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Parsing Long-Term Tree Recruitment, Growth, and Mortality to Identify Hurricane Effects on Structural and Compositional Change in a Tropical Forest

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Abstract: After hurricane disturbances in tropical forests, the size structure and species composition are affected by immediate mortality, and subsequent recruitment and individual growth. Often, immediate post-disturbance stand-level data are presented but understanding of the components that affect changes in growth and longer-term responses to forest structure and composition are lacking. To answer questions about how mortality, recruitment, and growth change among successional Plant Functional Types (PFT) through time after a hurricane disturbance, we use long-term census data (1989–2014) collected in the Luquillo Experimental Forest, Puerto Rico. We developed an algorithm to fill missing diameter data from the long-term data set that was collected three months after Hurricane Hugo; and subsequently at five-year intervals. Both the immediate hurricane-induced mortality and subsequent mortality were lower in stems with larger diameters, but varied among successional PFTs *Early*, *Mid*, *Late*, and *Palm*. Tree growth rates were observed to decrease with time since the hurricane disturbance. Five years after the hurricane, mortality was minimal but then increased gradually with time. In contrast, recruitment was highest five years after the hurricane and then decreased with time. The palm *Prestoea montana* became the most abundant species in the forest after the hurricane, as it had the lowest immediate hurricane-induced and subsequent mortality, and the highest recruitment. Twenty-five years after the hurricane, the palm and the *Late* PFT dominate the forest after shifting species composition from pre-hurricane conditions.

Keywords: forest disturbances; plant functional types; palms; hurricanes; Luquillo Experimental Forest; Bisley Experimental Watersheds; Puerto Rico

1. Introduction

Hurricanes have major effects on tropical forests [1–6]. Hurricane-force winds (compounded and aided by heavy rains, saturated soils, and loosened roots [4,7]) uproot and snap trees, break branches, and defoliate surrounding vegetation. The results are gaps in the forest and hence increasing light levels within the forest canopy [8]. Defoliation may recover in months to years [9–14], but forest structure and composition may shift over decades following three stages of species succession [15–19]. Early successional (pioneer) species establish and recruit in open gaps formed after hurricane disturbances, growing rapidly in the high light environment. Mid successional species, which have intermediate growth rate and are somewhat shade tolerant, gradually substitute early successional species as the gaps close and the canopy recovers. Late successional species, which have low growth rates and are shade tolerant, reach the canopy, and become dominant in the plant community as the forest matures until the next disturbance.

Forest composition and structure are also critical to hurricane-induced mortality– less wind-resistant structure and composition would lead to higher mortality, especially

when combined with higher exposure to hurricane winds [20]. Under the changing climate, hurricanes are expected to increase and become more intense over the Atlantic Ocean [21,22]. Damage from higher intensity and more frequent hurricane disturbances will change the structure and composition of the forest, inevitably affecting the resulting succession patterns and hence the conditions at the time of subsequent disturbances. Therefore, it is critical to understand the drivers of forest structure and composition during the succession.

A previous study pointed out that the demographic components such as recruitment, tree growth, and mortality drive the changes in biomass of second-growth tropical forests during the secondary succession [23]. Specifically, the biomass change was largely driven by tree growth in the early successional stage, and growth and mortality in the late successional stage. However, the forest structure and composition are not investigated. To understand how demographic components (mortality, recruitment, growth) contribute to the observed changes in forest composition and structure after a disturbance, we investigate the effects of hurricane Hugo on long-term patterns of forest structure and composition on a mature secondary forest at the Bisley Experimental Watersheds in the Luquillo Experimental Forest in Puerto Rico using long-term tree census observations.

Furthermore, topography affects species distribution and forest mortality from hurricane disturbances [11–15,24], and thus forest structure and composition in the long term. However, whether the demographic rates during the succession after a hurricane disturbance vary with topography has not been investigated. Therefore, we will also investigate the species distribution and demographic rates on different topographic settings (including valleys, ridges, and slopes) using the tree census observations at the study site.

The objectives of this study are to investigate the effects of hurricane Hugo on long-term patterns of forest structure and composition of a mature secondary forest in the Luquillo Experimental Forest in Puerto Rico. We examine the demographic dynamics of the most abundant species, and of successional Plant Functional Types (PFT)–*Early*, *Mid*, *Late*, and *Palm*–as palms are abundant components of tropical forests, have allometry and life history traits that appear to be important for hurricane disturbances, and are distinct from trees [25–27].

2. Materials and Methods

2.1. Study Site

The Bisley Experimental Watersheds (hereafter Bisley; 18°20′ N, 65°50′ W) are located in the Luquillo Experimental Forest, northeastern Puerto Rico. Bisley is part of the Luquillo Long Term Ecological Research (LTER) program and data sets from on-going and previous research are available (https://luquillo.lter.network/data-catalog/ accessed on 17 April 2022) [28]. The forest site ranges between 260 to 400 m above sea level, with a steep landscape that receives an average of 3500 mm precipitation per year, and it is exposed to storms, hurricanes, landslides, Saharan dust, and deposition from Caribbean volcanic activity [29,30].

The forest type at Bisley is found in other Caribbean islands [24,31] and it is locally known as tabonuco or *Dacryodes–Sloanea* vegetation association. The dominant species are *Dacryodes excelsa* (also known as tabonuco), *Sloanea berteriana*, and *Prestoea montana* var. *acuminata*, hereafter referred to as *Prestoea montana* [14,29]. The distribution of watershed-scale species composition, aboveground biomass, and forest turnover at Bisley have been associated to the characteristic geomorphic/terrain settings at the site: ridges, slopes, and valleys [14,32]. The geomorphology, soils, and disturbance history of Bisley are described in detail elsewhere [14,32–35].

The forest at Bisley had timber selectively removed, supported local-scale charcoal production and subsistence agriculture [33], and was noted to have sustained damage by Hurricanes San Felipe in 1928 and San Cipriano in 1932 (reported by Gerhart 1934 in [33]). Hurricane Hugo (category 3), passed over the site on 18 September 1989, was the largest storm to affect the area since the 1930s, and resulted in significant damage to the forest [29]. By the time of Hurricane Hugo, Bisley was a mature secondary forest that had

recovered its stem density and basal area after selective logging. Hence, the recovery of the forest from Hurricane Hugo is defined as secondary succession (a natural disturbance in mature native secondary forest) [36]. After Hugo in 1989, nine other named storms and hurricanes have passed near the area [30,37], but only Hurricane Georges (category 3), in 1998, resulted in localized defoliation and minimal mortality in the study area [14,38]. The most recent hurricanes at Bisley–Irma and Maria (September 2017)–are addressed in separate studies [20].

2.2. Diameter and Species Observations

Eighty-five permanent plots were established at Bisley in 1989 and censuses were conducted three months before Hurricane Hugo (pre-Hugo 1989), three months after the hurricane (post-Hugo 1989), and every five years since then (1994, 1999, 2004, 2009, and 2014). The pre-Hugo census was started in late 1988 and was completed in the summer of 1989 (three months before the hurricane), the post-Hugo census was started three months after Hugo and completed within five months. Other censuses were started in April and completed between June and July of their respective year. In addition, six more plots were established in 1994–one in 2009, and three in 2014–making 95 plots in total. The plots are 10-m diameter circles and 40 m apart in a grid extending over 13 hectares. The topographic location of each plot is recorded (i.e., valley, slope, and ridge). Stems in the plots with diameter at breast height (1.3 m above the ground) (DBH) equal to or greater than 2.5 cm were tagged, the species were identified, DBH measured (with a precision of 0.1 cm), and heights (H) of the two tallest stems per plot were measured. The tag number of each stem is unique at the plot level and provides the year the stem was first recorded in the census. The pre-Hugo 1989 census was completed three months before the hurricane, and the post-Hugo 1989 census was started three months after the hurricane, thus they directly measure the immediate mortality caused by the hurricane–mortality meaning that no recovery was found in later censuses.

The plots at Bisley were initially established to explore watershed scale biomass and forest standing stocks and protocols appropriate for that purpose were used. Previous studies at this site investigated the relative changes in standing stocks, estimates on stem density, basal area, aboveground biomass, and species richness and diversity in relation to succession after Hurricane Hugo [14,29,39,40]. Those studies, however, lacked long-term analyses of mortality, recruitment, and growth rates in response to hurricane disturbance.

2.3. Plant Functional Types (PFT) of Species

Sixty-six species were identified, including a species of herb (a banana species *Musa x paradisiaca*), a palm species *Prestoea montana*, two species of tree-ferns (*Cyathea arborea* and *C. portoricensis*), and 62 species of trees. The banana species disappeared from the forest after Hurricane Hugo in 1989. We categorized species into successional plant functional types (PFT) based on their documented response to disturbances [40–44]. The classification into PFT is a complementary approach to understand forest recovery and succession, and to contribute to on-going modeling efforts of vegetation dynamics [45–47]. The classifications of PFT have important applications for predictive ecology and modeling, serving to reduce the large numbers of plant species into a smaller quantity of functional classes based on ecological concepts [48,49]. Building upon a previous work [44], in a study of this same forest (Luquillo Experimental Forest) and same forest type (tabonuco), the species of trees and tree-ferns are categorized into one of three tropical successional PFTs: *Early*, *Mid*, or *Late* (Table S1 for the PFT of each species). *Early* PFT includes species that establish and recruit in open canopy and gaps formed after disturbances and grow rapidly in the high light environment. *Mid* PFT includes species that have intermediate growth rates and are somewhat shade tolerant. *Late* PFT includes species that have low growth rates and are shade tolerant. Very few species were not classified by previous studies [41–44], and in the rare case that a species was still not classified after the above two steps, we assigned a

PFT to the species based on descriptions of successional traits such as seed characteristics, recruitment, and growth [50,51].

Previous studies have either excluded palms from analyses [52] or considered palms as a mid or late successional species [41–44]. However, the palm *Prestoea montana* possesses some early successional traits, such as low "wood" density and high fecundity under open canopy [53,54], allowing them to recruit quickly when the canopy opens; and some late successional traits, such as tolerance to shade [26], which favor their growth and survival when the canopy closes. Therefore, following a previous study [20], we separate the palm species from the three broadly used successional PFTs and categorize it as *Palm* PFT.

2.4. Data Analyses

We estimated the missing values in the dataset (Supplementary Information S1) and calculated lower bounds for the measurement error (Supplementary Information S2). To study the mortality and recruitment changes with time since disturbance, we calculated the recruitment rate of each PFT in each five-year census interval, and the mortality rate of each PFT and of each DBH class. The recruitment rate was calculated as the percentage of the number of newly recruited stems to the number of stems that were alive in the previous census. Similarly, the mortality was calculated as the percentage of the number of stems that existed in the previous census but not in the current census to the number of stems that existed in the previous census. The immediate hurricane-induced mortality was calculated as the percentage of the number of stems that existed in pre-Hugo census but not in post-Hugo census to the number of stems that existed in pre-Hugo census.

Diameter growth was calculated as the diameter measurement difference between two consecutive five-year-interval censuses. Given the sampling rate of the census, our estimates of growth were cm per 5-years but expressed as cm per year (cm yr^{-1}) of each standing stem. The relative stem diameter growth rate (%) was calculated as the ratio of the absolute diameter growth rate to the previous-census diameter, expressed as a percentage. Similarly, we calculated the absolute basal area growth rates (cm^2 yr^{-1}) of each stem. Above-ground biomass (AGB) of each tree was calculated as $AGB = \exp(2.475 \ln(DBH) - 2.399)$ following the equations from Scatena et al. [29]. The growth rates of each species and PFT during each census interval were analyzed to identify the differences among species and among PFTs, and their changes with time since disturbance. Mortality and growth rates were calculated for each stem separately, and then grouped according to PFT. Note that height growth is more significant than diameter growth for the palm species [53,54]. However, since we do not have height information for all palms, we did not calculate the height growth for palms.

Lastly, to explore forest community structure and composition over 25 years, we selected the most abundant species to quantify the proportional changes in species composition. The most abundant species were defined as those whose individual abundance accounts for more than 5% of the total abundance in the forest in one or more censuses. Seven species were selected as abundant: two *Early* species (*Cecropia schreberiana* (CECSCH) and *Psychotria berteriana* (PSYBER)), one *Mid* species (*Ocotea leucoxylon* (OCOLEU)), three *Late* species (*Sloanea berteriana* (SLOBER), *Dacryodes excelsa* (DACEXC), and *Cyathea portoricensis* (CYAPOR)), and the *Palm* species (*Prestoea montana*, PREMON). The seven species in total account for 62%, 60%, 74%, 67%, 65%, 64%, and 66% of the total abundance in each of the seven censuses, respectively.

To identify the effect of topography on species distribution, we calculated the averages of the proportion of each species across plots with the same topographic setting; slopes, valleys, and ridges [38]. The species proportion in a plot is defined as the ratio between the number of stems of the species to the total number of stems in the plot. To identify the effect of topography on demographic rates, we calculated the distribution of growth rate for stems within each topographic setting and tested the difference of the distribution between any two settings using two-sample *t* test. For mortality and recruitment, we calculated the

rates using plots with the same topographic settings and tested the difference of the rates between any two settings using a z-score test [55] following Zhang et al. [20].

3. Results

3.1. Mortality and Recruitment over the Course of 25 Years

The overall immediate stem mortality from Hurricane Hugo (1989) was 58%. Mortality varied among PFTs, with *Early* PFT having the highest (82%), followed by *Mid* (55%), then *Late* (54%), and with *Palm* (42%) having the lowest mortality value (Figure 1a) overall. Immediate hurricane-induced mortality and subsequent mortality varied by diameter classes (Figure 1b). Smaller stems had higher mortality than larger stems for all censuses except censuses 1994 and 1999, where intermediate diameter stems (DBH between 5 and 10 cm) had the highest mortality among the four diameter classes.
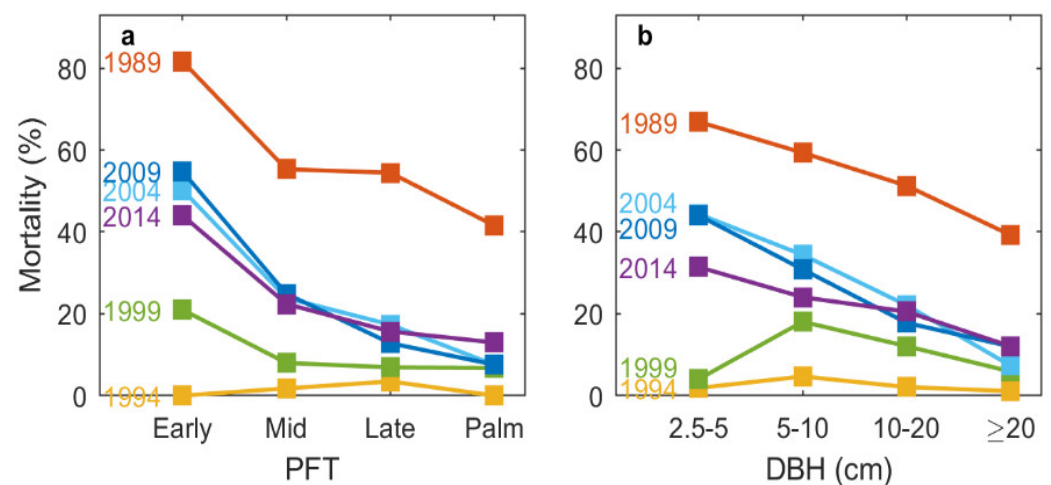
Figure 1. The mortality of (**a**) different PFTs and (**b**) different diameter (DBH) classes in each census at Bisley Experimental Watersheds, Luquillo, Puerto Rico. The mortality in 1989 refers to the immediate hurricane-induced mortality, and that in other census years refers to the mortality from the previous census year to current census year.

Five years after Hurricane Hugo (1994), all PFTs recruited new stems into the census. *Early* PFT had the highest recruitment rate (1665%), followed by *Palm* (95%), then *Mid* (45%), and then *Late* (16%) (Table 1). Meanwhile, mortality was very low for all PFTs (0%, 2%, 3%, and 0% for *Early*, *Mid*, *Late*, and *Palm*, respectively) five years after the hurricane (Figure 1a). Ten years after the disturbance (1999), the recruitment rate of *Early* (104%) decreased significantly, *Palm* (86%) decreased slightly, while *Late* (44%) and *Mid* (132%) increased significantly (Table 1). Although mortality was observed in more than half of the stems immediately after the hurricane, the decrease in basal area and aboveground biomass was only 42% and 40%, respectively (Table 2). After 15–20 years, the recruitment rate for the three successional PFTs decreased (5%, 8%, 10% for *Early*, *Mid*, and *Late*, respectively), while mortality increased (55%, 25%, 13% for *Early*, *Mid*, and *Late* PFTs, respectively); however, *Palm* had the highest recruitment rate (15%) and lowest mortality rate (8%) among the four PFTs (Table 1; Figure 1a). After 25 years, the recruitment rate and mortality rate became stable (Table 1; Figure 1a). The mortality of *Palm* remained the smallest among the four PFTs throughout the 25 years since the hurricane (Figure 1a).

Table 1. Recruitment rate (%) for each PFT during any two consecutive censuses of the 85 continually censused plots at Bisley Experimental Watersheds, Luquillo, Puerto Rico.

	Early	*Mid*	*Late*	*Palm*
1989–1994	1665.00	44.74	16.45	94.74
1994–1999	104.82	131.90	44.06	86.49
1999–2004	19.72	18.63	32.96	36.84
2004–2009	4.66	7.51	9.90	15.12
2009–2014	13.33	8.04	10.45	9.73

Table 2. Averages and standard deviations (in parentheses) of stem density, basal area, and aboveground biomass for the 85 continually censused plots in the Bisley Experimental Watersheds.

Census Year	Stem Density (# ha^{-1})	Basal Area (m^2 ha^{-1})	Aboveground Biomass (Mg ha^{-1})
Pre-Hugo 1989	1440 (702)	38 (33)	255 (271)
Post-Hugo 1989	604 (398)	22 (26)	152 (211)
1994	1275 (569)	32 (28)	199 (226)
1999	2254 (928)	36 (26)	217 (205)
2004	2072 (756)	38 (25)	228 (210)
2009	1645 (648)	39 (27)	238 (224)
2014	1440 (642)	39 (29)	246 (240)

3.2. Diameter Growth Rates

For all stems during the 25-year study period, average diameter growth rate decreased as time after the disturbance increased: 0.33 ± 0.02 cm yr^{-1} in 1994, 0.28 ± 0.01 cm yr^{-1} in 1999, 0.26 ± 0.01 cm yr^{-1} in 2004, 0.22 ± 0.01 cm yr^{-1} in 2009, and 0.19 ± 0.01 cm yr^{-1} in 2014. The differences between any two censuses are significant ($p < 0.05$) according to two-sample *t* test, except for censuses 1999 and 2004 ($p = 0.1437$), and censuses 2009 and 2014 ($p = 0.0891$). Growth rates also varied among PFTs and among stem sizes (Figure 2). The growth rate of the *Palm* PFT decreased with diameter (negative regression coefficient b) and the negative correlation was significant ($p < 0.05$) in all censuses. The growth rate of the three successional PFTs generally increased with diameter (positive regression coefficient b). The positive correlation of growth rate and diameter was significant ($p < 0.05$) in all censuses for the *Late* PFT. In contrast, the positive correlation of growth rate and diameter was significant only 10 and 15 years after the hurricane (1999 and 2004) for the *Early* PFT, and 20 and 25 years after the hurricane (2009 and 2014) for the *Mid* PFT (Figure 2). However, in the cases with a statistically significant regression coefficient, the coefficient of determination and the regression coefficient itself are very small, denoting a very weak relationship.

For all stems with diameter less than 20 cm, the average growth rate was the highest in census 1994, five years after the hurricane. Average growth rate decreased with time since the hurricane disturbance for all PFTs, especially for the *Early* and *Palm* PFTs (Figure 3). For stems with diameter between 20 and 40 cm, the growth rate of the *Early* PFT decreased with time since disturbance (Figure 3a), while the growth rate of the *Mid* and *Late* PFTs first decreased and then increased with time since disturbance (Figure 3b,c). For stems with DBH larger than 40 cm, the growth rate of *Late* increased with time since disturbance.
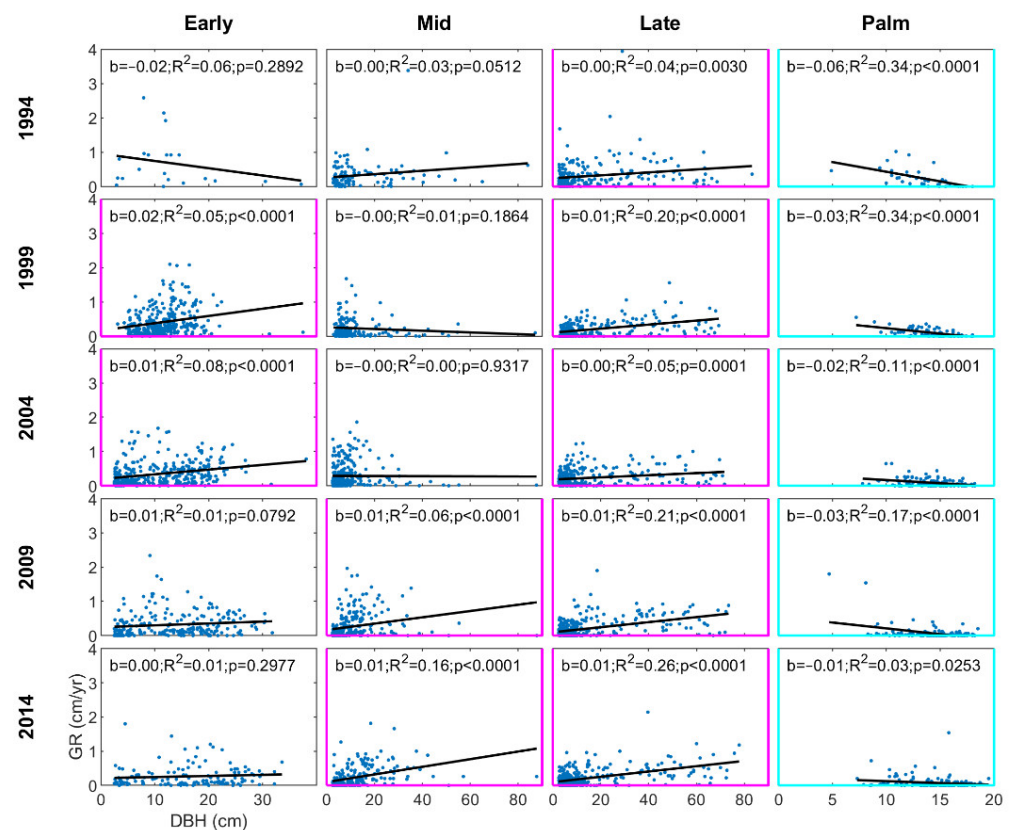
Figure 2. Scatter plots of diameter (DBH) growth rates (GR, cm per year) and DBH values (cm) for the four PFTs in the five censuses at Bisley Experimental Watersheds, Luquillo, Puerto Rico. The linear regression of GR on DBH for each PFT and census is estimated, and the regression coefficient (b), the coefficient of determination (R^2), and the *p*-value are shown in the panels. Linear regression models that are significant at 95% confidence interval ($p < 0.05$) are identified with a blue box for negative regression coefficient and a magenta for positive coefficient. Grey boxes do not have statistically significant coefficients.
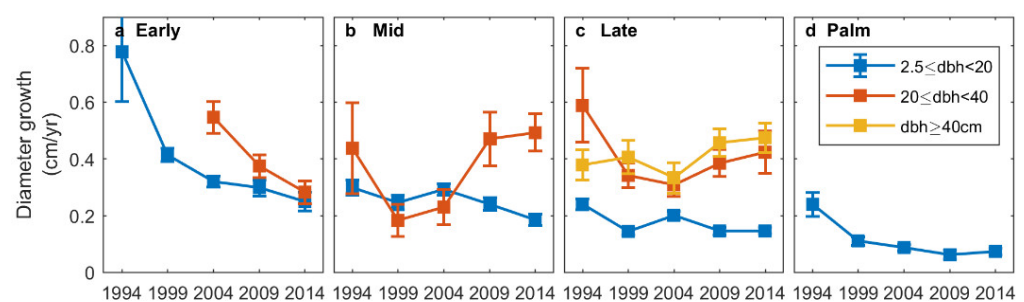
Figure 3. Diameter growth rates (cm per year) in five censuses for each diameter (DBH) size of (**a**) *Early*, (**b**) *Mid*, (**c**) *Late*, and (**d**) *Palm* PFTs. The markers and the bars indicate the mean and standard error, respectively; only values with more than 10 samples are shown.

Larger stems have lower relative growth rates as observed in *Late* PFT stems (Figure S6c). Like the absolute growth rate, the relative growth rate also decreased with time since disturbance, especially for *Early* and *Palm* PFTs, and *Mid* and *Late* PFTs with small diameters (Figure S6a–d). Basal area growth is derived from diameter and is highly correlated with diameter growth (Figure S6e–h).

3.3. Shifts in Species Composition

Shifts in species composition of the forest were quantified by focusing on the proportions of the seven most abundant species through time (Figure 4). In terms of abundance, the forest was originally dominated by two *Late* successional species, *Sloanea berteriana* (SLOBER) and *Dacryodes excelsa* (DACEXC) (Figure 4a). For the ten years following Hurricane Hugo (Figure 4c,d), *Early* successional species *Cecropia schreberiana* (CECSCH) and *Psychotria berteriana* (PSYBER) recruited and increased and then started to decrease 20 and 25 years later (Figure 4f,g). *Mid* successional species *Ocotea leucoxylon* (OCOLEU), which was less abundant after the hurricane (Figure 4b), recruited and increased in proportion ten years after the hurricane (Figure 4d) and then maintained its abundance (Figure 4e–g). The *Late* successional species SLOBER and DACXEC also began to increase their abundance 15 years after the hurricane, surpassing the *Early* successional CECSCH and PSYBER, then maintaining their abundance 25 years later (Figure 4e–g). Another *Late* successional species, the tree-fern *Cyathea portoricensis* (CYAPOR), surpassed its pre-disturbance abundance and became a dominant species in the forest in 2014 (Figure 4g). The *Palm* species PREMON increased its dominance in the forest after the disturbance (Figure 4b) and continued to increase throughout the 25 years after the disturbance and became the most abundant species in the forest by 2014 (Figure 4c–g).
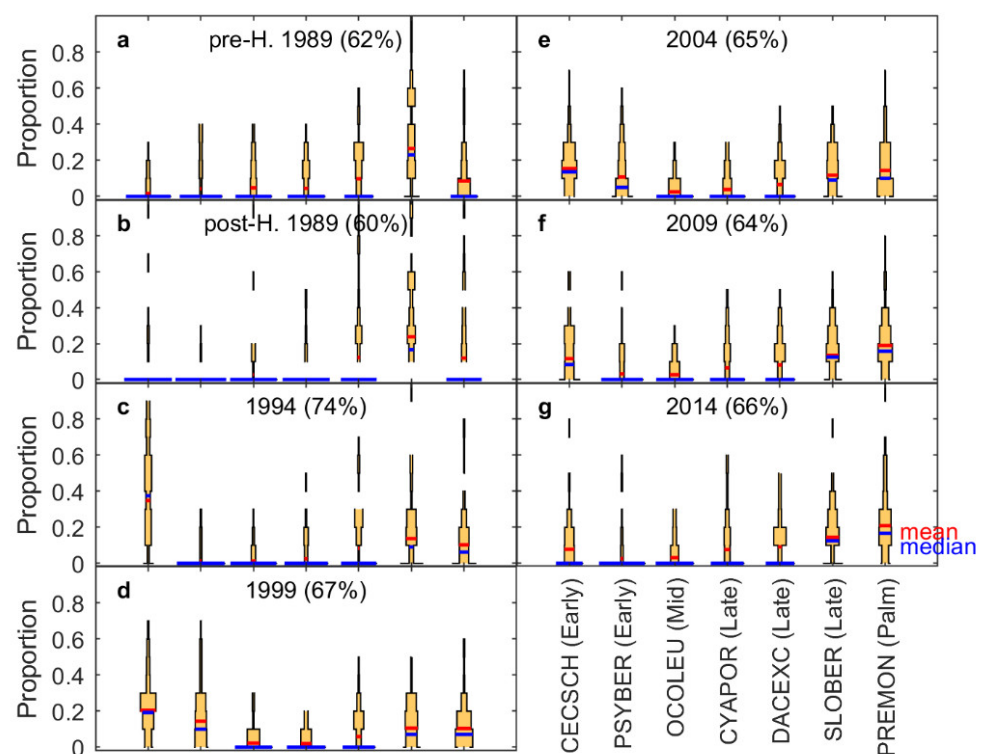
Figure 4. The probability density proportions for the seven most abundant species in each of the seven censuses at Bisley Experimental Watersheds, Luquillo, Puerto Rico. The seven censuses are (**a**) Pre-Hugo 1989, (**b**) post-Hugo 1989, (**c**) 1994, (**d**) 1999, (**e**) 2004, (**f**) 2009, and (**g**) 2014. The percentage of the abundance comprised by the top seven species in the forest per census is shown in parenthesis at the top of each panel. The x-axes are the seven species, with plant functional type (PFT) in parentheses, and the y-axes represent the proportion in 10 bins from 0.0001 to 1 and one bin for 0 proportion. The width of the yellow area represents the probability for each proportion bin; red and blue lines are the mean and median values of the proportion for all the 85 plots. A value of 0-median for a species indicates that the species is absent in more than half of the plots for that census.

3.4. Impact of Topography

The demographic rates vary among the topographic settings (i.e., valley, ridge, and slope) (Tables S2–S4). Specifically, *Mid* PFT has significantly lower growth rate on ridges (0.18 cm yr^{-1}) than on slopes (0.29 cm yr^{-1}) ($p < 0.0001$), *Late* PFT has significantly lower growth rate on valleys (0.16 cm yr^{-1}) than on ridges (0.25 cm yr^{-1}) ($p = 0.0053$), and *Palm* PFT has significantly higher growth rates on valley plots (0.16 cm yr^{-1}) than on slope plots ($p = 0.0015$). Mortality was generally lower on ridges than on slopes or valleys, and the difference was significant in 1989 ($p = 0.0001$), 2004 ($p < 0.0001$), and 2009 ($p = 0.0022$). Recruitment was the highest in valleys in the first five years after the hurricane (1994; $p < 0.0001$). These variations are linked with the shifts of species distribution among the topographic settings after the hurricane disturbance (Figure 5).
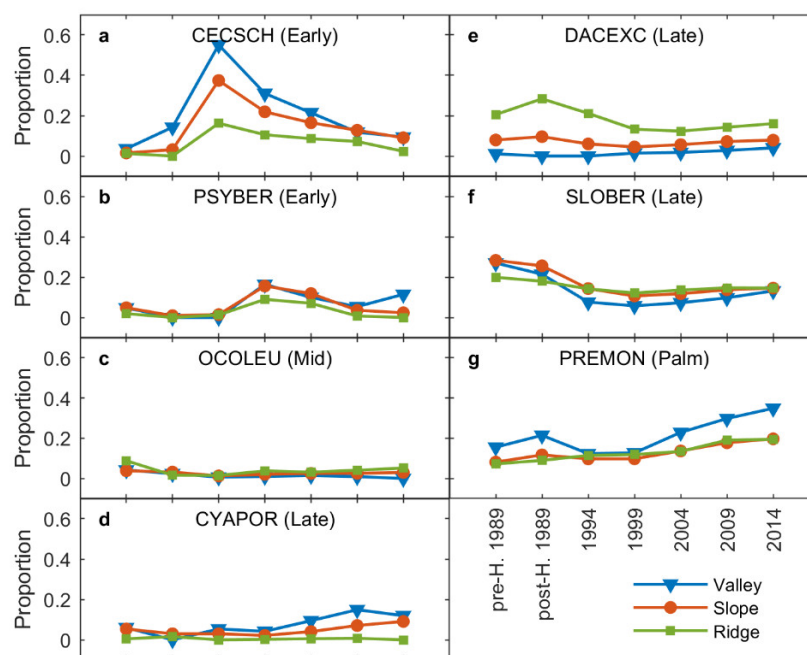
Figure 5. Mean values of species proportion across plots grouped by different topographic settings: valleys, slopes, and ridges. The x-axes are the seven census years, and the y-axes are the proportion. The seven most abundant species are (**a**) CECSCH: *Cecropia Schreberiana*, (**b**) PSYBER: *Psychotria berteriana*, (**c**) OCOLEU: *Ocotea leucoxylon*, (**d**) CYAPOR: *Cyathea portoricensis*, (**e**) DACEXC: *Dacryodes excelsa*, (**f**) SLOBER: *Sloanea berteriana*, and (**g**) PREMON: *Prestoea montana*. For taxonomic plant families and PFTs classification, please see Table S1.

The *Early* successional species CECSCH increased its proportional abundance in valleys and slopes, but never dominated on ridges (Figure 5a). The proportion of CECSCH in ridge plots is significantly lower than that in valley or slope plots ($p < 0.0001$). The tree fern CYAPOR (Figure 5d) increased the proportion of its abundance in valleys and slopes after the hurricane. The proportion of CAYPOR in valley/slope plots is significantly higher than in ridge plots ($p < 0.0001$). This is in contrast to the *Late* successional species DACEXC, which had significantly lower proportion in plots in valleys and slopes than in plots on ridges ($p < 0.0001$). This dominant topographical distribution of the *Late* species DACEXC remained unchanged during the 25-year post-hurricane study (Figure 5e). The palm PREMON was more abundant in valley plots (Figure 5g) before the hurricane and increased its proportional abundance in valley plots as time after the hurricane increased. The proportion of PREMON in valley plots is significantly higher than slope plots ($p = 0.0011$) and ridge plots ($p = 0.0091$). Further, palms recruited and maintained a significant abundance in all the topographical settings and an increase in proportion of palms relative to all stems was recorded in every census up to 25 years after the hurricane (Figure 5g).

4. Discussion

4.1. Patterns of Forest Structure following a Hurricane Disturbance

Changes in recruitment, growth, and mortality through time explain Hurricane Hugo's long-term effects on the forest structure and composition. Variation in the immediate mortality among PFTs and among stem sizes resulted in an immediate change of forest size structure and species composition. The variation in diameter growth and recruitment with time resulted in a shift in size structure as the forest recovered. Before Hurricane Hugo, the forest at Bisley was dominated by *Late* PFT with diameters less than 10 cm (Figure 6). Because *Early* had the highest mortality and *Palm* had the lowest mortality among the four PFTs during the hurricane disturbance, *Early* PFT decreased in abundance right after the hurricane, while *Palm* increased its proportion in the forest. As smaller stems had higher immediate mortality, the size structure of the forest shifted from being dominated by small stems (2.5–5 cm) to a uniformly distributed size structure immediately post hurricane (Figure 6). In an experimental manipulative study of hurricane effects, Shiels et al. [3] found that forest responses to hurricane effects were driven by changes in the canopy structure and openness of the canopy, more than from fallen hurricane debris. In our study, when the canopy opened due to the disturbance, both *Early* and *Palm* had higher recruitment than mortality, which resulted in increases in their abundance five years after the disturbance. Twenty years after the hurricane disturbance, the forest was again dominated by *Late* PFT with diameters less than 10 cm, which may be the beginning of the self-thinning stage until it is interrupted by the next disturbance [56,57]. These changes in PFT abundances have been documented in other tropical forests in response to changes in climate [58]. In our study system, the response to changes in the post-disturbance abiotic environment, inherently altered forest composition which in turn lead to concomitant changes in forest structure. Despite these shifts, the proportion of larger stems from the *Late* PFT did not change significantly throughout the 25-year study period. The maintenance of "non-pioneer" or *Late* PFT is associated to their documented post-hurricane resistance responses including resprouting or direct regeneration [57,59,60].
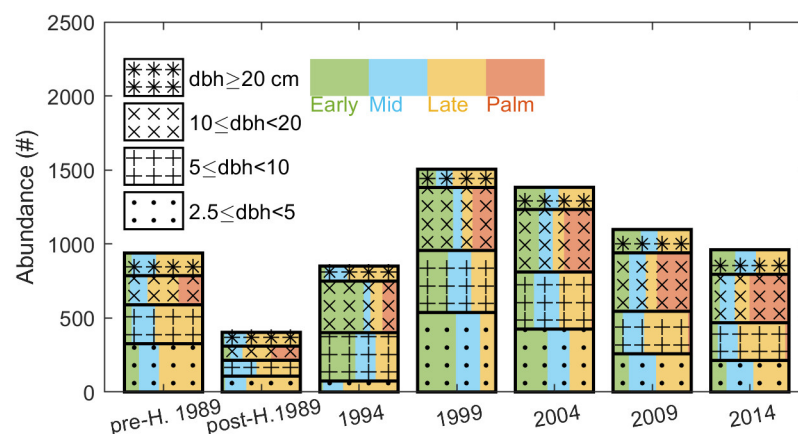
Figure 6. Bar chart of stem abundance (#) in each census at Bisley Experimental Watersheds, Luquillo, Puerto Rico. The stem abundance is calculated as the total number of stems in the 85 plots that were established in pre-Hugo 1989. For each census along the horizontal axis, the stem abundance is composed of four diameter (DBH) classes identified by the stacked bar pattern fills, and within those are the four plant functional types (PFTs) represented in colors.

4.2. Composition Dynamics of Dominant Species and Plant Functional Types

Changes in subsequent mortality and recruitment among the PFTs resulted in further shifts of species composition in the forest. As the canopy closed with progression of successional trajectories after the hurricane disturbance, the mortality rate of all PFTs increased. This brought compositional change, as mortality rates of *Early* and *Mid* PFTs exceeded their recruitment rates. Meanwhile the consistently lower mortality and higher

recruitment of *Palm* resulted in making it the most dominant species during the post-hurricane successional trajectory, as palms increased in all topographic settings (ridge, slope, valley) in the forest, and tolerated shade under a closing canopy which contributed to their low subsequent/background mortality. The resistant and resilient characteristics of palms favored their dominance in the successional post-hurricane forest, and this is reflected in their distribution in the steep, sloped and rugged montane terrain [4,54,61]. Twenty years after the disturbance (in 2009), mortality rates of *Late* and *Palm* began to exceed their recruitment rates, which decreased their relative total abundance in the forest.

Although there was an increase in *Palm* during post-hurricane succession, it occurred within the established hierarchical dominance of the same species that consistently remained the most abundant in the forest during the 25-year period of documented succession. The *Late* PFT species–*D. excelsa* and *S. berteriana*–are characteristic species that define the vegetation association of this forest type [24], and they maintained proportional dominance along with the increase in palm abundance. Burslem et al. [17] also found that over a 30-year period, there was a constancy of the most abundant species after a hurricane disturbance. The observed heterogeneity of species composition and shift in abundances of the dominant species at the study site may respond to changes in the forest environment during succession. Changes in forest climate and abiotic environment, similar to those observed in post-hurricane canopy and associated understory light conditions, have been identified as drivers of change in PFT successional patterns [62]. Local topographical variation in tropical forests has been known to mediate structure and composition [63,64], and also play a role in the effects from disturbances such as hurricanes and climatic conditions [14,38,65,66].

4.3. Concluding Remarks

In this study, we linked the changes in structure and composition of the forest with the changes in demographic components (i.e., recruitment, growth, and mortality). We showed that the structural and compositional change in the first 5–10 years after the disturbance were due to the high recruitment of *Early* successional species, which leads to compositional change where *Early* PFT dominates, and to structural change where small stems dominate the forest. During succession, mortality increases with time due to canopy closing, which is mostly from new recruits, leading to the forest thinning and structural change to a median-size dominated forest. The growth rate decreases with time, making the basal area and aboveground biomass accumulation slow. Even though the biomass and basal area are reaching steady state, the structure and composition are still changing with different recruitment and mortality rates among different PFTs. Throughout the 25 years of this study, *Early* PFT consistently maintained the highest mortality and *Palm* had the lowest. The low hurricane-induced mortality, high recruitment rate, and low subsequent mortality of palms explain their increased abundance in the forest after the hurricane disturbance and during the following decades. Palms have demonstrated resistance and resilience to hurricane disturbance [4,61,67], and are likely to maintain their high abundance in the forest with frequent hurricane disturbances in the future, unless density dependent mortality sets in as with the effect of pathogens [68].

A warming climate will probably lead to increased intensity and frequency of hurricanes that make landfall [21,22]. In fact, before the forest could fully recover after Hurricane Hugo, the successional trajectory of the forest was reset by two subsequent hurricanes, Irma and María, in 2017. The way forests respond to future disturbances will be affected by the size structure and species composition [20], which are continually changing in response to past disturbances [6,38,69]. Tropical forests worldwide continue to be important carbon sinks and contribute to climate change mitigation [70]. Therefore, enhancing knowledge about tropical forest structural and compositional responses to hurricane disturbances under a changing climate is fundamental to understanding their future outcomes and their complex role in the global carbon balance [71–75].

Institutional Review Board Statement: Not applicable.

Informed Consent Statement: Not applicable.

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