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Demographic trade-offs and functional shifts in a hurricane-impacted tropical forest

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- **Background and Aims:** Understanding shifts in the demographic and functional composition of forests after major natural disturbances has become increasingly relevant given the accelerating rates of climate change and elevated frequency of natural disturbances. Although plant demographic strategies are often described across a slow–fast continuum, severe and frequent disturbance events influencing demographic processes may alter the demographic trade-offs and the functional composition of forests. We examined demographic trade-offs and the shifts in functional traits in a hurricane-disturbed forest using long-term data from the Luquillo Forest Dynamics Plot (LFPD) in Puerto Rico.
- **Methods:** We analysed information on growth, survival, seed rain and seedling recruitment for 30 woody species in the LFDP. In addition, we compiled data on leaf, seed and wood functional traits that capture the main ecological strategies for plants. We used this information to identify the main axes of demographic variation for this forest community and evaluate shifts in community-weighted means for traits from 2000 to 2016.
- **Key Results:** The previously identified growth–survival trade-off was not observed. Instead, we identified a fecundity–growth trade-off and an axis representing seedling-to-adult survival. Both axes formed dimensions independent of resprouting ability. Also, changes in tree species composition during the post-hurricane period reflected a directional shift from seedling and tree communities dominated by acquisitive towards conservative leaf economics traits and large seed mass. Wood specific gravity, however, did not show significant directional changes over time.
- **Conclusions:** Our study demonstrates that tree demographic strategies coping with frequent storms and hurricane disturbances deviate from strategies typically observed in undisturbed forests, yet the shifts in functional composition still conform to the expected changes from acquisitive to conservative resource-uptake strategies expected over succession. In the face of increased rates of natural and anthropogenic disturbance in tropical regions, our results anticipate shifts in species demographic trade-offs and different functional dimensions.

Key words: Functional traits, LFDP Puerto Rico, seedling recruitment, seed rain, tree growth, tree survival.

INTRODUCTION

As the coverage of disturbed tropical forests grows rapidly (IPCC, 2022) and model projections forecast continued increases in the severity and frequency of disturbance events in the years to come (Altman *et al.*, 2018; Kossin *et al.*, 2020), an important challenge in ecology is to understand the effects of disturbance on forest communities and their recovery (Chazdon, 2003). Many forests worldwide have been subjected to intense anthropogenic activities and have also experienced natural disturbances due to hurricanes and tropical storms (Zimmerman *et al.*, 1994; Foster *et al.*, 1999; Thompson *et al.*, 2002; Bradford *et al.*, 2014). Regimes of frequent disturbances increase the spatial and temporal heterogeneity of resources for trees, which then influence tree demography, phenotypic diversity and species community composition (Loehle, 2000). Identifying the demographic and functional strategies that characterize frequently disturbed forests is necessary to anticipate shifts in communities subject to the predicted increase in disturbance events.

Plant demographic strategies are generally organized along a slow–fast continuum, in which plant growth trades off with survival, such that species with slow growth rates typically show higher survival rates, and species that grow fast have lower survival rates (Hubbell and Foster, 1992; Wright *et al.*, 2010; Salguero-Gómez *et al.*, 2016; Rüger *et al.*, 2018). However, previous studies have questioned the generality of this slow–fast spectrum by showing that the growth–survival trade-off weakens in disturbance-prone forests and suggest that frequent disturbance events may operate as an important selecting force, modifying the demographic strategies of communities (Bellingham *et al.*, 1995; Batista and Platt, 2003; Russo *et al.*, 2021; Kambach *et al.*, 2022). Disturbance events can directly affect populations and communities through increased tree damage and mortality (Walker, 1991; Bellingham *et al.*, 1995; Uriarte *et al.*, 2019). In some cases, severely injured trees may be unable to recover, so their performance (growth rate and reproduction) would decrease over time until death (Walker, 1995; Uriarte *et al.*, 2004; Tanner *et al.*, 2014; Yap *et al.*, 2016). Yet high tree mortality might be accompanied by high seedling recruitment rates that may eventually compensate for the tree loss, as was shown for a forest in the Solomon Islands after a cyclone (Burslem *et al.*, 2000). In other cases, less-damaged remnant trees may resprout and take advantage of the abundance of temporarily available resources, such as light and nutrients, that typically occur after disturbance, contributing to increased growth and survival (Walker, 1991; Whigham *et al.*, 1991; Yih *et al.*, 1991; Bellingham *et al.*, 2000). For example, tree crown damage and green leaf fall during a hurricane create high light conditions within the forest and increase soil nutrients through litter deposition, which temporarily boosts the growth and reproduction of many species (Lodge *et al.*, 1991, 1994; Whigham *et al.*, 1991). Frequent disturbance events, then, can generate severe damage and temporary high-resource conditions that alter not only species' growth and survival but also reproductive patterns (Comita *et al.*, 2009; Uriarte *et al.*, 2012).

The characterization of forest species demography is complex, as diameter growth and survival probability tend to be size-dependent (Stephenson *et al.*, 2014; Johnson *et al.*, 2018). This size-dependent demographic variation may ultimately contribute to changes such as rank reversals of species in demographic rates over trees' life cycles. Rank reversals occur when demographic characteristics for a given species switch over life stages, making it difficult to disentangle the contribution of these processes to forest dynamics (Lusk, 2004; Baraloto *et al.*, 2005; Pérez-Ramos *et al.*, 2012; Chen *et al.*, 2018). For instance, Lasky *et al.* (2015) showed that at the seedling stage, species with short stature and small seed mass had greater survival, but this relationship was reversed for adult trees in a hurricane-disturbed forest in Puerto Rico. This rank reversal is likely the manifestation of regeneration niches (Grubb, 1977), where, after the occurrence of a disturbance, shade-intolerant tree species (those with short stature and small seed mass that require full access to light when establishing) have a survival and growth advantage over shade-tolerant species (those that can prevail under shade). Explicitly accounting for potential changes in demographic rates over plants' life cycles fosters understanding and the potential to predict forest recovery after major disturbances.

As disturbed forests typically undergo rapid changes in species composition and diversity through succession and recovery, the predominance of certain trait values in the forest community should also change in response to disturbance (McGill *et al.*, 2006). Functional traits mediate the species' responses to their environment and are key to determining species' success during community assembly after hurricanes (Paz *et al.*, 2018). Species can follow a shade-intolerant and shade-tolerant strategy to deal with light intensity, which is crucial to explain the succession dynamics of a forest, with pioneer shade-intolerant species prevailing after disturbance and shade-tolerant species prevailing once the canopy has closed (Brokaw, 1987; Finegan, 1996; Hubbell *et al.*, 1999). Yet shade-tolerance to -intolerance strategies have been linked to a wide range of functional traits, including specific leaf area, wood density and seed mass (Zimmerman *et al.*, 1994; Wright *et al.*, 2010), that typically represent independent functional dimensions. For example, leaf economics traits (Wright *et al.*, 2004), such as specific leaf area and leaf nitrogen content, are often organized into a functional dimension different from wood density and seed mass (Díaz *et al.*, 2016). It remains unknown whether hurricanes and forest recovery may still drive consistent changes across different trait dimensions.

In this study, we sought to identify the demographic trade-offs that characterize a hurricane-prone tropical forest and the changes in community-wide functional composition following a hurricane disturbance. The study period encompassed the post-hurricane disturbance phase after the impact of a major hurricane, Hurricane Georges, in September 1998 (category 3) on Puerto Rico but before Hurricanes Irma and María (category 4) in 2017. We compiled growth, survival, recruitment and seed production information for 30 woody species representing more than 50 000 individuals, including adults and seedlings (Table 1). We integrated this information with functional traits that capture key resource and reproductive strategies for the forest community. Our specific questions were: (1) What demographic processes characterize communities in a forest repeatedly damaged by tropical storms and hurricanes? (2) How does community trait composition change during the post-hurricane period of forest recovery?

MATERIALS AND METHODS

Study site

The study used data from the 16-ha Luquillo Forest Dynamics Plot (LFDP) (18°20′°N, 65°49′°W) located in the Luquillo Experimental Forest (LEF) in north-eastern Puerto Rico. This site is part of the ForestGEO network and the Luquillo Long-Term Ecological Research (LTER) Program. According to the Holdridge life-zone system, the forest is classified as subtropical wet with a mean annual rainfall of 3500 mm and a range of elevation from 333 to 428 m.a.s.l. (Ewel and Whitmore, 1973; Thompson *et al.*, 2002). The soil is formed from volcanoclastic rock and the palm *Prestoea acuminata* var. *montana* and the tabonuco tree (*Dacryodes excelsa*, Burseraceae) are the most abundant species (Thompson *et al.*, 2002).

The forest has experienced both anthropogenic and natural disturbances. The north part of the LFDP was logged or used for coffee and kitchen gardens with fruit trees that were abandoned by 1934, while minimal selective logging occurred in the southern portion of the LFPD between 1937 and 1953 (Thompson *et al.*, 2002). In addition, heavy tropical storms and hurricanes have frequently impacted the forest. After the forest tract was purchased in 1934 and anthropogenic disturbances ceased (Thompson *et al.*, 2002), three major hurricanes have affected the forest area since the establishment of the LFDP: Hurricane Hugo (1989, category 3), Hurricane Georges (1998, category 3), and Hurricanes Irma and María

Table 1. *Species list and abundance for seedlings and trees for 2000 and 2016. Seedling abundance was calculated as the sum of free-standing individuals across 150 plots of 2 × 1 m^2. Total tree abundance was calculated as the sum of individuals of each of the focal 30 species in the 16-ha LFDP*

Code	Species	Family	Tree abundance		Seedling abundance	
			2000	2016	2000	2016
ALCLAT	*Alchornea latifolia*	Euphorbiaceae	541	165	87	2
BYRSPI	*Byrsonima spicata*	Malpighiaceae	474	255	89	6
CASARB	*Casearia arborea*	Salicaceae	4167	2651	45	29
CASSYL	*Casearia sylvestris*	Salicaceae	1721	770	13	9
CECSCH	*Cecropia schreberiana*	Urticaceae	3011	839	11	1
CORBOR	*Cordia borinquensis*	Boraginaceae	1070	358	14	8
DACEXC	*Dacryodes excelsa*	Burseraceae	1559	1432	49	276
DRYGLA	*Drypetes glauca*	Putranjivaceae	296	143	1	3
EUGSTA	*Eugenia stahlii*	Myrtaceae	569	279	10	11
FAROCC	*Faramea occidentalis*	Rubiaceae	363	352	6	31
GUAGLA	*Guarea glabra*	Meliaceae	340	110	10	1
GUAGUI	*Guarea guidonia*	Meliaceae	521	362	1238	512
HIRRUG	*Hirtella rugosa*	Chrysobalanaceae	816	667	18	22
HOMRAC	*Homalium racemosum*	Salicaceae	242	175	26	23
INGLAU	*Inga laurina*	Fabaceae	1308	844	357	362
IXOFER	*Ixora ferrea*	Rubiaceae	273	176	44	32
MANBID	*Manilkara bidentata*	Sapotaceae	1796	1740	73	34
MATDOM	*Matayba domingensis*	Sapindaceae	252	163	47	23
MICPRA	*Miconia prasina*	Melastomataceae	1343	235	4	1
MYRDEF	*Myrcia deflexa*	Myrtaceae	482	283	5	10
MYRLEP	*Myrcia leptoclada*	Myrtaceae	203	209	10	28
MYRSPL	*Myrcia splendens*	Myrtaceae	329	158	22	3
OCOLEU	*Ocotea leucoxylon*	Lauraceae	861	410	86	154
PSYBER	*Psychotria berteroana*	Rubiaceae	11 587	548	287	8
PSYBRA	*Psychotria brachiata*	Rubiaceae	3251	194	106	27
SCHMOR	*Schefflera morototoni*	Araliaceae	3090	760	108	11
SLOBER	*Sloanea berteroana*	Elaeocarpaceae	3350	2438	51	14
TABHET	*Tabebuia heterophylla*	Bignoniaceae	745	294	144	31
TETBAL	*Tetragastris balsamifera*	Burseraceae	604	547	30	92
TRIPAL	*Trichilia pallida*	Meliaceae	750	455	80	48
Total			**45 914**	**18 012**	**3071**	**1812**

(2017, Maria category 4) (Hurricane Irma did not make landfall in Puerto Rico but its winds affected the LFDP) (Foster *et al.*, 1999; Uriarte *et al.*, 2019). This study focused on the post-hurricane period after Hurricane Georges (1998), between 2000 and 2016, and before the impact of Hurricanes Irma and Maria.

Seed production and census data

We compiled information on tree and seedling censuses and seed production for woody tree and shrub species of the LFDP.

Seed production. We calculated the mean seed production per species for nine years from 2007 to 2016 using the phenology dataset that contains information on seed rain into 120 0.5-m^2 traps set at 1 m above the ground located at regular intervals along the main trail through the LFDP (Muscarella *et al.*, 2013). All seeds were collected every 2 weeks for each trap, identified to species, and counted. We calculated the mean flux of seeds arriving (seeds per year per m^2 of trap area) as the mean density of seeds per basal area of trees per area of the 16-ha LFDP (density, m^2 of reproductive basal area per m^2 of plot area) (following Visser *et al.*, 2016). To calculate tree basal area, we used the census of trees recorded in 2011 because that was the only census that took place during the period used for estimating seed production: 2007–16 (see below for the description of tree census data).

Seedling censuses. Data from 150 seedling plots (2 × 1 m) were used to assess seedling dynamics. The plots were located at the centre of each 20 × 20 m LFDP subplot along 500-m south–north transects with plots separated by 60 m (Comita *et al.*, 2009). These seedling plots were established across the LFDP in March 1999, 6 months after Hurricane Georges, when the seedlings were counted. From 2000 all seedlings at least 10 cm tall and with a diameter <1 cm at 1.3 m from the ground were tagged, mapped within the seedling plot, identified to species, and measured for total height and root collar diameter. We used data from complete seedling censuses in 2000, 2004, and every year from 2007 to 2016.

Seedling recruits. We calculated the species-specific mean recruitment (from seed to seedling) as the mean of newly recruited seedlings per year per m^2. We used data from the 150 2 × 1 m plots censused in 2000, 2004 and every year from 2007 to 2016 and scaled the recruitment value to the average basal area of trees from the whole 16 ha of the LFDP from the tree censuses (see below) conducted in 2000, 2005, 2011 and 2016 (following Rüger *et al.*, 2018).

Tree censuses. At ~5-year intervals since 1990, all the free-standing woody stems ≥1 cm in diameter at breast height (dbh, at 1.3 m from the ground) within the LFDP have been tagged, mapped and identified to species and diameter has been measured within the LFDP (Thompson *et al.*, 2002). We used tree census intervals from 2000, 2005, 2011 and 2016 that encompass the study period for this study after Hurricane Georges (1998) and before Hurricanes Irma and Maria (2017) and corresponding to the same period as the seedling census data. Across censuses, a total of 145 species of 47 families have been identified. These census datasets are referred to as the tree data.

Trait data

Seven functional traits were collected for the tree species present in the LFDP (Swenson *et al.*, 2012; Umaña *et al.*, 2016). These traits included leaf area (LA, cm^2), leaf C content (LC, %), leaf N content (LN, %), leaf P content (LP, %), seed mass (SM, g), specific leaf area (SLA, cm^2 g^{-1}) and wood specific gravity (WSG, g cm^{-3}). The data were collected using standardized protocols to measure functional traits (Cornelissen *et al.*, 2003; Swenson and Enquist, 2008) using 25 individuals for leaf traits and ten individuals for wood-specific gravity. While we also have seedling trait data, these data are only available for a subset of traits (LA, SLA and leaf thickness) and fewer species (23 species). To check for consistency between adult and seedling datasets, we performed the analyses for seedling communities (see below) using seedling traits. The seedling and adult trait data results were largely consistent (Supplementary Data Fig. S1). Also, previous studies have shown that both datasets (adult and seedling traits) are strongly correlated for this forest community (Umaña *et al.*, 2016). Thus, we opted for using the adult trait data for all the functional trait analyses. To reduce redundancy among traits, we performed a principal component analysis (PCA) and selected the first three principal components (PCs), which explained 63.37 % of the variation (Supplementary Data Fig. S2 and Table S1). For the PCA, we scaled all traits and log-transformed LA, SLA and SM before the analysis to reduce the skewness of the data. The first axis represents the well-known leaf economics spectrum (LES), with positive values representing more acquisitive species (referred to as the LES–PC axis), the second axis loaded positively for LA and SM, and the third axis loaded positively for LC (Supplementary Data Fig. S2).

Analyses

Our analyses consisted of two main steps: (1) identification of demographic dimensions for tree species in the LFDP; and (2) examining shifts in community functional composition over the post-hurricane study period. All analyses were carried out in R (R Development Core Team, 2017).

Step 1. To characterize the demographic rates for tree species in the LFDP, we first identified the variation in survival of seedlings, and survival and growth of trees. We opted not to use seedling growth data because seedling height and basal diameter growth are subject to observation error due to variation in the depth of the litter layer and frequent stem breakage (Comita *et al.*, 2009; Lasky *et al.*, 2015). To obtain robust estimates for these demographic processes, we focused our analysis on species with at least 200 adult individuals (30 species) but excluded palms as it does not show diameter growth (Table 1).

For seedlings, we fitted a linear model for survival that accounted for the variation in seedling height using all seedling censuses available (for further details see Supplementary Data Methods S1 and Figs S3–S5). For trees, we fitted size-dependent survival models to each species following Needham *et al.* (2018, 2022) for each census interval and averaged the demographic parameter estimates across all census intervals (for further details see Supplementary Data Methods S1, Table S2 and Figs S6 and S7). Growth rates were estimated following Needham *et al.* (2018, 2022) by dividing each species into the fastest-growing 5 % of individuals and the slowest-growing 95 % of individuals and fitting gamma distributions to each group (Supplementary Data Methods S1, Table S2 and Figs S6 and S7). From these calculations, for each species we obtained demographic parameter estimates that represent key life-history characteristics of seedlings and trees: seedling survival, maximum survival, juvenile survival (survival at 10 mm dbh), maximum tree size or stature (evaluated as maximum dbh), and slow and fastest growth for trees (Supplementary Data Fig. S6 and Table S3). The demographic parameters were estimated for each of the census intervals. These demographic parameter estimates were not significantly different across censuses (Supplementary Data Fig. S6); therefore, the values were averaged across all census intervals at the species level. These demographic parameter estimates for each species were posteriorly combined with the fecundity data (seed production and seedling recruitment; see above) in a PCA to define the main axes of demographic variation. For the PCA, we scaled all variables, log-transformed seedling recruitment and seed production variables to reduce skewness and retained the orthogonal demographic axes that explained at least 80 % of the total variation in tree demography. To assess the robustness of our results, we performed two additional PCAs using the parameters estimated from the first (2000) and the last (2016) census separately.

Step 2. To examine how functional community composition had changed after disturbance (after Hurricane Georges) (question 2), we first calculated community-weighted means (CWMs) for individual and multivariate functional traits using species abundance data from the initial (2000) and the final (2016) censuses of seedlings and trees. That is, we weighted the position of species along each trait and PC axis by their abundance in each census (2000 or 2016) to calculate the community means. The CWM for seedlings was calculated at the 1 × 2 m scale and for trees at the 20 × 20 m LFDP subplot scale. Next, we separately calculated the change in CWM between the 2000 and 2016 censuses for seedlings and trees by subtracting the CWM values in 2000 from the CWM in 2016. We assessed if these changes were significant using bootstrap by randomly selecting CWM values 999 times with replacement within each group (seedlings or trees). If the 95 % confidence intervals of bootstrapped values included zero, the value was considered not significant.

RESULTS

Overview

We analysed demographic and functional data for 30 tree species (Table 1). In 2000, 45 914 free-standing trees of these 30 species with dbh ≥1 cm were alive, while in 2016, 18 493 were alive, and from these a total of 15 357 trees survived from 2000 to 2016 (Table 1). For seedlings, a total of 3071 individuals were recorded in 2000, while by 2016 the total number of alive seedlings had decreased to 1812, and from these only 105 seedlings survived from 2000 to 2016 (Table 1).

Demographic axes

We retained the two first axes of the demographic PCA, which together explained 83 % of the demographic variation in LFDP tree species (Fig. 1, Supplementary Data Table S4). The variation in parameter estimates across censuses was not significant (Supplementary Data Figs S3–S7), and these identified axes were the same as when using parameter estimates obtained by using only the first or last census intervals (Supplementary Data Fig. S8). The first demographic axis explained 59 % of the demographic variation and represented the variation between fecundity and growth + stature, with negative values of this axis indicating short-stature species with slow growth and high fecundity (combined high seed production and high seedling recruitment) and the opposite for positive values (hereafter referred to as the fecundity–growth axis, F–G). The second demographic axis explained 25 % of the demographic variation and was positively loaded for seedling survival, juvenile survival and maximum adult survival (hereafter referred to as the survival axis, S).

Changes in community-wide functional composition

We examined changes in trait CWM over the post-disturbance study period from 2000 to 2016 after Hurricane Georges (1998). Over time, the functional community composition changed consistently for seedlings and trees towards species with larger seeds and conservative leaf economic trait values (Fig. 2, LN, SLA, LES–PC1). While we detected significant changes in other traits (LA, LC, WSG), these changes were not consistent for communities of both seedlings and trees. We also found that the trend was stronger for multivariate traits (e.g. LES–PC1) than for univariate leaf economics traits (e.g. LN, LP, SLA).

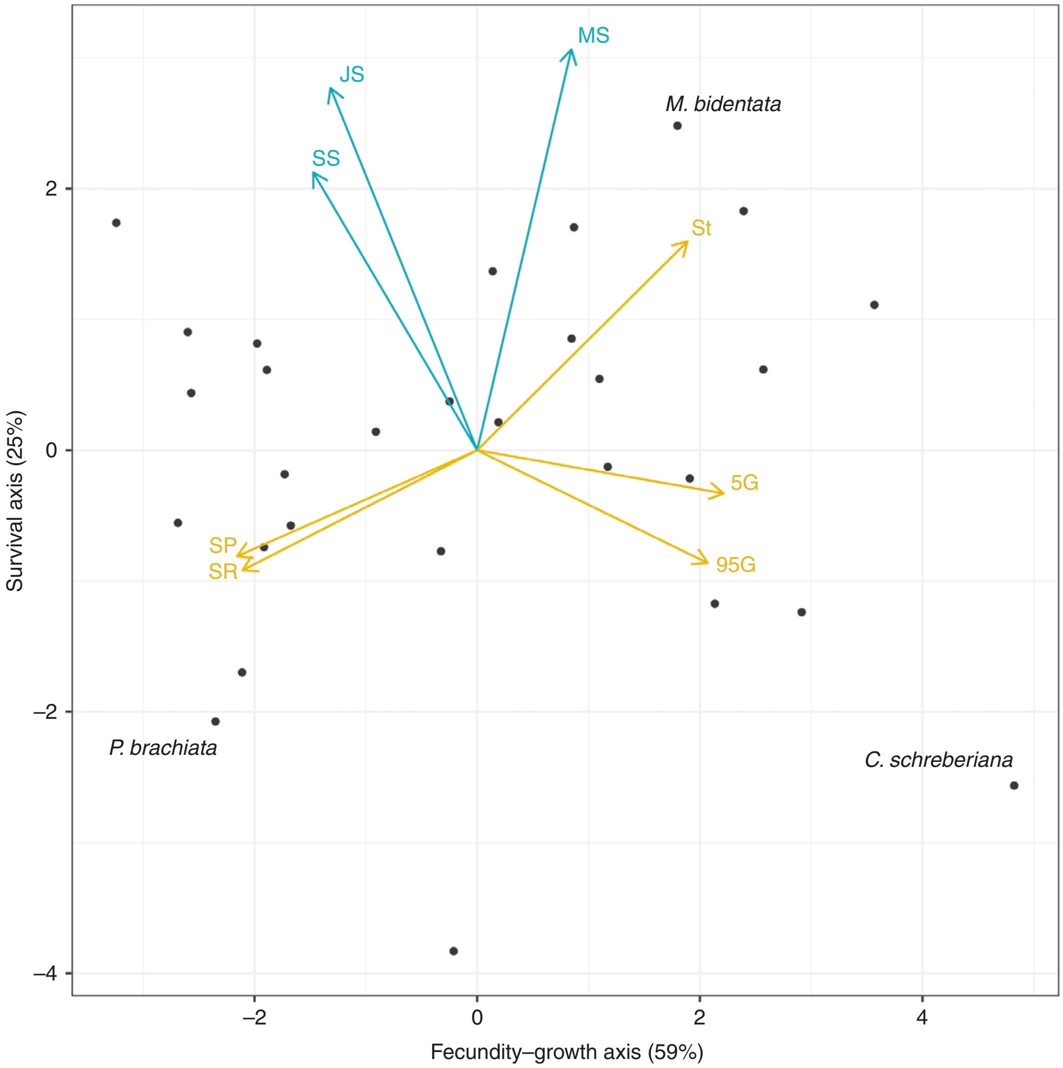
DISCUSSION

Identifying demographic strategies and changes in community-level functional traits after hurricane disturbance is necessary to understand mechanisms that promote diversity and predict the fate of frequently perturbed forest systems (Vandermeer *et al.*, 2000; Tanner *et al.*, 2014), especially when an increasing rate of disturbances is predicted (Balaguru *et al.*, 2018; Kossin *et al.*, 2020). Here we show that the demographic strategies of tree species from a disturbance-prone forest do not conform to the well-known growth–survival trade-off found in old-growth forests. Instead, we evidenced a fecundity–growth trade-off and an independent survival axis that promoted shifts in functional traits over time from acquisitive to conservative strategies following typical trends of forest succession.

A fecundity growth trade-off and a survival axis characterizing a disturbance-prone forest

The trade-off between fecundity and growth (and stature) (F–G) describes the range of demographic strategies where in one extreme species are typically represented by small shrubs that have minimal diameter growth but produce many seeds (e.g. *Psychotria brachiata*, Rubiaceae), while at the other extreme species are represented by pioneer species that grow fast, but have lower seed production and seedling recruitment on average (*Cecropia schreberiana*, Urticaceae). Our interpretation is that this axis has likely been shaped by the action of frequent and severe disturbance events (i.e. hurricanes) and represents diversification in demographic strategies relevant to forest communities that have prolonged stages of early succession. For example, after disturbance, high light levels select for fast-growing species with limited seed production but, simultaneously, high-recruitment species with slower growth can do well in shaded areas less affected by the hurricane (Uriarte *et al.*, 2012). Given the predicted increase in frequency and intensity of hurricanes worldwide (Kossin *et al.*, 2020) and the elevated rates at which secondary forests are replacing old-growth forests, it would be important to examine if the results obtained in this study could be extended to other frequently disturbed forests.

Disturbance may also act as a selecting force by modifying tree survival rates and contributing to decoupling survival and growth. For example, the boost of resources (e.g. light and soil nutrients) generated by the hurricane enables fast-growing species, which typically have low survival rates, to prolong their life via resprouting or rapid repair. The ability of trees to sprout is known as an adaptive strategy to deal with different types of disturbance (Bond and Midgley, 2001; Del Tredici, 2001; Vesk and Westoby, 2004; Mårell *et al.*, 2018) and previous studies



Variable	PC1	PC2
MS: maximum survival	0.17	**0.59**
JS: juvenile survival	–0.26	**0.54**
St: maximum stature	**0.37**	0.31
95G: 95% slowest tree growth	**0.40**	–0.17
5G: 95% fastest tree growth	**0.43**	–0.07
SR: log(mean seedling recruitment)	**–0.41**	–0.18
SP: log(mean seed rain)	**–0.42**	–0.16
SS: mean seedling survival at average neighbourhood density	–0.28	**0.41**

Fig. 1. Demographic dimensions for 30 tropical tree species in Puerto Rico. The first axis (fecundity–growth axis) explains 59 % of the variation and represents the trade-off between fecundity and growth. The second axis (survival axis) explains 25 % of the variation and represents the variation in survival for seedlings and trees. The vectors indicate the direction and strength of the correlations between the demographic variables and the multivariate axes. Vectors in yellow are associated with the fecundity–growth axis, and vectors in blue are associated with the survival axis. The loadings for each variable can be found in the table included in the figure.

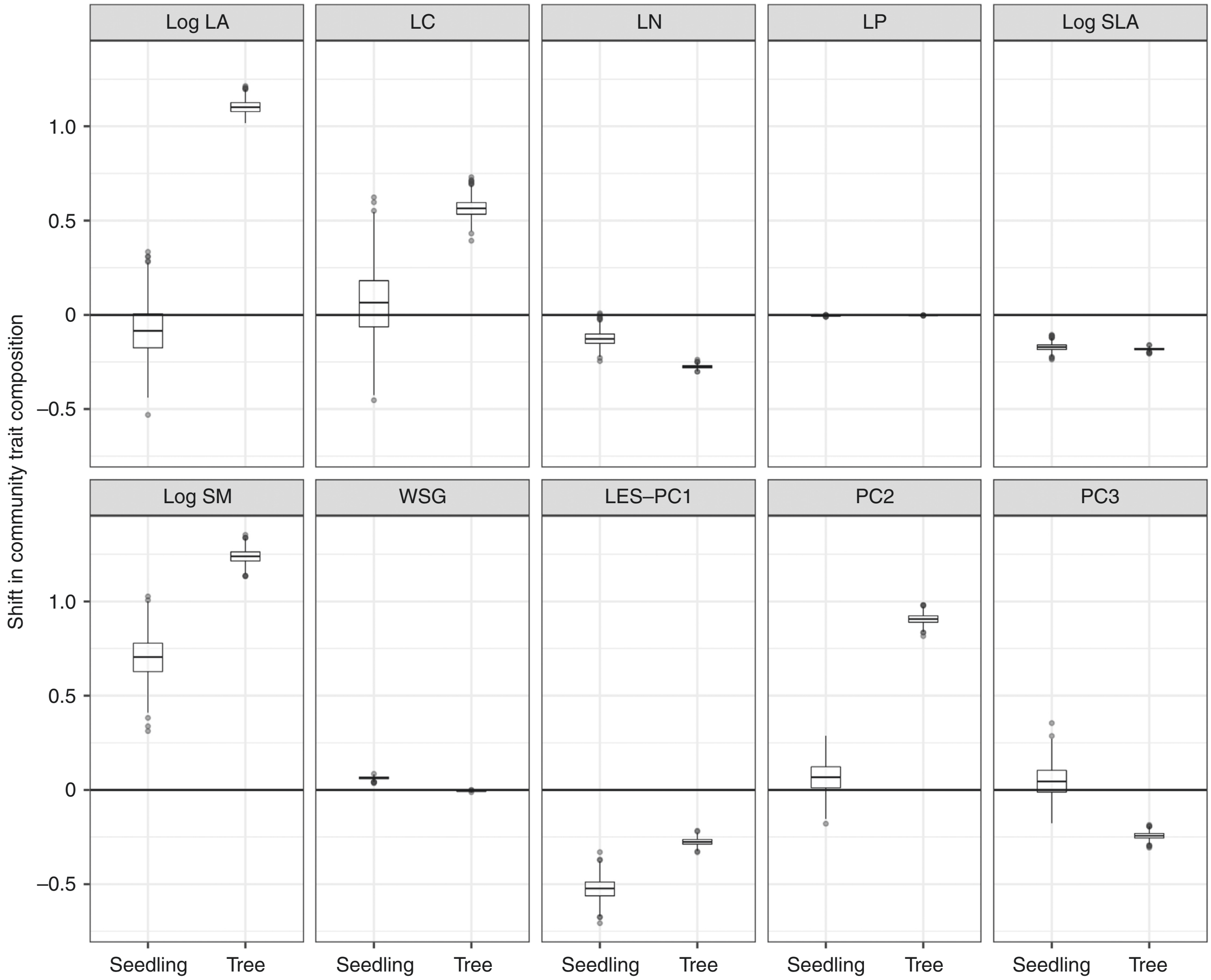


FIG. 2. Shifts in community functional composition for seedlings and trees during the recovery process after Hurricane Georges (2000–16). Positive values indicate that communities are shifting towards positive values of a given trait while negative values indicate the opposite. LA, leaf area (cm^2); LC, leaf C content (%); LN, leaf N content (%); LP, leaf P content (%); SM, seed mass (g); SLA, specific leaf area ($cm^2\ g^{-1}$); WSG, wood specific gravity ($g\ cm^{-3}$). PC1 represents the leaf economics spectrum (LES), where positive values represent more acquisitive strategies and negative values represent more conservative strategies. PC2 is loaded positively for LA and SM and PC3 is loaded positively for LC. Boxes represent the interquartile range (the range between the 25th and 75th percentile) The upper and lower whiskers represent scores outside the middle 50%.

suggest that sprouting plays a key role in determining life-history trade-offs in hurricane-impacted forests (Bellingham *et al.*, 1994, 2000; Uriarte *et al.*, 2012). We examined the relationship between resprouting ability (evaluated as the mean proportion of stems that sprout per species across all censuses) and the rest of the demographic variables and found that resprouting forms a third dimension independent of the other two axes identified (F–G and S) (Supplementary Data Figs S9 and S10). This result suggests that resprouting could be maximized independently of the other demographic variables examined.

Similarly, the weakening of the relationship between growth and survival may also result from the increased growth rates of species that typically show slow growth (and high survival) but that, due to the boost of resources post-hurricane, could increase their growth (Zimmerman *et al.*, 1994; Yap *et al.*, 2016; Hogan *et al.*, 2018; Zuleta *et al.*, 2022). This appears to be the case for *Manilkara bidentata* (Sapotaceae), which, in our study, showed a combination of fast growth and high survival rates during the study period (Fig. 1). However, we should also note that growth and survival for seedlings and juveniles were still significantly correlated (Supplementary Data Fig. S11), suggesting that although the slow–fast continuum was not identified as a dominant axis of demographic variation, it may still operate at particular life stages (Needham *et al.*, 2022).

In addition to the major role of hurricanes shaping the structure and the dynamics of forest communities, the legacy effects of the land-use history and additional extreme climatic events impacting this forest (e.g. droughts) likely contributed to the tree demography patterns reported in this study (Beard *et al.*, 2005). Previous studies along an elevational gradient in the Luquillo forest have shown that severe droughts in this forest may have adverse effects on growth for several years, influencing the responses of trees to upcoming extreme events (Umaña and Arellano, 2021). Also, increased tree mortality linked to severe droughts has been reported for other tropical forests (Phillips *et al.*, 2009; Lewis *et al.*, 2011; Powers *et al.*, 2020), indicating that, in addition to hurricanes, other types of climatic extremes may modify the demographic characteristics of forests. The alteration in demographic trade-offs likely responds to the cumulative effect of multiple stresses, and we might anticipate changes in the demographic patterns of forest communities in the light of future climatic changes.

Community composition showed a consistent shift in leaf and seed traits post-hurricane but not in wood specific gravity

Species community composition shifted from being characterized by small-seeded species with efficient carbon-use strategies to communities with large-seeded species with conservative carbon strategies (Fig. 2). A similar shift in functional composition has been found in other tropical communities undergoing succession (Subedi *et al.*, 2019) and in this Luquillo forest over a shorter period (2000–05) (Swenson *et al.*, 2012), reflecting the important role of shifts in resource availability changes during the recovery process (Grubb, 1977; Bazzaz and Pickett, 1980; Shiels *et al.*, 2010; Shiels and González, 2014). These functional changes reflected a general trend from acquisitive to conservative resource use strategies and were captured by two independent functional dimensions – leaf and seed traits. The shift in leaf traits is likely responding to light changes during the recovery process (Grubb, 1977; Bazzaz and Pickett, 1980), where canopy opening post-disturbance favours carbon-use-efficient species that are subsequently replaced by more shade-tolerant species as recovery progresses (Walker, 1991). The advantage of small-seeded species during early stages of recovery is likely related to the prominent role of seed banks for pioneer species (Dupuy and Chazdon, 1998) that have shown successful recruitment in disturbed communities (Brokaw, 1998; Burslem *et al.*, 2000; Lomascolo and Aide, 2001). Wood specific gravity, however, did not show a significant trend in our field site, despite previous studies having reported a shift from light- to hard-wooded species over succession. The trends for WSG in the context of hurricane disturbance have received mixed support as, on one hand high-wood-density species suffer less damage and are generally more resilient to hurricane damage than low-wood-density species (Zimmerman *et al.*, 1994), but on the other hand hard-wooded species are less flexible and tend to break more with the strong winds of hurricanes (Paz *et al.*, 2018).

Caveats

Our study comes with two important caveats. The trait data used in the study were collected from adult individuals but, ideally, including seedling trait data for the seedling analyses would have been more appropriate (Supplementary Data Fig. S1), as some traits may show substantial variation over ontogeny (Fortunel *et al.*, 2019). Second, the analyses excluded palms and liana species, two functional groups representing key members of the plant community in this forest (Lugo *et al.*, 1998; Thompson *et al.*, 2002; Uriarte *et al.*, 2018) and other tropical forests (Ter Steege *et al.*, 2013). The palm *Prestoea acuminata* (Arecaceae) is the most abundant species recorded in the tree censuses, and lianas, together with this palm, are also common as seedlings (Thompson *et al.*, 2002; Umaña *et al.*, 2019). Despite their importance, the lack of radial growth of palms meant that we could not use diameter growth measurements in our analyses. Similarly, lianas are not free-standing, have a different growth habit from trees, and were not included in the tree censuses. The position of these organisms, as adults, in the multidimensional demographic space is not yet known for the LFPD. For seedlings, however, evidence suggests that lianas might have a demographic advantage relative to tree seedlings (Muscarella *et al.*, 2013). A study in a tropical forest in Panama (Gilbert *et al.*, 2006) identified a similar demographic trade-off between survival and growth for both lianas and trees. Future work on palm and liana demography is necessary to advance our understanding of the dynamics of these life forms and their contribution to tropical forest communities.

Conclusions

Identifying the key demographic factors that promote changes in species composition after disturbance will improve our ability to predict how forests respond to climate change. In this study, we observed that ~80 % of the variation in patterns of demographic rates for trees represented by the LFDP could be described through the fecundity–growth trade-off axis and a dimension describing the survival rates for seedlings and adults. Further, we found consistent and significant community changes for seedlings and trees towards forests characterized by fast growth (at the expense of fecundity), high survival rates and conservative leaf and seed traits. Under the current global forest situation in which the coverage area of hurricane-disturbed forests will keep increasing in the years to come (Kossin *et al.*, 2020), we should anticipate shifts in species demographic trade-offs and different functional dimensions.

SUPPLEMENTARY DATA

Supplementary data are available online at https://academic.oup.com/aob and consist of the following.

Methods S1: identification of demographic dimensions for tree species in the LFDP.

Table S1: PC scores for PCA of functional traits.

Table S2: priors for Bayesian parameter estimation.

Table S3: demographic parameters for seedlings and trees used for the PCA.

Table S4: PC scores for demographic PCA. Figure S1: analyses with seedling trait data.

Figure S2: PCA for traits.

Figure S3: seed rain over time.

Figure S4: seedling recruitment over time.

Figure S5: histograms of parameters for seeds and seedlings.

Figure S6: parameter estimates for trees across censuses: 2000, 2005, 2011 and 2016.

Figure S7: histograms of demographic parameters for trees.

Figure S8: demographic PCA for the first and last censuses.

Figure S9: proportion of sprouted stems across censuses.

Figure S10: PCA combining demographic variables and sprouting.

Figure S11: pairwise correlation between demographic variables.

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