

Long-term shifts in the functional composition and diversity of a tropical dry forest: a 30-yr study

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Abstract. Over the past three decades, there has been a concerted effort to study the long-term dynamics of tropical forests throughout the world. Data regarding temporal trends in species diversity, species composition, and species-specific demographic rates have now been amassed. Such data can be utilized to test predictions regarding the roles the environment and demographic stochasticity play in driving forest dynamics. These analyses could be further refined by quantifying the temporal trends in the functional composition and diversity in tropical forests. For example, we have only a handful of studies that quantify directional shifts in the functional composition in tropical forests in response to global change drivers. The present study uses data from three censuses spanning 30 yr in a Neotropical dry forest dynamics plot to provide novel insights into how the functional diversity and composition of a tropical forest has changed through time. Specifically, here we aim to (1) quantify population dynamics and compare it to that expected from environmental or demographic variance; (2) quantify long-term trends in species richness and functional diversity; (3) test whether there have been directional changes in the functional composition of the forest through time and the population changes that are responsible for these changes; and (4) place these long-term results into the context of the successional and climatic history of the forest.

Key words: community dynamics; functional trait; population dynamics; seasonally dry tropical forest.

INTRODUCTION

Tropical forests serve as a significant carbon sink slowing the accumulation of carbon dioxide, a greenhouse gas, in the atmosphere (Phillips et al. 1998). A recent paradigm in global change biology is that tropical forests are extremely sensitive to climate change and that small natural or unnatural perturbations to these ecosystems can have a large impact on the global carbon cycle (Overpeck et al. 1990, Phillips et al. 1998, Lal et al. 2000). As such, an increasing emphasis has been placed on quantifying species-specific responses to natural and unnatural disturbance in tropical tree communities and to determine whether these responses vary in a predictable manner (e.g., Losos and Leigh 2004, Condit et al. 2006, Laurance et al. 2006, Enquist and Enquist 2011, Swenson et al. 2012a, Katabuchi et al. 2017). This research program, therefore, requires long-term monitoring of the biodiversity in large forest plots and an

intimate knowledge of species-specific variability in plant functional strategies.

Since the late 1970s, several large long-term forest dynamics plots (FDPs) have been established across the tropics largely to study tropical tree demography (Losos and Leigh 2004). One of the, if not the, first tropical FDPs was installed in a seasonally dry tropical forest in Santa Rosa National Park, Costa Rica in 1976 to study leaf cutter ants and plant selection (Rockwood and Hubbell 1987). Hubbell's work in a nearby dry forest plot, which is now cattle pasture, spurred decades of debate regarding the relative importance of demographic stochasticity as a driver of tree population and forest dynamics (Hubbell 1979).

The clearest evidence that tropical tree populations and forest dynamics can deviate from the expectations of neutral theory come from instances where populations respond nonrandomly to perturbations such as hurricanes, drought, fragmentation and fire (Zimmerman et al. 1994, Condit et al. 1996, 2004, Condit 1998, Ravindranath and Sukumar 1998, Laurance et al. 2006, Swenson et al. 2012a). Such studies have often quantified changes in the abundance, diversity, and

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distributional patterns of the species in the FDP. This provides a strong basis for rejecting demographic stochasticity or neutrality, but it does not always clearly indicate how the forest is nonrandomly changing (but see Zimmerman et al. 1994, Laurance et al. 2006, Swenson et al. 2012a).

Numerous studies have assessed the physiological responses of relatively few focal species to climatic change or forest disturbance (e.g., Bullock 1997, Enquist and Leffler 2001, Gilbert et al. 2001, Engelbrecht and Kursar 2003). These physiological studies have generally found that individual species have distinct responses to climate change. Fewer studies have been conducted on the responses of entire tropical forest communities to climate change or disturbance. Some of the best examples come from Condit (1998) and Feeley et al. (2011) who describe compositional shifts in the Barro Colorado Island (BCI) FDP in response to El Niño events and long-term declines in precipitation. These studies and those of other forests (e.g., Swenson et al. 2012a) have analyzed the shift in forest-wide composition, but they have not analyzed how the traits of individual species are related to their changes in abundance. Thus, it has not been possible from that work to know whether the observed changes in functional composition are due to large changes in the populations of a few species or changes across all species related to their functional traits.

Recent work by Katabuchi et al. (2017) analyzing the BCI FDP has provided a pathway for disentangling the population-level drivers of whole-forest functional compositional change. Specifically, they show how the contribution of population size changes combined with trait values can influence the whole forest functional composition. Previous work analyzing the functional composition of BCI had come to conflicting inferences with Feeley et al. (2011) detecting an increase in forest-wide wood density composition through time and Swenson et al. (2012a) detecting no significant change. The results from Feeley et al. (2011) could be interpreted as evidence that the composition of BCI was becoming increasingly drought tolerant, while the results from Swenson et al. (2012a) would indicate stasis. Katabuchi et al. (2017) resolved this debate by showing very minor shifts in forest-wide wood density were driven almost entirely by population crashes in three species that so happened to have light wood while other light wooded species did not change substantially in population size. These results indicate the importance of linking population dynamics data to trait data to understand the drivers of forest functional compositional change and not solely analyzing the aggregate outcome (e.g., a shift in forest-wide mean trait values).

As stated above, the emergence of multiple tropical FDPs has allowed tropical ecologists to reap the benefits of having the critical baseline long-term data necessary to understand the response of tropical forests to climatic variability. Despite this progress these FDPs have been

disproportionately placed in tropical rain forests with very few active FDPs in what is perhaps the most threatened tropical forest type, the seasonally dry tropical forest. Seasonally dry tropical forests have been particularly susceptible to destruction largely due to their relatively more hospitable climates, susceptibility to fire, and comparatively rich soils (Murphy and Lugo 1986, Janzen 1988, Pennington et al. 2006). This makes the few existing dry forest FDPs quite valuable, as they are the only ongoing efforts to collect the baseline needed to understand dry forest temporal dynamics. In the Neotropics, the dry tropical forests in Central America have been subjected to anthropogenic disturbance in the form of fire and ranching leaving approximately only 2% of these forests intact with less than 50% of that designated as protected land (Janzen 1988, Miles et al. 2006, Portillo-Quintero and Sanchez-Azofeifa 2010). Thus, many Central American dry forests are now highly degraded and those that are located in protected land are regenerating from previous disturbance. The functional composition of these forests is, therefore, likely shifting as they regenerate.

Previous work on tropical dry forest succession conducted in Mexico has shown that the recently abandoned land (i.e., early successional dry forests) tends to have an environment favoring conservative functional strategies (Lebrija-Trejos et al. 2011, Lohbeck et al. 2013). For example, wood density decreased when comparing forests aged 5–63 yr reflecting an initial filtering due to xeric conditions that is relaxed as the forest matures (Lohbeck et al. 2013). Thus, early succession in tropical dry forests may show the reverse pattern typically found in tropical wet forests where pioneer-type species with acquisitive functional strategies initially dominate and, ultimately, give way to more conservative functional strategies (Grubb 1977, Bazzaz and Pickett 1980, ter Steege and Hammond 2001).

Compounding the problem of the direct destruction of the seasonally dry tropical forest in Central America by humans are potential long-term changes in the climate. For example, some have argued that there has been a long-term drying trend along the Pacific coast of Costa Rica likely due to the increased frequency of El Niño events (Vargas and Trejos 1994, Borchert 1998, Oberbauer et al. 1999). Such a drying trend in Costa Rican dry forests would be problematic because the local tree species phenology, physiology and life history is tightly linked to seasonal rhythms in precipitation (e.g., Reich and Borchert 1984, Sobrado 1986, Borchert 1994, Holbrook and Franco 2005). The data from our study site in Área de Conservación Guanacaste in Costa Rica do not show a strong shift in precipitation over the 26 yr analyzed in this study (Fig. 1). However, there has been a long-term increase in mean annual temperatures, which should result in a directional shift in the functional composition of the forest (Fig. 1). Specifically, we expect compositional changes in the forests to be related to species-specific functional traits related to temperature,

which influences water use as temperature will directly impact the water economy of plants through an increase in transpiration rates. Specifically, we would a general decline in community-wide leaf area and specific leaf area (fresh leaf area divided by dry mass) values and a general increase in community-wide wood density (ter Steege and Hammond 2001). Ultimately, the effect of the warming trend on the fate of primary and regenerating Central American tropical dry forests cannot be understood without detailed long-term data from these forests and an in depth understanding of how these same forests are functionally altered during succession and as the climate shifts.

The following study utilizes 30 yr of data from a FDP in the dry forests of northwestern Costa Rica. We begin by asking whether the population dynamics in this forest match expectations derived from neutral theory regarding population variance scaling. Next, we provide the first detailed analysis of long-term trends in the species and functional components of biodiversity in a tropical dry forest. We then examine how species-specific population changes have contributed to the functional composition changes and how this information, combined, informs us as to the drivers of long-term forest change in this system. Specifically, we ask (1) has the species and functional diversity declined through time in this forest? (2) If so, has the forest lost peripheral functions

potentially due to increasingly warm conditions during the 1980s and 1990s or have similar functions or lineages been thinned through time as would be expected in a successional forest? And (3) has the mean function of forest assemblages shift, and if so, have the traits shifted in a direction expected from successional processes and/or increasingly xeric conditions?

METHODS

Study location

This study was conducted in the San Emilio Forest Dynamics Plot (SEFDP) located in Santa Rosa National Park, Área de Conservación Guanacaste, Guanacaste Province, Costa Rica. The forest is a seasonally dry tropical forest with a distinct wet (June–December) and dry (January–May) season with the annual rainfall totaling approximately 1,500 mm. The annual rainfall over recent decades seems to have declined in this region (Borchert 1998) likely due to an increasing El Niño frequency, but this declining trend may have leveled off during the late 1990s and 2000s and is not evident when examining deviations from a 26-yr mean running from 1979 to 2006 (Fig. 1). However, there has been a long-term increase in mean annual temperatures in this forest over that time period (Fig. 1). The SEFDP has a dynamic history with portions of the plot being heavily disturbed. Based upon observations by local inhabitants, approximately one-third of the plot was used for cattle grazing and banana cultivation until ~1910 (Enquist and Enquist 2011; D. Janzen, *personal communication*) and this age estimate has been independently confirmed via tree rings (Enquist and Leffler 2001). Given the species composition, a second one-third of the plot is 125-to 175 yr old and the final third is of intermediate age (Enquist and Enquist 2011). Thus the SEFDP, like most Central American dry forests, is a successional forest with the stage of succession varying spatially, but it is considerably older than trait-based successional studies in other tropical dry forests (e.g., Lohbeck et al. 2013).

The SEFDP was originally censused in 1976 by George Stevens and Stephen Hubbell, where all woody stems greater than or equal to 3 cm diameter at 1.3 m off the ground including lianas had their diameter measured and their spatial location in the plot recorded (Rockwood and Hubbell 1987). The area of the plot is 14.4 ha. In 1996, the SEFDP was recensused by B. J. Enquist using the same methodology as the first census (Enquist et al. 1999). A third census of the SEFDP was conducted by NGS between 2006 and 2007 using the same methodology. In Table 1, we provide baseline data from each census excluding lianas (Table 1). For the purposes of this study, we examine the tree and shrub community in the SEFDP and not the lianas due to a lack of trait information

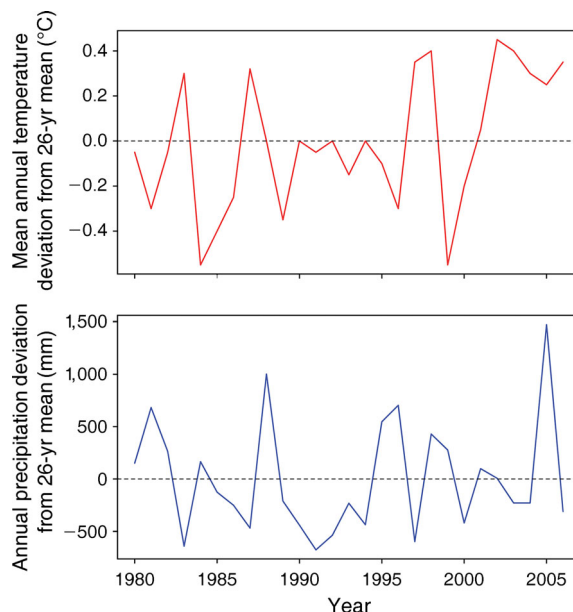


FIG. 1. Long-term climatic trends in the study area plotted as the deviation from the 26-yr mean for mean annual temperature (top) and annual precipitation (bottom) from 1980 to 2006. The data were downloaded from the Área de Conservación Guanacaste website (www.acguanacaste.ac.cr). There is a long-term increase in temperature deviation through time (slope 0.0172; $P = 0.017$; $r^2 = 0.177$), but no trend in precipitation deviations (slope 4.547; $P = 0.739$; $r^2 = 0.005$).

TABLE 1. Baseline descriptive statistics for each census regarding the number of species and stems.

Census	1976	1996	2006
Total number of species	130	137	135
Average number of species per hectare	75.57	73.92	71.33
Total number of stems	23,437	17,200	21,969
Average number of stems per hectare	1,116.16	819.05	1,046.14

for liana species and reliable population estimates for liana species through time.

Population variation scaling and demographic and environmental variance

The predictions of neutral theory are often tested using static data representing the relative abundance of species at one point in time (e.g., Hubbell 2001, Volkov et al. 2003, Adler et al. 2007). Repeat censuses of FDPs allow for dynamic analyses of populations that provide stronger tests of neutral theory. Here, we followed the theoretical and analytical framework outlined by Chisholm et al. (2014) for studying the scaling of abundance variation and initial abundance. Specifically, the theoretical expectation arising from a model of demographic stochasticity is that variation in squared abundance changes should scale linearly with initial abundance (Lande et al. 2003, Engen et al. 2005, Chisholm et al. 2014). Thus, when fitting a power law function to these data, a slope of one is expected under demographic stochasticity. Conversely, if population changes arise solely from environmental variation through time, then squared abundance changes should scale quadratically with initial abundance thereby generating a slope of two when fitting these data with a power law function. To test these expectations, we fit power law functions of squared abundance change against initial abundance where both axes were \log_{10} transformed. This was repeated using changes from 1976 to 1996, 1996 to 2006, and 1976 to 2006. Each time the slope of the function and the confidence intervals around the slope were recorded. Because robust population change estimates can be challenging to make for rare species, we also conducted the above analyses only using species that had 10 or more individuals in each of the three censuses.

Functional trait measurements

Six plant functional traits were selected for this study during the June and July 2007. The six traits were: leaf area, the specific leaf area (SLA), leaf succulence, wood density, maximum height, and seed mass. Each trait we generally measured on three to five individuals of each species known to occur in the SEFDP, but only on one individual for extremely rare species (Swenson and Enquist 2009). For all leaf traits in this study, we

collected sun-exposed leaves from the outer portion of the canopy and leaves with heavy damage were not collected. The petiole was not included in any measurement and the rachis and petioles were also excluded if the leaf was compound. The fresh area of the leaves was measured using a handheld leaf area meter and then dried for 2 d at 60°C or until their mass stabilized. These measurements were used to calculate leaf area, specific leaf area (SLA; ratio of area to dry mass) and leaf succulence ((wet mass – dry mass)/leaf area).

The wood density was determined in most cases using wood cores collected using an increment borer at 100 cm from the ground for two to three individuals of each tree species. In shrubs, we took a basal stem section from two to three individuals that were located in areas outside of the plot along road sides and near fire breaks because of the destructive methodology (Swenson and Enquist 2008). The cores and sections had their length and diameter measured immediately in the field after the cortex was removed allowing for an estimation of the fresh wood volume. The wood samples were then dried in a drying oven at 60°C for 2 d or until their mass stabilized. The wood density was calculated as the ratio of dry mass to green volume. We obtained the maximum height of each species using literature sources. If there was substantial variation in the reported maximum heights for a species we utilized the value from the region most climatically similar to the SEFDP (i.e., tropical dry forest).

The seed mass data were obtained for 54 species in the SEFDP from the KEW Millennium Seed Database (Kew 2005) and field collections by N. G. Swenson and C. M. Hulshof. These species accounted for 78%, 85%, and 84% of the stems in the plot for the three censuses, respectively. For those remaining species where we did not have a species-specific value, we estimated the value as the mean of the congeneric values. This was not a preferred method, but we argue that most of the global variation in seed mass is contained in taxonomic levels higher than genera (Moles et al. 2005) and the results from this study would not likely deviate greatly from what is presented if data for the remaining species were available.

As some of the six functional traits measured are highly correlated, we conducted a principle components analysis (PCA) between the species as a way of reducing the redundant trait data and to provide a multivariate metric of function. The first axes of the PCA space explained 66.2% of the variance (leaf area and seed mass) and the second axis captured an additional 24.0% of the variance (leaf area, seed mass, and maximum height) (Swenson and Enquist 2009; Appendix S1: Table S1).

Functional composition of San Emilio over 30-yr

We began by plotting a kernel density estimate of each trait for each census. Specifically, we assigned a species-level trait value to each individual of that species. These

data were then used to plot the kernel density estimate. Bandwidth was assigned following Silverman's rule of thumb (Silverman 1986), but multiplied this value by 4 as in Swenson et al. (2012a) to reduce noise due to con-specific individuals having the same trait value.

Next, at the 20×20 m quadrat scale, we quantified shifts in abundance-weighted mean trait values, often referred to as the community weighted mean (CWM) trait value. Prior to analyses we quantified the spatial autocorrelation in the CWM values using a spatial simultaneous autoregressive model with a queen's case neighborhood relationship. This model was used to adjust the observed CWM values to account for the observed spatial autocorrelation, and these adjusted values were used in all subsequent analyses. We utilized a binomial test to quantify whether there have directional shifts in the mean trait values in 20×20 m through time. This test was repeated for each census interval (i.e., 1976–1996, 1996–2006, and 1976–2006). The expected rate of shift in CWM values in quadrats was 50% for the first two intervals and 25% for the last interval that tests for consecutive shifts in means. The P values were adjusted using a Holm adjustment (Holm 1979).

The relationship between changes in species abundance and their trait values was quantified using generalized linear models (GLMs) with negative binomial error distributions. To accomplish this, the abundance of species in 2006 was modeled as a function of the each trait and their interactions with the log(abundance of the species in 1976) as the baseline intercept value. A stepwise AIC procedure was used to select the best model (Burnham and Anderson 2002) and a 10-fold cross-validation was used to assess fit. Specifically, 20×20 m subplots were divided into 10 groups. Nine of these groups were then used to fit the model, and the remaining group not used in the model was used to assess fit. A cross-validated r^2 was calculated as $1 - (\text{predicted error sum of squares} / \text{total sum of squares})$.

Functional diversity through time

We quantified the functional trait diversity of the SEFDP through time using three different metrics. First, we quantified the range of individual traits in 20×20 m quadrats. Next, we quantified the convex hull volume containing the trait space, now commonly referred to as functional richness (Laliberté and Legendre 2010), in each of the 20×20 m quadrats using the first two PC axes to define the trait space. Then we used the mean pairwise distance (MPD) in trait space between all species in a sample weighted by their abundance. This metric gives an overall measure of diversity and is more relevant to questions pertaining to habitat filtering and competitive exclusion (Weiher et al. 1998; Swenson 2014). Second, we use a mean nearest neighbor distance (MNND) in trait space between all possible species pairs in a sample weighted by their abundance (Weiher et al. 1998; Swenson 2014). This metric is an indicator of niche differences

and limits to similarity. Because the expected mean and variance of these metrics can be sensitive to the species richness (Swenson 2014), we then used a null model to standardize our measures across samples through space and time. The null model was generated by using a trait matrix containing all species that have been found in the SEFDP from 1976 to 2006. Species names were randomized 999 times, and each time a random MPD and MNND was calculated for each sample and each year. Next, a standardized effect size (SES) was calculated where the mean of the null MPD or MNND values was subtracted from the observed MPD or MNND for a sample and this value was divided by the standard deviation of the random MPD or MNND values (Swenson 2014). Thus, positive values indicate more than expected diversity and negative values indicate less than expected diversity. We used the entire trait matrix including all species from 1976 to 2006 in order to detect shifts towards clustering in trait space due to long-term drying in the region. All analyses were conducted at the scale of 20×20 m. Analyses at smaller and larger spatial scales were conducted and the median SES values shifted to higher and lower values, respectively (Swenson and Enquist 2009). However, in this work, we were interested in trends in SES values across time and therefore only report the trends at the 20×20 m scale because they were similar across scales. The analyses were conducted on each individual trait and the first two PC axes. They were also conducted using the Euclidean distance between species in the two dimensional PC space defined by the first two PC axes. A binomial test was used to test for trends in MPD, MNND, and their respective SES values through time using the same approach described above for the CWM analyses including the adjustment of values for observed spatial autocorrelation. Again, a Holm correction of P values was used due to multiple tests being conducted.

Species-level contributions to functional shifts

Previous work has shown that examining only forest- or community-wide trait shifts can lead to flawed inferences regarding the drivers of forest change (Katabuchi et al. 2017). Thus, we quantified the contribution of individual species and their population size changes through time to forest-level changes in functional composition. To accomplish this, we computed the contribution index developed by Katabuchi et al. (2017). It is calculated as

$$\text{contribution index} = (f_{i,2006} - f_{i,1976}) \times (t_{ij} - \bar{t}_j)$$

where $f_{i,A}$ is the relative abundance of species i in the plot at time A , t_{ij} is trait j in species i , and \bar{t}_j is the CWM of trait j in the first of the two censuses considered. Thus, a negative value indicates a species with low trait values increased in abundance or a species with large trait values decreased in abundance. The absolute value of the contribution index is maximized when species with

extreme trait values have large changes in abundance. Here, we show the equation for comparing the contribution to the change in CWM from 1976 to 2006. However, we also calculated this index for the 1976–1996 and 1996–2006 intervals.

RESULTS

Species richness and population changes through time

The overall species richness in the San Emilio Forest Dynamics Plot experienced little change from 1976 to 2006. There was, however, a 27% reduction in stem number from 1976 to 1996 and a 28% increase in stem number from 1996 to 2006 resulting in an overall 6.3% reduction from 1976 to 2006 (Table 1). Discrete population growth (i.e., $\lambda = N_{t+1}/N_t$) varied tremendously during each census interval (0.006–145.00 for 1976–1996; 0–13.00 for 1996–2006; and 0–53.00 for 1976–2006; Fig. 2).

When we regressed \log_{10} -transformed squared abundance change for each species against their initial abundance we found that the slopes of the power law functions were 1.60 (95% CI, 1.39–1.80) for 1976–1996, 1.68 (95% CI, 1.52–1.85) for 1996–2006, and 1.57 (95% CI, 1.39–1.76) for 1976 to 2006. Thus, the slopes did not include the expectation for pure demographic stochasticity (i.e., a slope of 1) or from pure environmental

variation (i.e., a slope of 2; Fig. 3). When considering only those species with 10 or more individuals during each census, we found that the power law functions were 2.32 (95% CI, 1.94–1.67) for 1976–1996, 1.90 (95% CI, 1.53–2.27) for 1996–2006, and 1.60 (95% CI, 1.20–2.00) for 1976 to 2006. Thus, when removing rare species, the confidence intervals on the slopes always included a slope expected given environmental variation (i.e., a slope of 2; Appendix S1: Fig S1).

Functional compositional change through time and abundance change

To analyze changes in the functional composition of the SEFDP through time, we plotted the distribution of traits at the plot scale using kernel density plots (Fig. 4) and then using community weighted mean trait values (CWM) at the 20×20 m quadrat scale for each census (Fig. 5). During the first census interval from 1976 to 1996 the CWM of leaf succulence, seed mass, SLA, PC1, and PC2 decreased and the CWM of maximum height, leaf area and wood density increased (Table 2). During the second census interval from 1996 to 2006, the CWM of leaf area, SLA, and PC1 decreased and the CWM of leaf succulence, wood density, maximum height, seed mass, and PC2 increased. Finally, consecutive decreases from 1976 to 1996 and 1996 to 2006 in the CWM of leaf

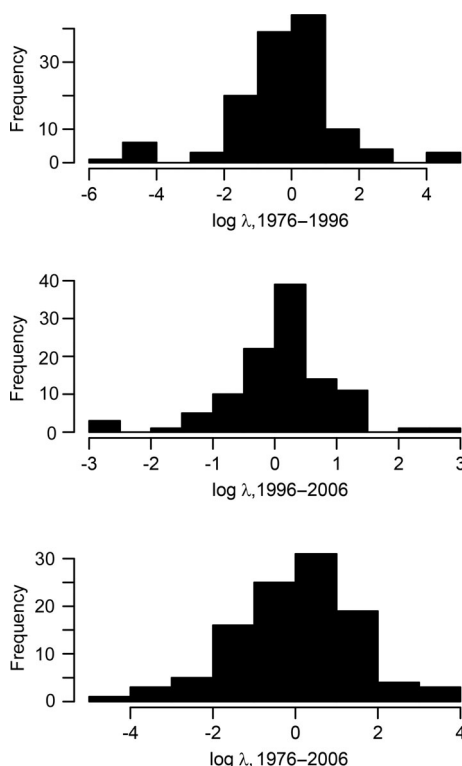


FIG. 2. Histograms of the discrete population growth parameter (λ) from 1976 to 1996 (top), 1996–2006 (middle), and 1976–2006 (bottom).

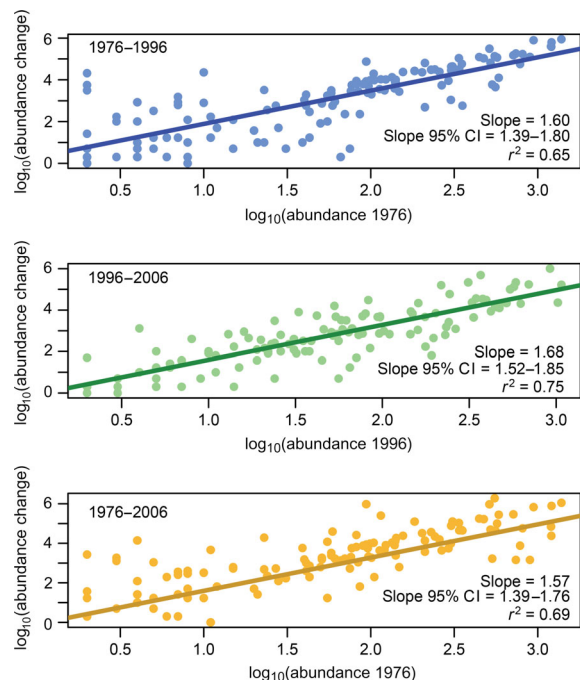


FIG. 3. The squared change in abundance for individual species from 1976 to 1996 (top), 1996–2006 (middle), and 1976–2006 (bottom) plotted against the initial abundance plotted on \log_{10} axes with a power law function. If population change is driven purely by demographic stochasticity, then we would expect a slope of 1. If population change is driven purely by environmental variation, then we would expect a slope of 2.

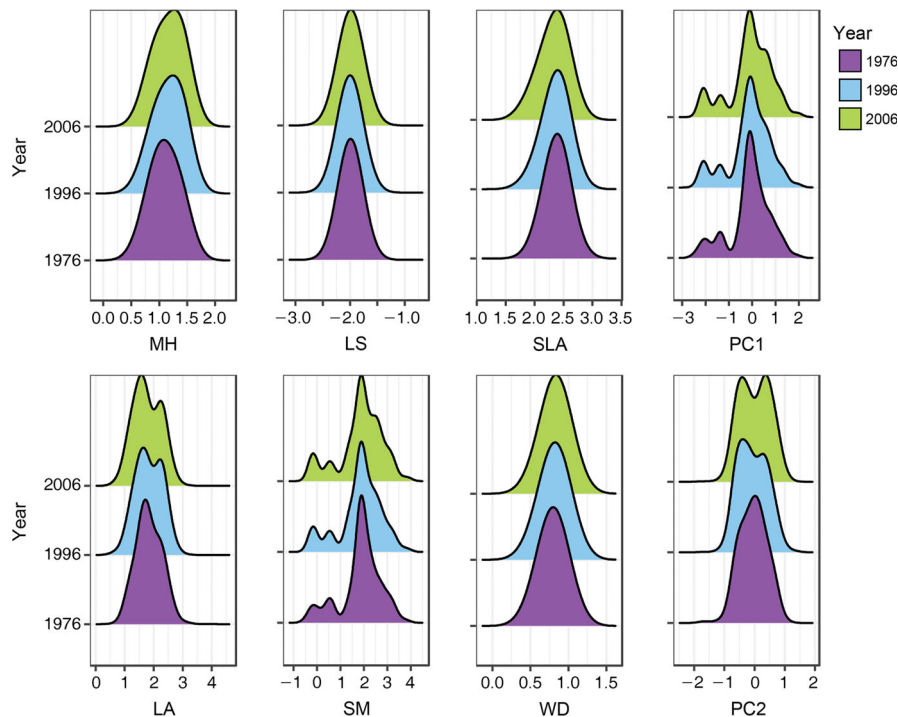


FIG. 4. Kernel density estimates of trait data using all individual from a census. All traits except wood density are \log_{10} -transformed. LA, leaf area; LS, leaf succulence; MH, maximum height; SM, seed mass; SLA, specific leaf area; WD, wood density; PC1, principal components axis 1 scores; and PC2, principal components axis 2 scores.

area and SLA were detected as were consecutive increases in the CWM of maximum height, wood density, and PC2 (Table 2). Thus, there have been long-term trends in mean trait values related to drought tolerance (i.e., smaller leaves, lower SLA and higher wood density) or heat dissipation (i.e., smaller leaves, lower SLA). Furthermore, seed mass, a trait expected to change with succession, has had no directional change through time.

Next, we asked whether changes in species abundance from 1976 to 2006 were related to their traits. The best supported model included leaf area (estimate = -1.13 ; $P < 0.001$), maximum height (estimate = 0.82 ; $P = 0.07$), and wood density (estimate = 1.92 ; $P = 0.09$). However, the r^2 from the cross-validation analysis was negative (-0.34 ; 95% CI, -0.64 to -0.05). This indicates that the models were overfit. That is the traits (i.e., the estimated parameters) had almost zero ability to predict changes in abundance. We then modeled changes in abundance using the first two PC axes with the best model had both axes (PC1 estimate = 0.15 , $P = 0.21$; PC2 estimate = 0.99 , $P < 0.01$) and the interaction term (PC1 \times PC2 estimate = 0.38 , $P = 0.08$). The cross-validation r^2 was negative (-0.51 ; 95% CI = -0.90 to -0.12).

Functional diversity through time

The functional diversity of the forest plot was measured at each census point at the scale of 20×20 m.

There was a significant decrease in functional richness from 1976 to 1996 and a significant increase in functional richness from 1996 to 2006, which lead to no overall change from 1976 to 2006 (Table 3; Fig. 6). There was a significant increase in the multidimensional trait mean pairwise distance (MPD) during each time step and overall (Table 3; Fig. 6). The mean nearest neighbor distance (MNND) in multidimensional trait space increased slightly from 1976 to 1996 and decreased from 1996 to 2006 leading to a slight increase overall from 1976 to 2006.

All tests were then performed on individual traits to quantify if the diversity in a single trait has changed directionally through time. There has been an increase in the total trait range for all traits through time (Table 4; Appendix S1: Fig. S2). The MPD for individual traits in 20×20 m increased for all traits with the exception of maximum height, which had no change through time (Appendix S1: Table S2 and Fig. S3). The MNND increased in leaf succulence, seed mass, SLA, wood density, PC1, and PC2 and decreased for maximum height and leaf area (Appendix S1: Table S3 and Fig. S4). Thus, while the overall functional diversity in the plot changed moderately through time, the increases in diversity for individual traits was more evident.

The functional dispersion of assemblages (SES values) in the forest at the scale of 20×20 m was generally underdispersed when using the mean pairwise distance measure with the exception of wood density for all

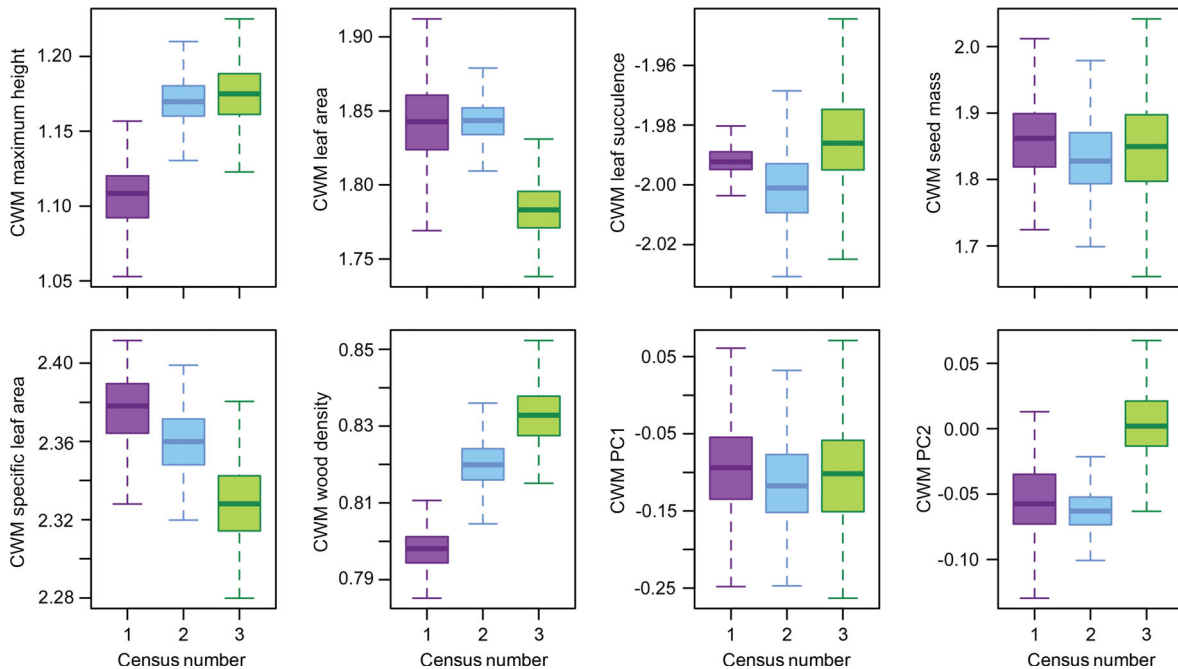


FIG. 5. Box plots representing the community weighted mean trait value (i.e., an abundance-weighted mean trait value) in 20×20 m quadrats during each of the three censuses. All traits except wood density are \log_{10} -transformed. Box plot components are mid line, median; box edges, first and third quartiles; whiskers, maximum and minimum values.

censuses, seed mass and SLA in 2006 and SLA (Fig. 7; Appendix S1: Table S4). Thus, species in 20×20 m quadrats were more similar in their traits than expected. The results were similar when using the mean nearest neighbor distance measure with the exceptions that wood density was underdispersed in 1976 and leaf area and PC1 were underdispersed in 1996 and 2006, respectively (Fig. 8; Appendix S1: Table S5).

Contributions of individual species to functional compositional change

Given that community mean trait values were changing, we then asked what individual species are driving to these changes given their changes in abundance and trait values. We quantified these contributions for the two census intervals and over the entire 30-yr period using the contribution index developed by Katabuchi et al. (2017).

The major changes in CWM traits from 1976 to 1996 were an increase in maximum height and wood density and a decrease in leaf succulence and SLA (Fig. 5). One way of representing which species drive overall CWM shifts is to record those species that contribute to a trait shift that exceeds that shown in the overall assemblage (Katabuchi et al. 2017). We show these species for the 1976–1996 interval in Table S6. The leaf succulence, maximum height, SLA, and wood density shifts were driven by 2, 10, 3, and 11 species, respectively (Appendix S1: Table S6). The population increase of

Astronium graveolens (Anacardiaceae; $\lambda = 2.09$) during this period played a major role in shifting leaf succulence, maximum height, and wood density CWM and *Malvaviscus arboreus* (Malvaceae; $\lambda = 0.06$) population decline played a major role in shifting the leaf succulence and wood density CWM. However, no other species played a consistently large role in the CWM shifts in multiple traits (Table S6).

The major changes in CWM traits from 1996 to 2006 were an increase in leaf succulence, wood density and PC2 and a decrease in leaf area and SLA (Fig. 5). The shifts in leaf area, leaf succulence, SLA, wood density and PC2 were largely due to 7, 3, 5, 7, and 6 species, respectively (Appendix S1: Table S7). Three species played major roles in shifting the CWM values of nearly all of these traits. Specifically, a population increase in *Capparis indica* (Capparidaceae; $\lambda = 2.91$) helped drive the leaf area, leaf succulence, SLA, wood density, and PC2 shifts. *Semialarium mexicanum* (Celastraceae; $\lambda = 2.09$) helped drive the leaf area, leaf succulence, SLA, and PC2 shifts. Finally, a decline in the population of *Bursera simaruba* (Burseraceae; $\lambda = 0.85$) helped drive the leaf area, SLA, wood density, and PC2 shifts (Appendix S1: Table S7).

The notable changes in CWM traits from 1976 to 2006 were an increase in maximum height, wood density, and PC2 and a decrease in leaf area and SLA (Fig. 5). These changes were largely driven by population changes in 3, 7, 4, 17, and 2 species, respectively (Table 5). Dramatic increases in the populations of *C.*

TABLE 2. Results from the binomial test of community weighted mean trait changes in 20 × 20 m quadrats through time.

Test	LA	LS	MH	SM	SLA	WD	PC1	PC2
1976–1996								
Success	193	279	357	228	305	358	213	230
Direction	inc.	dec.	inc.	dec.	dec.	inc.	dec.	dec.
<i>P</i>	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01
1996–2006								
Success	358	330	234	256	348	357	249	358
Direction	dec.	inc.	inc.	inc.	dec.	inc.	dec.	inc.
<i>P</i>	<0.01	<0.01	<0.01	<0.01	<0.001	<0.01	<0.01	<0.01
1976–2006								
Success	339	233	354	178	358	354	180	333
Direction	dec.	inc.	inc.	dec.	dec.	inc.	dec.	inc.
<i>P</i>	<0.01	<0.01	<0.01	0.91	<0.01	<0.01	0.87	<0.01

Notes: We note the number of quadrats with a directional change in the mean, whether increasing (inc.) or decreasing (dec.) and the *P* value. LA, leaf area; LS, leaf succulence; MH, maximum height; PC1, pc axis 1 scores; PC2, pc axis 2 scores; SLA, specific leaf area; SM, seed mass; WD, wood density.

TABLE 3. Results from the binomial test of functional diversity changes in 20 × 20 m quadrats through time.

Interval	Trait	Direction	Success	<i>p</i>
1976–1996	functional richness	decrease	330	<0.01
1996–2006	functional richness	increase	310	<0.01
1976–2006	functional richness	increase	191	0.34
1976–1996	MPD	increase	314	<0.01
1996–2006	MPD	increase	278	<0.01
1976–2006	MPD	increase	338	<0.01
1976–1996	MNND	increase	258	<0.01
1996–2006	MNND	decrease	209	0.02
1976–2006	MNND	increase	248	<0.01

Note: We note the number of quadrats with a directional change in the mean, whether increasing or decreasing, and the *P* value.

indica ($\lambda = 11.48$), *S. mexicanum* ($\lambda = 3.50$), and *Manilkara chicle* (Sapotaceae; $\lambda = 5.40$) have played key roles in changing the functional composition of the forest over this 30-yr period (Table 5).

DISCUSSION

In this study, we asked whether the species and functional composition and diversity of a long-term dry forest dynamics plot has changed nonrandomly through time, and if so, is this shift similar to that expected given the climatic history of the study region and the successional history of the forest. We find that the dynamics of this forest have been generated by nonrandom population dynamics. Furthermore, this has resulted in a clear shift in the functional composition of this forest over 30 yr. We show that these shifts are due to major population shifts of multiple species that are indicative of more conservative functional strategies, which are more indicative of a dry forest responding to long-term warming rather than expected functional trends with dry forest succession (e.g., Lohbeck et al. 2013). Last, the

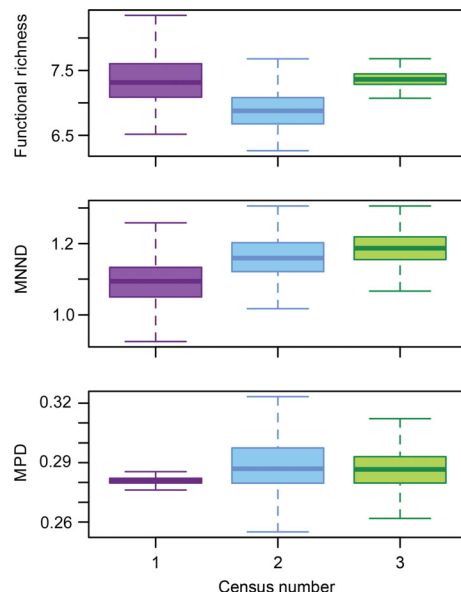


FIG. 6. Box plots representing the functional richness, mean nearest neighbor distance (MNND), and mean pairwise distance (MPD) in 20 × 20 m quadrats during each of the three censuses. The indices were calculated using distances between species with respect to their PC axis 1 and PC axis 2 scores.

functional diversity in the forest has shifted slightly through time, but it is, generally, lower than expected given the species richness at the quadrat scale. Taken together, the results show a strong shift in functional composition in a Neotropical dry forest that is indicative of a response to a warmer climate. In the following, we discuss the results in detail.

Species richness and population changes through time

The species richness in the San Emilio Forest Dynamics Plot has not changed dramatically through time.

TABLE 4. Results from the binomial test of trait range changes in 20 × 20 m quadrats through time.

Interval	Trait	Direction	Success	<i>P</i>
1976–1996	leaf area	increase	215	0.01
1996–2006	leaf area	increase	358	<0.01
1976–2006	leaf area	increase	346	<0.01
1976–1996	leaf succulence	decrease	187	0.66
1996–2006	leaf succulence	increase	203	0.11
1976–2006	leaf succulence	increase	209	0.03
1976–1996	maximum height	increase	244	<0.01
1996–2006	maximum height	increase	306	<0.01
1976–2006	maximum height	increase	295	<0.01
1976–1996	seed mass	increase	191	0.50
1996–2006	seed mass	increase	335	<0.01
1976–2006	seed mass	increase	301	<0.01
1976–1996	SLA	increase	344	<0.01
1996–2006	SLA	increase	358	<0.01
1976–2006	SLA	increase	354	<0.01
1976–1996	wood density	increase	314	<0.01
1996–2006	wood density	increase	351	<0.01
1976–2006	wood density	increase	350	<0.01
1976–1996	PC1	decrease	195	0.34
1996–2006	PC1	increase	335	<0.01
1976–2006	PC1	increase	284	<0.01
1976–1996	PC2	decrease	209	0.03
1996–2006	PC2	increase	354	<0.01
1976–2006	PC2	Increase	278	<0.01

Note: We note the number of quadrats with a directional change in the mean, whether increasing or decreasing, and the *P* value.

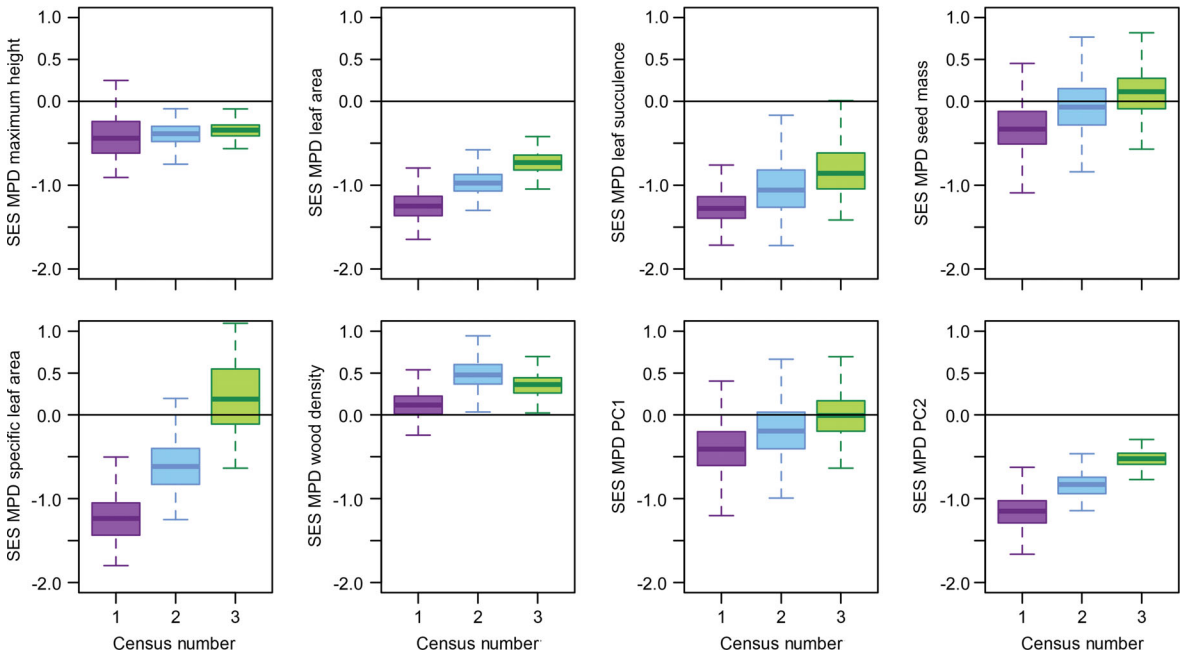


FIG. 7. Box plots representing the standardized effect size (SES) values for the mean pairwise distance (MPD) in 20 × 20 m quadrats during each of the three censuses for individual traits and the individual PC axis 1 and 2 scores. Negative values indicate lower than expected trait diversity, and positive values indicate higher than expected trait values. The mean values of the distributions were significantly ($P < 0.05$) different from the null expectation of zero (horizontal black line) in each case with the exception of PC1 in the final census.

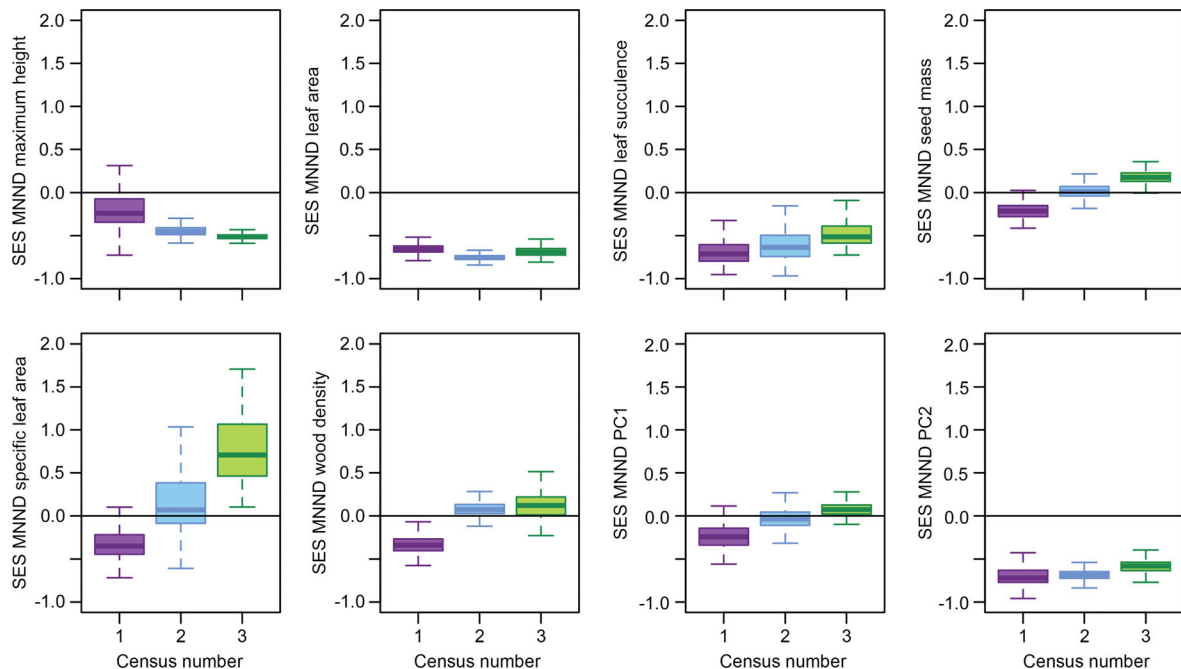


FIG. 8. Box plots representing the standardized effect size (SES) values for the mean nearest neighbor distance (MNND) in 20×20 m quadrats during each of the three censuses for individual traits and the individual PC axis 1 and 2 scores. Negative values indicate lower than expected trait diversity, and positive values indicate higher than expected trait values. The mean values of the distributions were significantly ($P < 0.05$) different from the null expectation of zero (horizontal black line) in each case with the exception of seed mass and PC1 in the second census.

However, the number of stems has declined considerably (Table 1). This decline is primarily due to a major decline in stem number from 1976 to 1996. This decline is in line with the thinning of a successional forest. However, previous work analyzing the shifts in species distributions in this plot from 1976 to 1996 has argued that while stem thinning due to succession undoubtedly has occurred, the species distributions across elevation over this 20-yr period are indicative of shifts in response to decreasing water availability (Enquist and Enquist 2011). The slight increase in stem number from 1996 to 2006 indicates that thinning of the forest has likely stopped and whatever successional dynamics were taking place may have greatly slowed.

Next, we wanted to examine the degree to which population dynamics in the forest have been nonrandom. Populations in the SEFDP have been very dynamic through time with large population increases and declines (Fig. 2), but this does not directly address whether these changes have been nonrandom. Theory predicts that when the squared change in population size is plotted against the initial population size and evaluated with a power law function, demographic stochasticity should give rise to a scaling slope of one. Conversely, if population changes are purely driven by environmental stochasticity the scaling slope should be 2 (Chisholm et al. 2014). Here, we have shown that the scaling of squared changes in population sizes vs. initial population sizes is significantly higher than a slope of 1 and

closer to, but significantly lower than, a slope of 2 (Fig. 2). However, when excluding species with fewer than 10 individuals in any census, the confidence intervals in each regression included a slope of 2 (i.e., environmental variation; Appendix S1: Fig. S1). Thus, we can reject a model of pure demographic stochasticity (Hubbell 2001) driving the dynamics of this forest and we fail to reject a model of pure environmental stochasticity when excluding rare species, but reject it when using all species. Therefore, the dynamics are likely driven primarily by environmental drivers with some stochastic dynamics, most likely for rare species.

Functional composition and diversity through time

Analyses of the changes of population size through time demonstrate nonrandom population dynamics in the SEFDP through time. However, the environmental drivers of population and forest dynamics cannot be understood purely from those analyses. Thus, we analyzed the changes in functional composition and diversity in the SEFDP from 1976 to 2006. We show at the forest and 20×20 m quadrat scale that the forest has shifted significantly through time in its functional composition. Specifically, there has been a large decline in mean leaf area and specific leaf area through time and a large increase in mean maximum height, leaf succulence, and wood density through time (Fig. 5). Additionally, PC2 has increased in its mean through time, but this PC

TABLE 5. Results from the contribution index analyses from 1976 to 2006.

Species	Family	Trait	λ	Individual contribution
<i>Capparis indica</i> (L.) Fawc.	Caparidaceae	leaf area	11.48	−0.02993929
<i>Semialarium mexicanum</i> (Miers) Mennega	Celastraceae	leaf area	3.50	−0.02466472
<i>Trichilia cuneata</i> Radlk.	Meliaceae	leaf area	0.14	−0.01326007
<i>Casearia corymbosa</i> H.B.K.	Salicaceae	maximum height	0.27	0.01645338
<i>Semialarium mexicanum</i> (Miers) Mennega	Celastraceae	maximum height	3.50	0.015963397
<i>Astronium graveolens</i> Jacq.	Anacardiaceae	maximum height	2.88	0.011282321
<i>Acacia collinsii</i> Safford	Fabaceae	maximum height	0.24	0.010101087
<i>Exostema mexicanum</i> A. Gray	Rubiaceae	maximum height	1.91	0.008330767
<i>Manilkara chicle</i> (Pittier) Gilly	Sapotaceae	maximum height	5.40	0.007576136
<i>Allophylus occidentalis</i> (Sw.) Radlk.	Sapindaceae	maximum height	0.23	0.006463805
<i>Capparis indica</i> (L.) Fawc.	Caparidaceae	SLA	11.48	−0.020899575
<i>Semialarium mexicanum</i> (Miers) Mennega	Celastraceae	SLA	3.50	−0.015219166
<i>Allophylus occidentalis</i> (Sw.) Radlk.	Sapindaceae	SLA	0.23	−0.007949487
<i>Manilkara chicle</i> (Pittier) Gilly	Sapotaceae	SLA	5.40	−0.007161062
<i>Astronium graveolens</i> Jacq.	Anacardiaceae	wood density	2.88	0.00610091
<i>Manilkara chicle</i> (Pittier) Gilly	Sapotaceae	wood density	5.40	0.004807851
<i>Exostema mexicanum</i> A. Gray	Rubiaceae	wood density	1.91	0.002869762
<i>Malvaviscus arboreus</i> Cav.	Malvaceae	wood density	0.13	0.002689345
<i>Cochlospermum vitifolium</i> (Willd.) Spreng.	Cochlospermaceae	wood density	0.37	0.002342443
<i>Allophylus occidentalis</i> (Sw.) Radlk.	Sapindaceae	wood density	0.23	0.002251372
<i>Capparis indica</i> (L.) Fawc.	Caparidaceae	wood density	11.48	0.001851938
<i>Cordia panamensis</i> Riley	Boraginaceae	wood density	0.57	0.001658996
<i>Calycophyllum candidissimum</i> (Vahl.) DC.	Rubiaceae	wood density	2.16	0.001540556
<i>Pisonia aculeate</i> L.	Nyctaginaceae	wood density	0.45	0.001435159
<i>Corida alliodora</i> (R. and P.) Oken	Boraginaceae	wood density	0.06	0.00141752
<i>Vernonia triflosculosa</i> Kunth	Asteraceae	wood density	0.03	0.001338105
<i>Tabebuia ochracea</i> Standl.	Bignoniaceae	wood density	1.93	0.001201006
<i>Swartzia cubensis</i> (Britt and Wilson) Standley	Fabaceae	wood density	3.02	0.001014985
<i>Cecropia peltata</i> L.	Urticaceae	wood density	0.26	0.000837416
<i>Randia monantha</i> Benth.	Rubiaceae	wood density	1.38	0.000748326
<i>Alibertia edulis</i> A. Rich.	Rubiaceae	wood density	4.41	0.000733296
<i>Capparis indica</i> (L.) Fawc.	Caparidaceae	PC2	11.48	0.03311067
<i>Semialarium mexicanum</i> (Miers) Mennega	Celastraceae	PC2	3.50	0.02720056

Notes: We provide the species name and family, the discrete population growth parameter (λ) for the time interval, and the individual contribution in to the overall change in the mean trait value over the interval. Negative individual contribution values indicate how much the change in the population of that species reduced the average trait value in the forest. Positive individual contribution values indicate how much the change in the population of that species increased the average trait value in the forest.

axis is heavily weighted by leaf area (Appendix S1: Table S1). An increase in temperature through time would be expected to produce shifts in these trait distributions in the directions found. Specifically, smaller and thicker more sclerophyllous leaves should be expected in environments where increased transpiration due to higher temperatures occurs. Furthermore, denser wood is expected as well in such environments, as it is indicative of resistance to xylem embolism (e.g., Hacke et al. 2001, Swenson and Enquist 2007, Chave et al. 2009). The increase in maximum height is not necessarily expected in a forest undergoing a gradual warming, and it may even be considered the direct opposite of the expected result. We note that the major increase in maximum height through time occurs from 1976 to 1996 (Fig. 5) when a major thinning of the forest occurred (Table 1). We suspect that the increase in maximum heights, therefore, may be due to successional processes

playing out from 1976 to 1996 and/or a thinning of shrub species over these 20 yr. We also note that the decrease in specific leaf area and the increase in wood density may be expected in a successional wet forest (ter Steege and Hammond 2001, Swenson et al. 2012a), but not a dry forest (e.g., Lohbeck et al. 2013). Thus, our results not reject the expected functional trajectories for dry forests. However, the human disturbance to our forest plot is several decades older than other successional dry forests where functional trajectories have been studied (i.e., Lohbeck et al. 2013). Thus, it might be more reasonable to expect functional trajectories more similar to that found in a wet forest due to less xeric environment in our original census than the youngest plots in chronosequence studies. That said, we also do not find functional trajectories that are wholly consistent with that expected from a successional wet forest. For example, we note that the seed mass distribution in the

SEFDP has not changed through time. The seed mass distributions in a successional wet forest should shift from small-seeded light-demanding species to large-seeded shade-tolerant species through time (ter Steege and Hammond 2001, Swenson et al. 2012a). Thus, the finding that seed mass distributions have not changed through time indicates that the shifts in SLA and wood density are likely more linked to long-term warming of the forest rather than purely successional dynamics. Last, other work in the forests around the SEFDP by Buzzard et al. (2016) has shown an increase in the CWM SLA with stand age, whereas we have found a decrease in the CWM SLA through time.

Next, we asked whether abundance changes in this forest could be predicted strictly from trait information and which species and their associated abundance changes had the greatest contribution to CWM trait shifts at the 20×20 m scale during each census interval and overall from 1976 to 2006. While our best fit model of abundance change included significant trait effects from leaf area and height, our cross-validation analyses indicated that these models overfit the data and we, ultimately, had little ability to predict the abundance changes of individual species based upon the traits we considered in this work despite the clear community-level shifts in these traits. This points to two nonmutually exclusive scenarios. First, the traits measured simply do not relate to demographic performance and therefore population change. However, there is evidence indicating these traits are related to growth and survival rates in tropical trees (e.g., Wright et al. 2010, Iida et al. 2014, Liu et al. 2016), but there is additional evidence that the strength of these relationships is often very weak (e.g., Swenson 2012, 2013, Paine et al. 2015, Yang et al. 2018). Second, weak correlations between major functional spectra (e.g., leaf and wood economics; Reich et al. 1997, Chave et al. 2009) may indicate that multivariate approaches are necessary to disentangle how traits relate to forest dynamics. Here, we have used a multivariate analyses, but the approach was statistical in nature and could be improved by models of plant phenotypes that include whole plant allocation and organ-level trait data (e.g., Enquist et al. 2007, Yang et al. 2018).

The functional diversity of the SEFDP though time was analyzed next. We utilized three different metrics: a convex hull volume (i.e., the functional richness), the mean pairwise distance (MPD), and the mean nearest neighbor distance (MNND). We found no large shifts in functional richness, a slight increase in MNND, and an increase in MPD through time when analyzing the distance between species in two dimensional principle component space (Fig. 6). When examining individual traits we found an increase in MPD for all traits except for maximum height (Appendix S1: Fig. S2). We also found increases in the MNND for most traits (Appendix S1: Fig. S3) and subtle changes in individual trait ranges (Appendix S1: Fig. S2). Thus, while individual traits did moderately increase in diversity through time, forest-

wide the diversity of overall trait space increased very little through time. Thus, the functional changes in the forest are primarily due to a shift of the overall distribution of traits and not necessarily an expansion of the range of traits in the forest. A notable exception to this is SLA where there has been an increase in the overall range in values through time and a shift in the mean as well (Fig. 5 and Appendix S1: Fig. S2).

Functional dispersion through time

To gain a deeper insight into the functional dynamics in this forest we analyzed the long-term trends in functional dispersion in local assemblages (i.e., the 20×20 subplot scale). Specifically, we asked whether the observed MPD and MNND deviated from a null expectation and how that dispersion did or did not change through time. We found a significant increase in the SES values for seed mass, SLA and PC2 through time in 20×20 m subplots using both metrics of functional diversity (Appendix S1: Tables S4 and S5). Using the MPD measure, we also found increases in the SES values for leaf area, leaf succulence, and PC1 through time (Appendix S1: Table S2). Using the MNND, we also found increases in the SES values for wood density. Thus, functional diversity has increased in this forest more than expected given the, subtle, changes in species richness. The increase in SLA diversity through time could indicate successional dynamics where limited water in dry forests may select for divergent leaf strategies: high SLA deciduous (avoider) species and low SLA evergreen (tolerator) species (Swenson et al. 2012b). Though, as noted above, the long-term shift in SLA values in this forest runs in a direction opposing that found in communities with increasing stand ages in this same area (Buzzard et al. 2016). Thus, while functional diversity increases through time, it does not appear to be consistent with successional processes and more likely due to an increase in the abundances of very drought tolerant species with high wood density and low SLA values.

Contributions of individual species to functional compositional change

Previous work has demonstrated how it can be difficult to infer the processes driving the functional compositional changes in a forest from community-level metrics. For example, Katabuchi et al. (2017) have shown that the forest-level shifts in trait distributions on Barro Colorado Island, Panama could largely be attributed to the population crashes of approximately three species out of the ~300 in that forest plot and that these few species just so happened to have low wood densities while other species with low wood densities did not experience similar population crashes. Here, we have shown that trait distribution shifts through time in the San Emilo Forest Dynamics Plot can be attributed to many species changing in abundance. For example, the shift in

higher wood density in the forest from 1976 to 2006 can be attributed to 17 species (>10% of the species in the forest; Table 5). In nearly all cases, the shift in trait distributions was driven by both population increases and decreases for species on the peripheries of trait space (Table 5, Appendix S1: Tables S6 and S7). Combined, this evidence indicates that the shifts in the functional composition in the forest plot are not simply due to the anomalous crash of one to a few species as it was in Barro Colorado Island over decades.

The species-level contribution analyses provide further insights into the potential drivers of forest change. It is clear that some pioneer species, *Cecropia peltata* (Urticaceae), *Vernonia triflosculosa* (Asteraceae), and *Cochlospermum vitifolium* (Cochlospermaceae), have declined in abundance and have contributed to an increase in wood density through time. This may indicate a role of successional dynamics. However, there was also a major increase in drought-tolerant species such as *Capparis indica* (Capparaceae), *Manilkara chicle* (Sapotaceae), *Astronium graveolens* (Anacardiaceae), and *Semialarium mexicanum* (Celastraceae). These species also played a key role in reducing the forest-level mean SLA value, which is a result opposite of that in successional dry forests in the same national conservation area (Buzzard et al. 2016). Thus, while some trait shifts may have been promoted via successional processes from 1976 to 1996, the largest shifts are more indicative of a forest functionally responding to increased temperatures and reduced water availability.

CONCLUSIONS

In this study, we have provided one of the first documentations of long-term trends in the species and functional composition and diversity in a tropical dry forest. We began by demonstrating population dynamics that reject a neutral model of pure demographic stochasticity. Next, we demonstrated clear directional shifts in the functional composition and moderate-to-no changes in functional diversity in this forest that are in line with what is expected of a forest undergoing a long-term decline in water availability and less in line with successional dynamics. Last, we were able to demonstrate that the shift in the functional composition of this dry forest over 30 yr can be attributed to large changes in abundance for multiple species on the periphery of trait space, which indicates the functional shifts are not driven by a few anomalous population expansions or collapses. Ultimately, the work demonstrates that long-term forest dynamics data must be integrated with detailed trait data to understand the drivers of forest change and, critically, analyses of individual population changes are critical for drawing robust inferences.

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SUPPORTING INFORMATION

Additional supporting information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/ecm.1408/full>

DATA AVAILABILITY

Data are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.h44j0zpg3>