinulosa* L. were lost over the 21-yr period.

temporal patterns. Agreement statistic values were relatively low, although values of 0.1 are not uncommon in community ecology (McCune et al. 2002). The overall tendency is for areas of differing land-use intensity within the LFDP to differentiate over time in terms of community composition, in the absence of a hurricane disturbance between censuses.

The ISA revealed species-specific responses that determined the pattern observed in the MRPP (Figs. 7 and 8). A maximum of three indicator species were present for cover class 1,

showing stability in community composition over the 21-yr time period for the northeastern part of the LFDP, the area with the most intense level of past land use (Figs. 7 and 8). Cover class 2 ranged from five to seven indicators over time, with minor variability in the species that played roles as indicators. A decreasing trend from nine to five in the number of indicators present in cover class 3 occurred over time. Cover class 4 showed the most stability in community composition and community rank of indicator species, with the number of indicators ranging
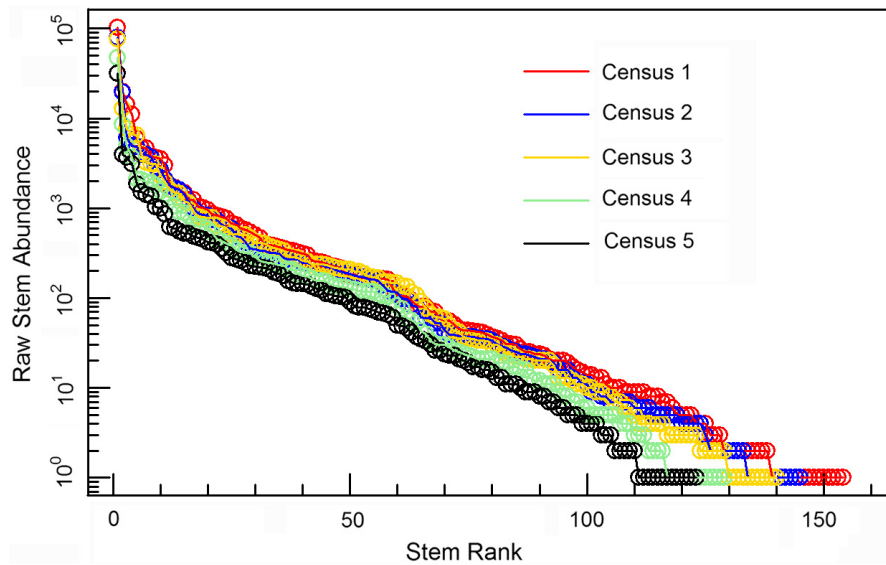
Fig. 5. Dominance curves by census for the LFDP. Species rank (or community position) is shown on the *x*-axis, and its raw abundance is shown on the *y*-axis (log-scale). Colors represent census year (red, 1990; blue, 1995; yellow, 2000; green, 2005; black, 2011).

from 13 to 17, depending on the census. Thus, overall, hurricane disturbance does not strongly affect community composition of individual land uses, separately, as shown by the consistent differences in indicator species.

Combining cover classes, as suggested by De Cáceres et al. (2010), increases the community sample size to better capture species of higher rank (greater abundance) in the community within the indicator species analysis (Figs. 7 and 8). This is especially evident when cover classes 1, 2, and 3 are combined, yielding a range of 22–29 significant indicator species, many with fairly high community rank. Variation in species composition was evident over time in the combined grouping, with pioneer species becoming stronger indicators of land-use differences after Hurricane Georges before moving down in abundance over time thereafter. Maps of two of these species show their concentration in the area of high land-use intensity (Fig. 9), particularly cover class 3, explaining the dynamics of small stems there (Fig. 3) and the change in values of *A* over time (Fig. 6).

Percent coverage, or the proportion of quadrats within each cover class where indicator species of that cover class are present, was calculated for each cover class and the two selected cover class

Table 2. MRPP statistics for the four cover class comparisons based on 999 permutations.

Census	Observed (δ)	Expected (M_δ)	A	Significance (of delta)
1	0.628	0.642	0.0219	≪0.001
2	0.604	0.612	0.0252	≪0.001
3	0.630	0.643	0.0193	≪0.001
4	0.584	0.596	0.0226	≪0.001
5	0.557	0.567	0.0226	≪0.001

combinations (Fig. 10). Percent coverage for indicator species for the four cover classes separately showed that not all indicator species occurred in all quadrats within that cover classes, with each cover class having coverage values ranging, on average, between twenty and eighty percent. Percent coverage increased to one hundred percent, or perfect indicator species presence within site-group, when a comparison of high (cover classes 1, 2, and 3) vs. low (cover class 4) land use was used (Fig. 10, Appendix S1).

DISCUSSION

The legacies of past land use in the LFDP described by Thompson et al. (2002) are shown in this study to be resilient to frequent high
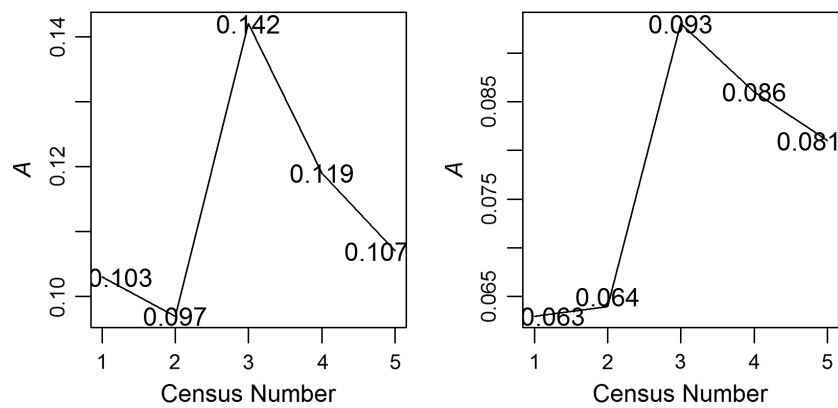
Fig. 6. Chance-correlated within-cover class agreement (*A*) for forest communities within the LFDP over time from the multiple response permutation procedure. Four land-use comparisons (all four cover classes) are shown in the left panel, and the two land-use comparisons are shown (cover class 4 vs. cover classes 1, 2, and 3) on the right.

wind disturbance. Despite two severe hurricanes since 1989, only small changes have been detected in the overall community composition of large trees within the LFDP. In terms of forest structure, the majority of the dynamics occurred in the abundance of small stems that, at the plot level, exhibit transient dynamics with initial increases and subsequent thinning of stem densities in response to the first hurricane. These changes are reflected in a reduction in overall species richness of the plot, which declined 25% over the 21-yr period. Some loss of species included heliophilic plants that were quite abundant after Hurricane Hugo, species that were lost from the plot despite the subsequent disturbance by Hurricane Georges. The remaining species lost from the plot were rare, whose loss was barely reflected in calculated diversity indices, but which influenced the shape of dominance–diversity curves at the tails.

Despite community stability at the whole-plot level, forest species composition within the LFDP was highly variable and directly related to past land use (Thompson et al. 2002, Comita et al. 2010). Thompson et al. (2002) found the northern half of the LFDP, in particular cover class 3, to be dominated by the secondary forest species *Casearia arborea* (CASARB). The abundance of *C. arborea*, with to its low wood density and susceptibility to uprooting (Zimmerman et al. 1994), created a forest that is structurally different in terms of canopy structure and diameter

size-class distribution. Average canopy openness was statistically greater in cover classes 1–3 after Hurricane Georges (1999) and also in 2004 and 2007 (see figure 2 in Comita et al. 2010). Hurricane disturbances created large canopy openings leading to the recruitment of both understory and canopy pioneers (Zimmerman et al. 1994, 2010, 2014), species that persisted in secondary forest areas for a longer period of time after the hurricane had passed, than in mature tabonuco forest (cover class 4). The indicator species analysis clearly identified this pattern of response. Understory pioneer species, including *Psychotria berteriana* (PSYBER), *Psychotria brachiata* (PYSBRA), and *Palicourea crocieoides* (PALRIP), and canopy pioneers such as *Schefflera morototoni* (SCHMOR) and *Cecropia schreberiana* (CECSCH) appeared alongside the dominant *C. arborea*, with their indicator values increasing to peak at the third census (Appendix S1). This pattern of response explains the changing magnitude of *A* derived from the MRPP.

Many previous analyses using LFDP data have grouped cover classes 1, 2, and 3 together in a broader, high vs. low use distinction (e.g., Uriarte et al. 2004, 2009). We compared values of *A* from MRPP for two vs. four classes of human disturbance and found the patterns over time to be very similar. ISA showed that the differences in key species distinguishing individual cover classes 1–3 were species of low rank and, in the case of cover class 1, species associated with silviculture

Census	1	2	3	4	5
Year	1990	1995	2000	2005	2011
CC 1	CALCAL (67) HIBTIL (65) GENAME (110)	CALCAL (64) HIBTIL (62)	CALCAL (65) HIBTIL (38)	CALCAL (64)	CALCAL (50) GENAME (98)
CC 2	MALFUR (108) LONLAT (109) HETCYM (93) CITCAU (103) WALPEN (118)	COCSWA (59) MICRAC (81) MALFUR (101) COCSPP (79) LONLAT (112) HENFAS (96) WALPEN (109)	COMGLA (66) COCSWA (60) FICCIT (82) MALFUR (98) CITFRU (115) LONLAT (120)	COCSWA (59) COMGLA (70) MICMIR (82) MALFUR (99) OCOMOS (81)	MICTET (34) ARDGLA (38) COCSWA (46) COMGLA (65) MALFUR (88) OCOMOS (72) MICMIR (87) LONLAT (105)
CC 3	FAROCC (47) ORMKRU (30) SYMMAR (84) SYZJAM (54) MICAFF (79) MARNOB (77) SOLRUG (90) CINMON (117) CASDEC (124)	FAROCC (37) ORMKRU (30) SYMMAR (83) SYZJAM (53) MICAFF (72) MARNOB (80) CINMON (108)	PIPGLA (22) LAEPRO (43) FAROCC (29) MICAFF (64) SYMMAR (75) SYZJAM (48) MARNOB (77) CINELO (94)	FAROCC (23) LAEPRO (43) SYZJAM (45) SYMMAR (80) MICAFF (76) MARNOB (90)	PSYBRA (13) FAROCC (20) SYZJAM (36) SYMMAR (78) MARNOB (77)
CC 4	SLOBER (9) DACEXC (12) EUGSTA (25) TETBAL (27) CROPOE (51) MRYLEP (50) MATDOM (38) CSSGUI (62) CALSQU (68) MIRGAR (69)	SLOBER (7) DACEXC (12) EUGSTA (78) TETBAL (24) CROPOE (55) MYRLEP (48) MATDOM (32) CSSGUI (61) CALSQU (66) MIRGAR (65)	SLOBER (5) DACEXC (11) EUGSTA (23) GUAGLA (24) MYRLEP (41) MATDOM (39) CROPOE (59) CSSGUI (63) CALSQU (70) MIRGAR (67)	SLOBER (3) DACEXC (9) EUGSTA (21) MYRLEP (38) DRYGLA (30) MATDOM (40) CROPOE (60) CSSGUI (62) GUEVAL (48) CALSQU (71)	DACEXC (5) EUGSTA (21) MYRLEP (27) MATDOM (31) CSSGUI (45) CROPOE (49) GUEVAL (40) MIRGAR (57) CALSQU (71) RHEPOR (54)
CC 1+2+3	CASARB (4) CASSYL (10) PALRIP (1) PSYBRA (7) PREMON (5) PSYBER (2) CECSCH (3) SCHMOR (6) INGLAU (14) ALCLAT (15)	CASARB (3) CASSYL (8) PSYBRA (5) PALRIP (1) PREMON (2) CECSCH (4) PSYBER (6) INGLAU (14) TRIPAL (18) OCOLEU (16)	PSYBER (1) CASARB (4) PSYBRA (3) CASSYL (8) SCHMOR (7) CECSCH (6) PREMON (2) INGLAU (13) OCOLEU (15) MICPRA (9)	CASARB (2) CASSYL (4) PSYBRA (5) PREMON (1) PSYBER (6) INGLAU (11) SCHMOR (10) CECSCH (8) OCOLEU (15) TRIPAL (17)	CASARB (2) CASSYL (6) PREMON (1) INGLAU (8) CECSCH (7) SCHMOR (9) TRIPAL (15) OCOLEU (11) CORBOR (14) TABHET (19)

Fig. 7. Indicator species for the LFDP by cover class (CC) (1–4) and combined cover class (1+2+3). Indicator species listed in order of indicator strength (highest indicator values toward the top). Numbers in parentheses indicate species rank, and species color represents species-specific life histories; blue, anthropogenically associated; tan, small trees; brown, large trees; green, pioneer species; and gray, palm trees. A maximum of 10 indicator species shown for each group. Complete indicator species analysis results are available in Appendix S1.

CODE	Species	Family
	Anthropogenically-associated	
CALCAL	*Calophyllum antillanum* Cambess.	Calophyllaceae
GENAME	*Genipa americana* L.	Rubiaceae
HIBTIL	*Talipariti tiliaceum* (L.) Fryxell	Malvaceae
SYZJAM	*Syzygium jambos* (L.) Alston	Myrtaceae
	Pioneer	
ALCLAT	*Alchornea latifolia* Sw.	Euphorbiaceae
CECSCH	*Cecropia schreberiana* Miq.	Urticaceae
HETCYM	*Clidemia eggersii* (Cogn.) F.S. Axelrod	Melastomataceae
MICAFF	*Miconia affinis* DC.	Melastomataceae
MICMIR	*Miconia mirabilis* (Aubl.) L.O. Williams	Melastomataceae
MICPRA	*Miconia prasina* (Sw.) DC.	Melastomataceae
MICRAC	*Miconia racemosa* (Aubl.) DC.	Melastomataceae
PALRIP	*Palicourea croceoides* Ham.	Rubiaceae
PIPGLA	*Piper glabrescens* (Miq.) C.DC.	Piperaceae
PSYBER	*Psychotria berteroana* DC.	Rubiaceae
PSYBRA	*Psychotria brachiata* Sw.	Rubiaceae
SCHMOR	*Schefflera morototoni* (Aubl.) Maguire, Steyerm. & Frodin	Araliaceae
	Small Trees	
ARDGLA	*Ardisia glauciflora* Urb.	Myrsinaceae
CASARB	*Casearia arborea* (Rich.) Urb.	Salicaceae
CASDEC	*Casearia decandra* Jacq.	Salicaceae
CASSYL	*Casearia sylvestris* Sw.	Salicaceae
CITCAU	*Citharexylum caudatum* L.	Verbenaceae
CITFRU	*Citharexylum spinosum* L.	Verbenaceae
COMGLA	*Comocladia glabra* Spreng.	Anacardiaceae
CORBOR	*Cordia borinquensis* Urb.	Boraginaceae
CSSGUI	*Cassipourea guianensis* Aubl.	Rhizophoraceae
FAROCC	*Faramea occidentalis* (L.) A. Rich.	Rubiaceae
GUAGLA	*Guarea glabra* Vahl	Meliaceae
MALFUR	*Malpighia fucata* Ker Gawl.	Malpighiaceae
MYRLEP	*Myrcia amazonica* DC.	Myrtaceae
RHEPOR	*Garcinia portoricensis* (Urb.) Alain	Clusiaceae
SOLRUG	*Solanum rugosum* Dunal	Solanaceae
TRIPAL	*Trichilia pallida* Sw.	Meliaceae
WALPEN	*Wallenia lamarckiana* (A. DC.) Mex	Myrsinaceae
	Large Trees	
CALSQU	*Henriettea squamulosum* (Cogn.) Judd	Melastomataceae
CINELO	*Cinnamomum elongatum* (Nees) Kosterm.	Lauraceae
CINMON	*Cinnamomum montanum* (Sw.) Bercht. & J. Presl	Lauraceae
COCSPP	*Coccoloba sp.*	Polygonaceae
COCSWA	*Coccoloba swartzii* Meisn.	Polygonaceae
CROPOE	*Croton poecilanthus* Urb.	Euphorbiaceae
DACEXC	*Dacryodes excelsa* Vahl	Burseraceae
DRYGLA	*Drypetes glauca* Vahl	Euphorbiaceae
EUGSTA	*Eugenia domingensis* (Kiaersk.) Krug & Urb.	Myrtaceae
FICCIT	*Ficus citrifolia* Mill.	Moraceae
GUEVAL	*Guettarda valenzuelana* A. Rich.	Rubiaceae
HENFAS	*Henriettea fascicularis* (Sw.) M. Gómez	Melastomataceae
INGLAU	*Inga laurina* (Sw.) Willd.	Fabaceae
LAEPRO	*Laetia procera* (Poepp.) Eichler	Salicaceae
LONLAT	*Lonchocarpus heptaphyllus* (Poir.) DC.	Fabaceae
MARNOB	*Margaritaria nobilis* L.f.	Euphorbiaceae
MATDO	*Matayba domingensis* (DC.) Radlk	Sapindaceae
MICTET	*Miconia tetrandra* (Sw.) D. Don	Melastomataceae
MIRGAR	*Micropholis garciniifolia* Pierre	Sapotaceae
OCOLEU	*Ocotea leucoxylon* (Sw.) Laness.	Lauraceae
OCOMOS	*Ocotea moschata* (Meisn) Mez.	Lauraceae
ORMKRU	*Ormosia krugii* Urb.	Fabaceae
SLOBER	*Sloanea berteroana* Choisy ex DC.	Elaeocarpaceae
SYMMAR	*Symplocos martinicensis* Jacq.	Symplocaceae
TABHET	*Tabebuia heterophylla* (DC.) Britton	Bignoniaceae
TETBAL	*Tetragastris balsamifera* Oken	Burseraceae
	Palm Trees	
PREMON	*Prestoea acuminata* (Wiild.) H.E. Moore var. *montana* (Graham) Henderson and Galeano	Arecaceae

Fig. 8. Scientific names of species and corresponding species codes for reference in Fig. 7. Species code color corresponds to species-specific life histories; blue, anthropogenically associated; tan, small trees; brown, large trees; green, pioneer species; gray, palm trees.
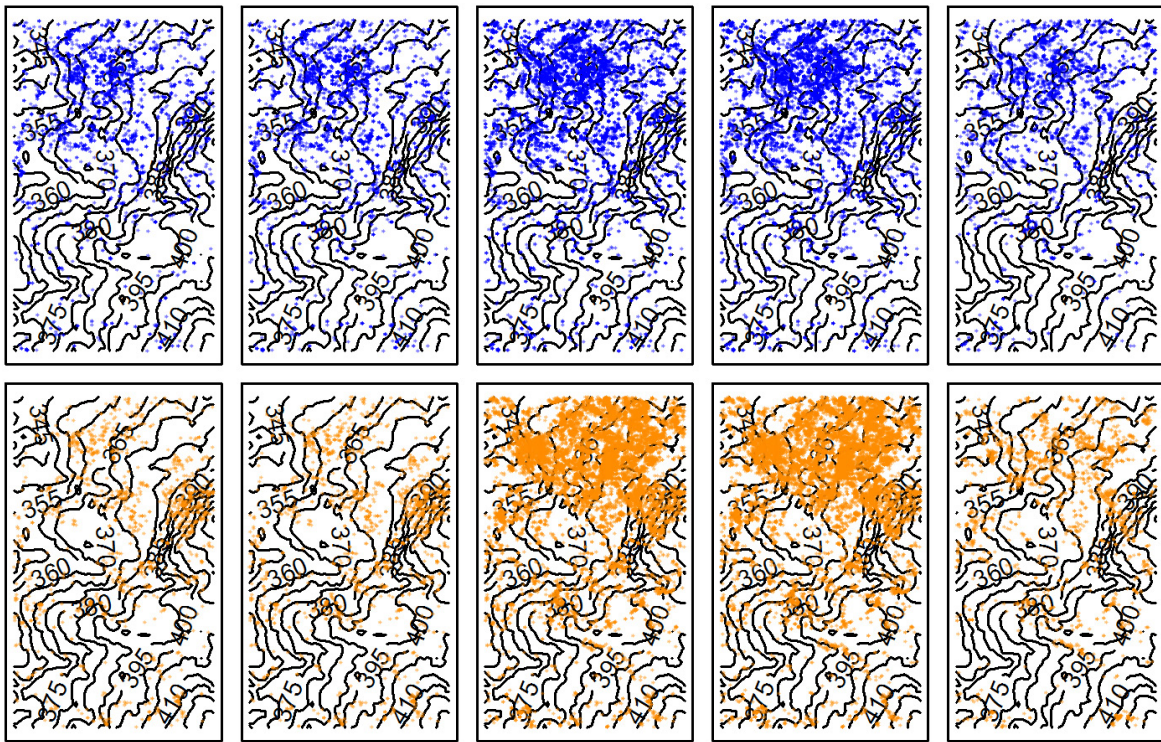
Fig. 9. Distribution maps for two understory pioneer species (Rubiaceae) in the LFDP. Censuses progress from left to right (Census 1: 1990–1992, Census 2: 1995, Census 3: 2000, Census 4: 2005, and Census 5: 2011). *Psychotria berteroana* DC is shown in blue (top), and *Psychotria brachiata* Sw. is shown in orange (bottom).

(i.e., the presence of planted *C. antillanum*). When all secondary forest areas were combined into a single category, the ISA extracted a large number of species of high community rank as contributing to the land-use pattern, including *C. arborea* and several shrubs and pioneer trees. This strongly suggests that all secondary forest is responding similarly to hurricane disturbance, regardless of its canopy cover appearance from the aerial photographs in 1936, and any differences in management since that time. Thus, not only was it convenient to combine cover classes 1–3 for past analyses, but it also strongly suggests that this combination captures emergent properties of secondary forest in terms of their response to human land-use legacies, hurricane disturbance, and their subsequent dynamics (Chazdon 2003, 2014).

This pattern supports the idea that hurricane disturbances "reset" successional trajectories by facilitating canopy damage, sometimes resulting in mortality and individual turnover that result from altered environmental (e.g., light) conditions. In doing so, hurricane disturbances

have preserved the landscape-scale community compositional differences attributed to past land use (Foster 1988, Zimmerman et al. 1995, Pascarella et al. 2004). When these differences were explored with indicator species analysis, community stability for the areas with most and least intensive past land-use pressure (cover classes 1 and 4, respectively) was highest, demonstrating the long-term effects of past land use. The stability in cover class 1 illustrates how the land-use signal has remained strong in the area with the highest levels of human disturbance. Similarly, in cover class 4, the natural tabonuco forest community has dominated. The ISA for the combination of cover classes 1–3 highlights how past land-use legacies have helped facilitate "novel," or anthropogenically selected, secondary tropical forest communities that are more affected and take longer to recover from hurricane disturbance (Lugo and Helmer 2004, Lugo 2009). This can be inferred to illustrate the compromised resistance but increased resilience of secondary forest communities to cyclonic storms.
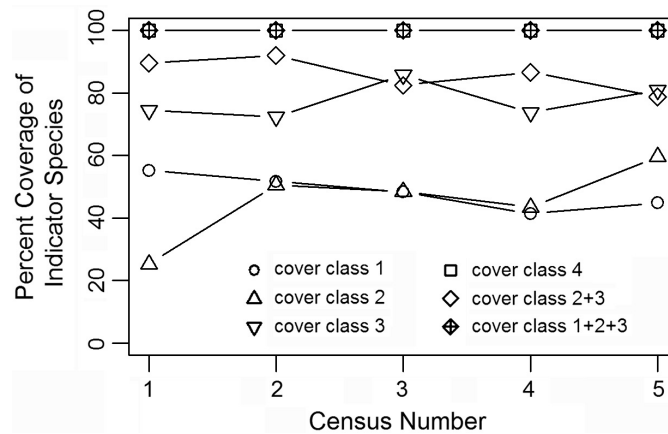
Fig. 10. Coverage of indicator species for each cover class over time. Census numbers correspond to successive census years on the *x*-axis. The *y*-axis shows the percent of sites within each cover class that contained the indicator species for any given census. Perfect coverage for cover class 4 and for cover classes 1, 2, and 3 combined.

In summary, dynamic changes in both forest composition and structure are evident in the LFDP over the 21-yr study period, being predominately determined by past land use (Thompson et al. 2002). Hurricane disturbances interact with community differences to preserve past land-use differences in forest community structure and composition (Foster 1988, Uriarte et al. 2009). The MRPP has shown how community heterogeneity increases after hurricanes, and the ISA attributes this to a disproportionate recruitment of pioneer species in areas of more intense past land-use pressure (i.e., the northern part of the LFDP). We currently understand these differences in recruitment of pioneer species among cover classes in the LFDP to be directly related to differences in forest structure and species composition created by past logging and agricultural practices in the area.

CONCLUSIONS

The LFDP encompasses a patch of heterogeneous forest with differing structure and community composition, conditional on the varied effects of past human land use (Thompson et al. 2002, Chazdon 2003, Lugo 2009). Community responses to natural disturbances, in this case hurricanes, differ with respect to these land-use legacies (Uriarte et al. 2009), emphasizing the general idea that human land use is a long-term press type disturbance and natural disturbances

tend to be more of a short-term pulse (Foster et al. 1998, Grau et al. 2003). The LFDP exhibits an asymmetric response to hurricanes when areas are divided by past land use, despite showing a singular compounded response to both hurricanes at the whole-plot level. Infrequent and cyclic hurricane disturbances affecting the LFDP serve to maintain community differences resulting from past land-use pressures, yet the underlying mechanisms are poorly understood. Further research into the exact ways in which human land-use pressures alter the biotic and abiotic conditions (Comita et al. 2010, Uriarte et al. 2012) is recommended for a better understanding of how land-use legacies are maintained within forest communities at ecologically long timescales after land-use cessation. Improved understanding of the mechanisms at play in regenerating secondary tropical forests is of interest as much of the tropical world continues to industrialize, and secondary forests with varied land-use histories increasingly dominate the region (Chazdon 2014).

ACKNOWLEDGMENTS

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