Long-term change within a Neotropical forest: assessing differential functional and floristic responses to disturbance and drought

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Abstract

Disentangling the relative roles of biotic and abiotic forces influencing forest structure, function, and local community composition continues to be an important goal in ecology. Here, utilizing two forest surveys 20-year apart from a Central American dry tropical forest, we assess the relative role of past disturbance and local climatic change in the form of increased drought in driving forest dynamics. We observe: (i) a net decrease in the number of trees; (ii) a decrease in total forest biomass by 7.7 Mg ha^{-1} but when calculated on subquadrat basis the biomass per unit area did not change indicating scale sensitivity of forest biomass measures; (iii) that the decrease in the number of stems occurred mainly in the smallest sizes, and in more moist and evergreen habitats; (iv) that there has been an increase in the proportion of trees that are deciduous, compound leaved and are canopy species, and a concomitant reduction in trees that are evergreen, simple-leaved, and understory species. These changes are opposite to predictions based on recovery from disturbance, and have resulted in (v) a uniform multivariate shift from a more mesic to a more xeric forest. Together, our results show that over relatively short time scales, community composition and the functional dominance may be more responsive to climate change than recovery to past disturbances. Our findings point to the importance of assessing proportional changes in forest composition and not just changes in absolute numbers. Our findings are also consistent with the hypothesis that tropical tree species exhibit differential sensitivity to changes in precipitation. Predicted future decreases in rainfall may result in quick differential shifts in forest function, physiognomy, and species composition. Quantifying proportional functional composition offers a basis for a predictive framework for how the structure, and diversity of tropical forests will respond to global change.

Keywords: climate change, community ecology, drought, El Niño, long-term forest dynamics, Pacific Decadal Oscillation, Tropical dry forest

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Introduction

An increasing number of studies have shown that tropical forests are dynamic and have undergone directional shifts in composition and structure (Phillips & Gentry, 1994; Condit, 1998; Phillips *et al.*, 2004). Linking observed changes in tropical forests with changes in climate would support a central contention in global change biology that tropical forests are sensitive to climatic change (Overpeck *et al.*, 1990; Hartshorn, 1992; Phillips *et al.*, 1998; Lal *et al.*, 2000; Enquist, 2002). Indeed, several studies have reported moderate to strong correlations between climatic variables and tropical tree growth. For example, variability in rainfall

and soil moisture are often correlated with rates of tropical tree growth and forest production (Frankie *et al.*, 1974; Opler *et al.*, 1976; Reich & Borchert, 1984; Enquist & Leffler, 2001; Chidumayo, 2005; Lawrence, 2005). The spatial and temporal variation in soil moisture has been cited as an important diver of functional differentiation and niche separation in tropical trees (Sobrado & Cuenca, 1979; Sobrado, 1986; Borchert, 1994; Holbrook *et al.*, 1995; Clark *et al.*, 1999; Jackson *et al.*, 1999; Meinzer *et al.*, 1999; Yavitt & Wright, 2008). Further, several studies have also shown that tropical forests appear sensitive to drought conditions stemming from changes in precipitation (Stowe & Brown, 1981; Leighton & Wirawan, 1986; Condit *et al.*, 1995, 1996a; Swaine, 1996; Condit, 1998; Nepstad *et al.*, 1999; Engelbrecht *et al.*, 2007; Phillips *et al.*, 2009) and/or increased temperatures (Clark *et al.*, 2003; Chidumayo, 2005). In addition, on short time scales, across many small plots throughout the Amazon, the aboveground

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forest biomass and productivity have decreased in response to the 2005 drought (Phillips *et al.*, 2009; see also Nepstad *et al.*, 2007).

In order to understand and ultimately predict how tropical forests and ecosystems respond to changes in climate it is important to assess if tree species are differentially sensitive to variation in climate due to their functional traits (Diaz & Cabido, 2001; Townsend *et al.*, 2008). Such understanding would not only allow ecologists to assess which taxa are more likely to experience changes in dominance but also to link how climate driven dynamics and functional differences in species composition then influence ecosystem functioning (Diaz & Cabido, 2001; Norberg *et al.*, 2001). Several studies have assessed how the functional composition of tropical forests changes as a result of recovery from past disturbance (Arroyo-Mora *et al.*, 2005) or spatial variability in temperature, precipitation and/or water availability influence the functional composition of tropical forests such as wood density (Swenson & Enquist, 2007), leaf traits, (Stowe & Brown, 1981; Leffler & Enquist, 2002; Kraft *et al.*, 2008; Townsend *et al.*, 2008; Fyllas *et al.*, 2009; Swenson & Enquist, 2009), as well as the degree of deciduousness (Condit, 1998). Other studies have assessed physiological or growth responses of different tropical tree species to climate variability (Zimmerman *et al.*, 1994; Bullock, 1997; Borchert, 1998; Enquist & Leffler, 2001; Gilbert *et al.*, 2001; Engelbrecht & Kursar, 2003; Yáñez-Espinosa *et al.*, 2006; Townsend *et al.*, 2008). Fewer studies have assessed either how climatic variation or disturbance differentially influences species-level and functional responses of entire tropical forest communities (Condit *et al.*, 1996b; Thompson *et al.*, 2002).

Perhaps the best example of the importance differential responses of tropical tree species to climatic change comes from Condit *et al.* (1996a, b) and Condit (1998). They described directional compositional shifts in the tropical tree community in the Barro Colorado Island (BCI) Forest Dynamics Plot in response to a particularly severe El Niño event in the early 1980s. Condit and colleagues found that species typically found in mesic habitats on BCI tended to have much lower stem densities post-El Niño that those species that are typically found in more xeric habitats. Taken together these results suggest that species-specific variability in function and life history may drive short-term nonrandom species-specific responses to disturbance and climatic change.

Assessing the effects of climate on forest dynamics and structure, however, is complicated as other dynamical features of forests may obscure any differential species-specific signal. The responses of forests to climatic change may be masked or complicated by succession or recovery of forests from past disturbances (Lawrence, 2005; Chave *et al.*, 2008). Further, locally, while many of the above studies have focused on a handful of species, a large fraction of tropical tree species may not show any clear local habitat preference or responses to local variation in topography/variation in soil moisture (Webb & Peart, 2000; Harms *et al.*, 2001; Valencia *et al.*, 2004). If neutral or dispersal assembly is important, then drift, and history might play more of a role in long-term compositional change in tropical forests than niche differences (Hubbell & Foster, 1986; Hubbell, 1997, 2001; Bell, 2001).

Here we report on the nature of a 20-year change observed within a long-term monitored tropical secondary forest plot across differing aged areas of within the forest. We assessed three separate hypotheses for temporal shifts in community floristic composition, dominance, and function.

Differential functional response to drought hypothesis

Several studies have indicated that if the forest species composition and dominance is primarily influenced by differential drought responses of species then: (H1a) the functional composition of the forest community should shift in dominance primarily along soil moisture gradients (Condit, 1998; Condit *et al.*, 2000); (H1b) Functionally, drought should disproportionately impact small stemmed understory species, and evergreen simple-leaved species (Stowe & Brown, 1981; Condit *et al.*, 1996b), which tend to have shallower rooting depths and cannot access deeper soil moisture (Poorter, 2005); Further, lianas should be less susceptible to and perhaps respond favorably to drought (Swaine & Grace, 2007) (H:1c) Spatially, rates of turnover should be greatest in more wet areas of the forest as these areas tend to have higher abundances of evergreen species (Borchert, 1994; Poorter, 2005; Engelbrecht *et al.*, 2007).

Recovery from disturbance hypothesis

Alternatively, if recovery from past disturbance (succession) has been more important, because of soil water and light changes associated with succession (Bazzaz & Wayne, 1994), then (H:2a) species composition and dominance of younger forest should, over time, come to approximate the dominance and composition of older forest (Austin, 1977; Bakker *et al.*, 1996; Franklin *et al.*, 1999); (H:2b) Functionally, with forest maturation we would expect an increase in more evergreen species, an increase or a constancy in the density of stems, the relative proportion of simple and evergreen leaved species will increase, but compound-leaved and deciduous species should decrease (Budowski, 1970;

Horn, 1971; Givinsh, 1978; Opler, 1978; Janzen, 1986; Arroyo-Mora *et al.*, 2005). Further, the density and proportion of liana stems should decrease with time (Letcher & Chazdon, 2009).

Neutral drift and dispersal hypothesis

If neutral drift and dispersal limitation (H:3a) has been more important (Bell, 2001; Hubbell, 2001) then changes in functional and floristic composition and dominance would not be uniformly directional across habitats and areas of the forest that differ in age. Further, there should not be a functional signal associated with forest dynamics. Instead, any directional changes observed within habitats, different aged areas would, and functional differences between species should effectively be independent of each other (Clark & McLachlan, 2003).

We show that between census periods the San Emilio Forest Dynamics Plot (SEFDP) has been witness to extended drought conditions including the driest year yet recorded as well as a longer-term drying trend that has occurred during the life span of many of the trees within the plot. The unique age and climate heterogeneity of the forest allows us to assess if changes in functional composition, species composition, and dominance are more consistent with predictions of changes expected from recovery to disturbance, response to climate shifts, or from drift. Specifically, we assess if (i) the observed drought conditions have been a more primary driver of forest dynamics than recovery from past disturbance; and (ii) that heightened drought has differentially shifted patterns of community floristic dominance and forest functional composition. We utilize multivariate techniques to quantify directional shifts in floristic composition and species dominance in both number of individuals and total biomass. While we observe some evidence for a secondary signal of recovery from disturbance our results suggest that the observed dynamics of the forest has been primarily influenced by several drought years and a longer-term decrease in rainfall. Our results largely are consistent with predictions (Borchert, 1998; Brando *et al.*, 2008) for how tropical forests will respond to predicted decreases in rainfall and reductions in water-balance due to climate change.

Methods

Study site

Data were collected from the Area de Conservación de Guanacaste (ACG), Sector Santa Rosa, Guanacaste Province of Costa Rica (10°45′N, 85°30′W). The study site is a long-term forest dynamics plot within seasonally dry tropical forest. The plot was established in the mid-1970s by S. P. Hubbell.

The specific study area is locally known as the San Emilio forest (Bosque San Emilio), a 16.32 ha tropical dry forest plot (240 m × 680 m) which included 386, 20 m² permanently staked quadrats. The plot is located at 10.84N, −85.61W and ranges from 240 to 300 m in elevation. In 1996, soil moisture surveys, at each of the 386 stakes that demarcate the SEFDP were conducted separately from the vegetation survey. Several habitat types were identified including slope, mesa top, and valley bottom see also Appendices S1 and S2, Figs S1–S3). The forest consists of areas of differing ages – ranging from 80 years to approximately 100–150 years old (see discussion in Appendix S1).

In total, ~150 tree species have been recorded in the plot (see Data Supplement 1 for a detailing of the taxonomy and authorities of the species within the SEFDP). Identification of all specimens of these species were conducted at the Herbario Nacional de Costa Rica, and in consultation with taxonomists affiliated with the Costa Rican Instituto de Biodiversidad (INBIO). Taxonomic and identification discrepancies between the 1976 and 1996 have been standardized to follow Enquist & Sullivan (2001) with voucher specimens deposited in the University of New Mexico herbarium and also accessible online at the University of Arizona herbarium (specimens, collection numbers and dates are currently being entered into the UofA database and accessible via a search on 'Enquist' as collector via http://ag.arizona.edu/herbarium/search).

To assess these three hypotheses we conducted four classes of analyses:

(i) Assessing precipitation variability and change in Guanacaste – To assess the climatic trend during the period of the lifespan of the trees found within the SEFDP up to 1996 we analyzed the longest climate record from lowland Guanacaste province (Borchert, 1998) W. Hagnauer & R. Borchert, unpublished results). The dataset is from near Cañas, Costa Rica (10°42′N, 85°09′W, ~90 m elevation, mean annual precipitation 1565 mm see Enquist & Leffler, 2001) approximately 70 km miles from the SEFDP. The mean annual precipitation and annual variation in precipitation at Cañas is essentially identical to observed rainfall patterns within the ACG (see Enquist & Leffler, 2001; Kalacska *et al.*, 2004). Rainfall is highly seasonal with an average of ~78% of rainfall within lowland Guanacaste falling between June and November (data from W. Hagnauer & R. Borchert, unpublished results). A summary of the climate of the ACG and area near the SEFDP can be found in Janzen (1986).

Soil Moisture and Canopy Cover Surveys – Soil moisture surveys within the SEFDP were performed during 1996: April (representing the dry season) and late June (representing the wet season). Following Thompson *et al.* (1996) we measured surface soil moisture at each of the 386 stakes in the plot. Four measurements were recorded each stake. Relative moisture values were then calibrated to gravimetric water content based on a calibration curve generated from soil samples taken from within SEFDP with increasing amounts added to known water content added to dried samples and allowed to equilibrate before measurements were made (see Appendix S1). This method allowed us to assess spatial and temporal variation in relative moisture content readings at a soil depth of approximately 15 cm.

(ii) Assessing variation in forest environment, mortality, and turnover – To assess spatial variation in forest structure and the physical environment we first measured spatial variation in soil moisture and percent canopy cover (see Appendices S1–S3). For both 1976 and 1996 data sets we also calculated the abundance, biomass (Brown, 1997), and functional group type of each species. Demographic rates were calculated from following the fates of approximately 8000 individuals within the SEFDP in 1976 (Appendix S1). Of these individuals, only trees that attained sizes over 10 cm dbh were included. We calculated mortality rate as: $\mu = [\ln(N_0) - \ln(N_t)]/t$, where N_0 is the initial number of stems at time 0 and N_t is the number of surviving stems at time t (Condit *et al.*, 1995). Similarly, recruitment rate, was calculated as $\omega = [\ln(N_t) - \ln(S_t)]/t$, where N_t is the number of stems for a given species at time t and S_t is the number of surviving stems at time t (Condit *et al.*, 1999). To evaluate correlations between the biotic and abiotic properties within the SEFDP we first conducted Pearson's product–moment correlations or, where appropriate, nonparametric Spearman's rank correlations. Further, we assessed proportional changes in the functional composition between sites and within the entire forest utilizing a likelihood ratio test or *G*-test. Unless noted, all statistical analyses were conducted in the R statistical package (R Development Core Team, 2009).

Lastly, to investigate forest-wide community dynamics in relation to the environmental heterogeneity, in both 1976 and 1996, within each of the 386 20 m^2 quadrats within the SEFDP, we calculated annual rate of change, α of individuals in units of individuals per unit area and biomass per unit area. Measures of α incorporate *all* individuals mapped. Following Condit *et al.*, (1996a, (b), we calculated: $\alpha_N^{\text{Plot}} = \ln(N_t/N_0)$ and $\alpha_B^{\text{Plot}} = \ln(M_t/M_0)$, where N_0 is the total number of individuals (or total biomass of individuals, M_0) within a quadrat in 1976 and N_t is the total number of individuals (or total biomass of individuals, M_t) in the same quadrat but at a future time, t (in this case, 1996). Any variation in α thus reflects absolute changes in plot stem density and/or biomass. We next mapped and analyzed the resulting α values in a Geographic Information System (GIS) using the ARC/INFO platform via ARCGIS 8.0 (SRI, Redlands, CA, USA) with respect to habitat types, relative forest age classes, and all continuous environmental variables (elevation, soil moisture, and percent forest canopy cover). Nonparametric logistic regressions were used to test the relationships between α and the nominal, categorical variables of habitat type.

(iii) Assessing changes in functional groups and focal species – We classified the majority of the species found within the study plot to coarse-grained functional groups based on leafing phenology (deciduous or evergreen), leaf type (simple or compound leaf), canopy position when mature (canopy, subcanopy, understory), and forest succession association (Smith *et al.*, 1997). Functional and successionary classifications follow Enquist & Sullivan (2001) and (Kalacska *et al.*, 2004). These classifications have been used previously for this forest, although less formally (Janzen & Leisner, 1980; Janzen, 1983; Sorensen, 1998). In addition we also conducted a preliminary analysis with wood density and leaf carbon isotope composition to assess the role of

functional traits on forest dynamics. Next, to assess the responses of some of the most abundant individual species, in both 1976 and 1996, we examined changes in relative abundance and size distribution of nine focal tree species. Each species represents the diversity of functional groups and forest succession stages (see Appendix S1). We also assessed geographic distributions of each focal species by consulting the literature and distributions listed within the Missouri Botanical Gardens Tropicos website [http://www.tropicos.com query (http://www.tropicos.org/) 12 January 2009].

(iv) Assessing directionality in multivariate shifts in species compositions – We assessed the degree of directionality in forest composition by using multivariate ordination analyses (see Appendix S1). Multivariate analyses were conducted using either species abundance or total species biomass. Using the program CANOCO v.4 for Windows (ter Braak & Similauer, 1998), we performed a detrended canonical analysis (DCA). To assess the degree of changes in the temporal relationships between focal species from 1976 and 1996, we conducted a simultaneous DCA on 1976 and 1996 species abundance units of number of individuals (N-DCA) and biomass (M-DCA).

Results

Abiotic variation

Long-term precipitation variability. We find two patterns within the long-term precipitation record (Fig. 1). First,
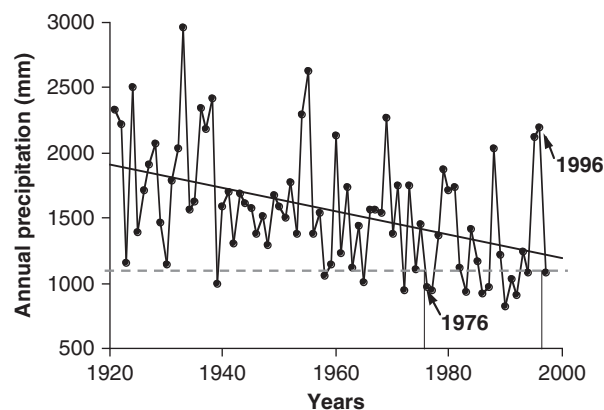
Fig. 1 Relationship between annual rainfall across 77 years in lowland Guanacaste. Data are from the Las Pomas weather station, near Cañas, Guanacaste (Borchert, 1998; W. Hagnauer & R. Borchert, unpublished results). Although there has been a wide degree of variability across years, within the life span of the trees within the SEFDP, between 1921 and 1997, there has been a decrease in mean annual precipitation ($N = 77$, $F = 16.48$, $r^2 = 0.180$, $P = 0.00012$, SD $= 470.04$, mean $= 1563.64$ mm, min $= 832$ mm, max $= 2962$ mm). In addition to the longer term-trend, in the 20 years *between* the two SEFDP census periods (1976 and 1996) there have been *nine* drought years where annual precipitation fell below 1 SD of annual rainfall (1 SD $= 470$ mm or 1100 mm annual rainfall; dotted line). SEFDP, San Emilio Forest Dynamics Plot.

between 1921 and 1997, within the life span of the trees in the SEFDP, there has been a decrease in mean annual precipitation (Fig. 1; $n = 77$, F = 16.48, $r^2 = 0.180$, $P = 0.00012$, SD = 470.04, mean = 1563.64 mm, min = 832 mm, max = 2962 mm). Second, between the two census periods of 1976 and 1996 there has been an increase is frequency of dry years. We defined dry years as those years where annual rainfall was <1 SD (470 mm) of the long-term mean 1563.64 or 1100 mm (the dotted line in Fig. 1). Comparing the prevalence of years with drier than usual annual rainfall before (1976) and during the census period (1976 to 1996) the prevalence of drier than usual years increased (G-test, $G = 12.743$, df = 1, $P = 0.0004$). In the 54 years up to the original survey in 1976, 7.4% of the years were dry years (a total of 4 dry years) whereas in the 20 years between 1976 to the second survey in 1996, the frequency of dry years increased to 45% (a total of 9 dry years). Further, not only did the driest year recorded occur in-between the census periods (1990, 832 mm) but also several of these dry years were consecutive, with the only *three* back-to-back drier than usual years (1990, 1991, 1992). The observed increase in dry years between 1976 and 1996 coincides with the increase in the intensity of the El Niño/Southern Oscillation (ENSO) conditions during this time including the intense 1982–1983 El Niño (Enquist & Leffler, 2001; Malhi & Wright, 2004; Heimann & Reichstein, 2008), a 'warm' Pacific Decadal Oscillation regime that occurred between 1976 till the mid 1990s (Mantua & Hare, 2002), as well as a heightened increase in temperatures throughout the tropics (Malhi & Wright, 2004). Together, these patterns indicate that, when compared with the past century, the trees within the SEFDP have likely experienced heightened drought conditions – especially in the time period between the two forest census periods.

Topography, forest age, soil moisture and %canopy cover. Similar to past findings in other tropical forests (Daws *et al.*, 2002) both wet and dry season soil moisture were significantly correlated with topography, % canopy cover, and to some extent forest age. Each of these environmental and physical attributes of the forest exhibited significant correlations and covariation (Table S1 and Fig. S2; see Appendix S1). Figs S1–S3 show GIS maps of these variables within the SEFDP.

Forest stem density, biomass, turnover, and recruitment

Changes in stem density and demography. Between 1976 and 1996 the San Emilio forest experienced a net *decrease* in the density of individual trees (Fig. 5). The total number of sampled individuals in the SEFDP, including lianas, decreased 27.2% from 25 746 in 1976 to 18 734 (Fig. 2a; Wilcoxon's rank sum test, $W = 113 213$, $P < 0.0001$). In 1976 the mean number of stems per 20 m^2 quadrat was 66.8. In 1996, this number declined to 48.5 stems per 20 m^2. This decrease was observed across all habitat types throughout the forest and forest ages (Fig. S6). Plotting the frequency distribution of stem diameters shows that
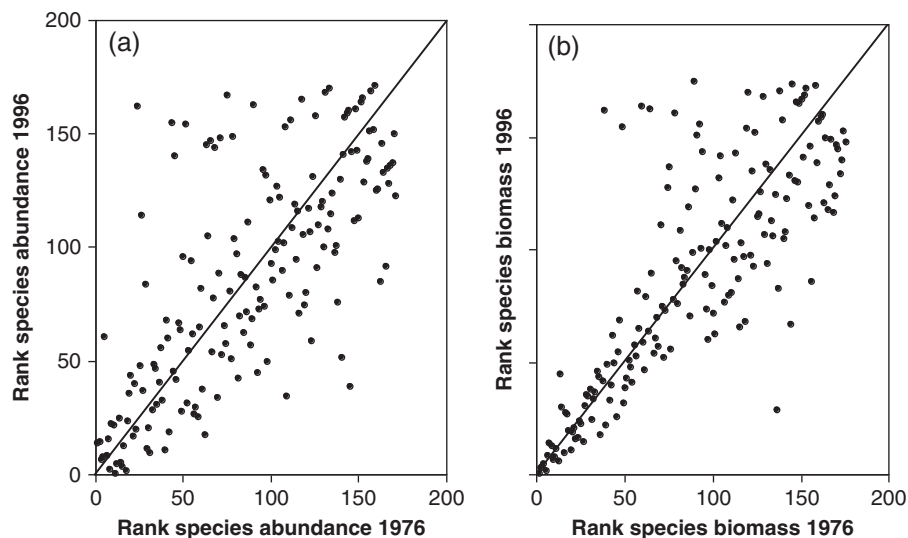
Fig. 2 Rank dominance plots of species community dominance. (a) Community rank abundance scores for each species from 1976 compared with 1996. (b) Community rank aboveground biomass scores from 1976 as compared with 1996. For each plot a 1 : 1 line is drawn. Points falling on the 1 : 1 line would indicate no change in community dominance for that species. Points falling either below the line or above the line would indicate species either increasing or decreasing in dominance, respectively. The distribution of points indicate much variation in species both above and below the 1 : 1 line indicating that there has been both increases and decreases in the proportional dominance of species within the forest.

most of the reduction of individuals appears to be associated with the smallest size classes (Fig. S4) with small stems between 3 and 4 cm dbh suffering the largest decreases in stem numbers. The forest-wide annual mortality rate, μ, for trees ≥ 10 cm dbh was 3.52%. Forest-wide annual recruitment, ω, however, was calculated as 3.05%. The difference between these numbers reflect the observed changes in stem density and indicate that tree mortality exceeded recruitment. Note, the observed SEFDP mortality rate is higher than the average tropical forests (Phillips, 1996; Stephenson & van Mantgem, 2005) which tend to have mortality rates of 1–2% per year (Condit *et al.*, 1995).

Changes in forest biomass. Despite the above decrease in stem numbers there does not appear to have been a strong directional change in forest biomass. The total biomass of the 16.32ha forest was 221.7 Mg ha^{-1} in 1976 and 214 Mg ha^{-1} in 1996. This range is similar to other reported values for topical seasonal forests (Brown & Lugo, 1984; Brown, 1997; Asner *et al.*, 2009). For the entire SEFDP the total aboveground biomass decreased by 7.66 Mg ha^{-1}, or 3.5%, which is consistent, although slightly higher than a recent observed decreased 5.3 Mg ha^{-1} in biomass of Amazonian forests in response to the 2005 El Niño drought (Phillips *et al.*, 2009). It is important to note that the observed decrease in the SEFDP, however, appears to be scale dependent and mainly driven by a one or a few large biomass quadrats (see Fig. 2b). When forest biomass was examined on a smaller spatial scale, a per unit quadrat basis (biomass per 20 m^2 quadrat), we find that the average biomass per quadrat did not significantly change between the two sample periods (Fig. 2b; Wilcoxon's rank sum test, $W = 71\,129$, $P = 0.277$) indicating that assessing changes in biomass is sensitive to the spatial scale of sampling and to the biomass estimates of the largest trees (Chave *et al.*, 2003). Figures 2B and S5 indicate that most areas of the forest did not experience decreases in biomass.

Dynamics of quadrat biomass and number of individuals. While there were no significant relationships between the change in plot biomass, α_B^{Plot}, and any environmental variable (see Table S1), variation in the rate of change in the number of stems per plot, α_N^{Plot}, was significantly related to variation in abiotic features. Together, these results indicate that low elevation, wet, and more evergreen areas of the forest experienced heightened mortality and larger *decreases* in the number of individuals (see additional discussion in Appendix S1).

Rates of change in plot density, α_N^{Plot}, and biomass, α_B^{Plot}, fluctuated across space in the San Emilio forest

plot (see Fig. S5). However, these rates varied depending on the measure. In change of the number of stems per unit area (α_N^{Plot}), nearly 90% of the quadrats examined exhibited negative values, reflecting a close to uniform reduction in the total number of stems across the plot. In contrast, only about 45% of these quadrats showed negative values in units of biomass (α_B^{Plot}). Interestingly, rates of change in plot biomass α_B^{Plot} showed no relationship with total plot biomass in 1976 ($r = 0.009$, df = 384, $P = 0.855$) but a slight positive correlation with total plot biomass in 1996 ($r = 0.122$, df = 384, $P = 0.016$) indicating that plots experiencing high turnover in plot biomass since 1976 tended to be characterized by higher amounts of biomass in 1996.

Change in species richness and dominance

Data Supplement 1 lists all of the species encountered in 1976 and 1996, and their authorities. The data presented in Data Supplement 2 provides a summary of the abundances, biomass, functional groupings, and successional associations of each species across years. Within the SEFDP, species dominance differed between habitats and successionary ages (see also multivariate results below). For example, the dominant species in the younger areas in 1976 were *Luehea speciosa*, *Lonchocarpus parviflorus*, *Casearia corymbosa*, *Guazuma ulmifolia*, *Allophylus occidentalis*, whereas the most abundant species in the older areas were *Malvaviscus arboreus*, *A. occidentalis*, *L. parviflorus*, *Trichilia cuneata*, *Ocotea veraguensis*. Species composition in more wet areas of the forest, slope habitats, included *Casearia sylvestris*, *A. occidentalis*, *O. veraguensis*, *Aphelandra deppeana*, *Lonchocarpus rugosus*. Dominant species in more dry areas, hill top/ridge, included *C. corymbosa*, *A. occidentalis*, *Bursera simaruba*, *L. parviflorus*.

Between 1996 and 1976 there were significant changes in patterns of species dominance within the community. Figure 3 shows there has been a shift in the relative dominance of many species with species increasing *and* decreasing in community dominance. Data for the species community rank based on abundance and biomass are given in Supplement 2. Analysis of changes in species abundance as measured by both numbers of individuals and biomass reveals a dynamic forest. While the forest community distribution of species biomass did not change over the 20-year interval ($D = 0.0756$, P-value = 0.7097) the distribution of species abundances was marginally significant (Kolmogorov–Smirnov test, $D = 0.1395$, $P = 0.07025$). While rare species appear to shift in dominance more than common species (Fig. 3), there has been some notable changes in dominance within even the most common species (see Appendix S1 and S4). For example, in 1976,
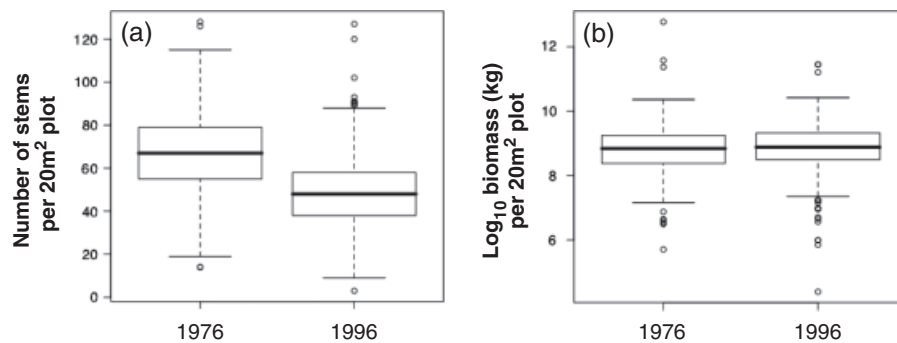
Fig. 3 Change in either stem numbers or biomass per 20 m² plot in the SEFDP plot. (a) Box plot showing the total number of stems >3 cm dbh per 20 × 20 m in 1976 and 1996. (b) Box plot comparing the distribution of total plot biomass (kg) for the number of stems >3 cm dbh per 20 m² in 1976 and 1996. For the entire 16ha forest the total aboveground biomass decreased by 7.66 Mg ha^{-1}. However, when analyzed on a per 20 m² there has not been a change in the mean biomass even though there has been a significant decrease in the total number of stems indicating that the total reduction of biomass of the forest is likely due to one or a few large biomass quadrats. SEFDP, San Emilio Forest Dynamics Plot.

the three most abundant tree species, in terms of number of individuals, were *A. occidentalis*, *Casearia nitida*, and *C. sylvestris* – all understory and tending to be evergreen tree species. However, in 1996, the top three abundant species changed to *Astronium graveolens*, *Bursera simarouba*, and *Semialarium mexicanum* each deciduous species.

Change in functional group abundance. Next, we assessed the nature of the change in community species dominance in Fig. 3 by assessing the proportional shifts in functional composition. We utilized a likelihood ratio test (*G*-test) to test if the proportions of forest composition of one variable in 1976 were the same in 1996. We observed several significant changes in proportional composition of the forest (Fig. 4; see also Fig. S4), both in terms of number of individuals and biomass, across each of the functional groups: (i) the proportion of evergreen trees in the SEFDP decreased from 21.2% to 14.2% but the proportion of deciduous trees increased from 64% to 67% (number of individuals, $G = 319.6$, df = 1, $P < 0.0001$; biomass $G = 6467$, $P < 0.0001$); (ii) the proportion of compound leaved individuals increased from 30.7% to 33.7% while simple leaved species decreased from 59.9% to 55.3% (abundance $G = 65.6$, df = 1, $P < 0.0001$; Biomass $G = 7215$, df = 1, $P < 0.0001$); (iii) the proportion of stems that were lianas increased from 7.0% to 10.2% ($G = 56.85$, df = 1, $P < 0.0001$); (iv) the relative dominance of canopy types changed (abundance $G = 431$, df = 2, $P < 0.001$; Biomass $G = 41379$, df = 2, $P < 0.0001$) – subcanopy, and understory trees all decreased in proportion while larger canopy species increased; and (v) the relative dominance of different successional classes (Abundance $G = 555$, df = 5,

$P < 0.0001$; Biomass $G = 43893$, df = 5, $P < 0.001$) also significantly changed but there were no clear directional patterns across groups. Functional shifts in composition were often due to disproportionate reductions in stem numbers and/or biomass between groups. For example, the number of individuals in both the evergreen and deciduous functional groups experienced declines in numbers (Fig. S4) but the reductions were larger in deciduous individuals (−22% and −46%, respectively; see Fig. S4). Similarly, both the compound- and simple-leaved functional groups experienced declines in numbers but the decline was greatest for simple-leaved individuals (−32% and −22%, respectively; see Fig. S4). Further, the increase in the proportion of trees in the forest that were canopy trees does not reflect an increase in their numbers (in fact their numbers remained about the same) but instead a dramatic reduction of subcanopy and understory individuals. Nonetheless, in contrast to evergreen and simple-leaved species, both deciduous and compound leaved categories as well as canopy trees increased in biomass (Fig. S4). Our conclusions do not change if we exclude from the analysis species that are partially evergreen or partial deciduous.

While there have been significant changes in the proportion of trees and biomass within each of the successional categories this change does not appear to follow expected directional successionary signal across all of the classes (Fig. 6, Fig. S4). While we do observe reductions in the proportion of trees within the SEFDP classified as pioneer and early successional species we do not see the expected in dominance of late succession species. We also did not find any significant correlations associated with percent change in species abundance or biomass with three functional traits related to plant
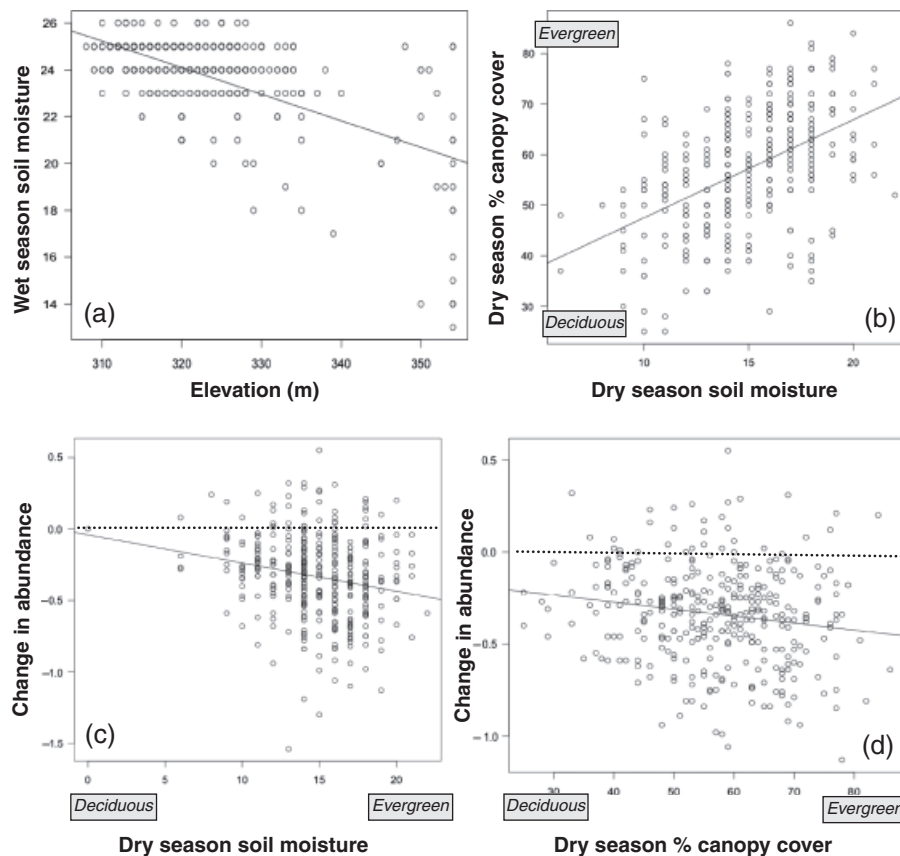
Fig. 4 (a) Negative correlation between quadrant elevation and wet season (June) average soil moisture content (mL 100 g^{-1}) at each of the 386 stakes that demarcates each of the quadrants within the SEFDP. (b) The relationship between dry season (April) soil moisture and seasonal percent canopy cover as measured across each of the 386 stakes at each 20 m interval throughout the SEFDP. Soil moisture is mL/100 g soil. (c) Significant negative relationship between dry season soil moisture and the change in stem density, α_N^{Plot} (see main text and Table S1 for a summary of the statistics). (d) Significant negative relationship between the percent canopy cover in the dry season (April) and the observed change in stem density, α_N^{Plot} (see main text and Table S1 for a summary of the statistics). The black dotted line is where $\alpha_N^{\text{Plot}} = 0$ (no change in stem density between census years). Points falling above the line are quadrants or subplots that have experienced a net increase in stem density. Those points below the dotted line (the majority of quadrants or subplots) have shown a decrease in stem density. The more evergreen and wet areas of the forest have experienced the greatest decrease in stem densities. SEFDP, San Emilio Forest Dynamics Plot.

water use strategies, leaf stable carbon isotope, and leaf thickness (see Leffler & Enquist, 2002) and wood density (Enquist *et al.*, 1999).

Changes in species dominance and size structure. For the most common species in the SEFDP, changes in abundance appear to be primarily related to the degree of deciduousness, and canopy position and tree size. Temporal changes in the size distributions of each of the nine abundant focal species significantly changed (Kolmogorov–Smirnov test, $P < 0.001$; see Fig. 7) but in differing ways and generally reflect the overall functional changes observed in the forest (Fig. 6). Those focal species experiencing reductions in abundance (disproportionately in their smallest size classes) were observed in primarily understory/sub canopy trees and

evergreen species whereas those species increasing in abundance were primarily deciduous, canopy species. Tables S2a–d provide the top-ten species relative dominance values (in terms of stem density and biomass) across each of these habitat types and relative age classes in 1976 and 1996. Comparing species relative rankings, both in terms of biomass and density, across all habitats and forest ages indicates that the forest has changed in species dominance appreciably between the two surveys. For example, there are several species, besides the focal species, that have notably decreased in abundance (density) including: *Cordia alliodora*, *G. ulmifolia*, *M. arboreus*, *L. rugosa*, *L. parviflorus*, *T. cuneata*, *Sciadodendron excesa*. Species that have notably increased across habitats include: *Calycophyllum*
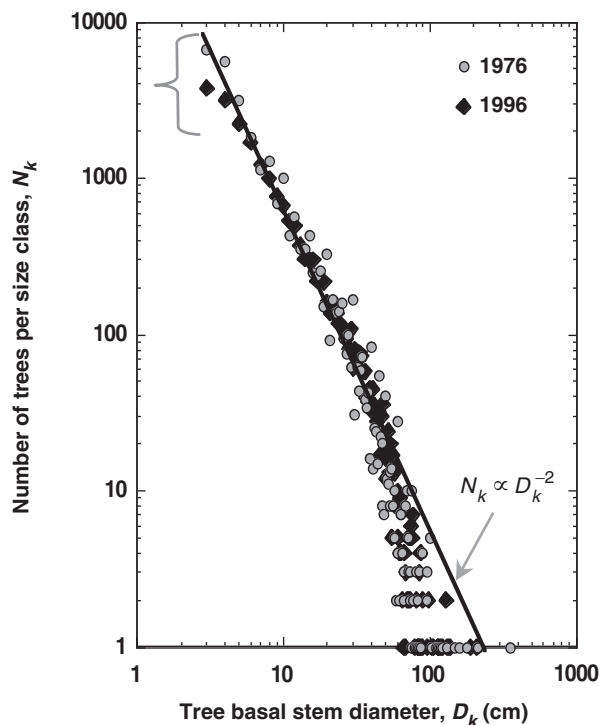
$N_k \propto D_k^{-2}$

Fig. 5 Size distribution of trees within the SEFDP. Frequency distribution for the forest in both 1976 and 1996. In both years, trees were binned at 2 cm increments. The overlaid line is of slope of –2, which is the hypothesized steady-state distribution (Enquist *et al.*, 2009a; West *et al.*, 2009). Across years only the smallest size classes have experienced a large decrease in numbers of individuals. The smallest size classes, 3 and 4 cm dbh, have each experienced a decrease in over 3000 individuals. Thus, most of the change in the number of individuals within the SEFDP has been within the smallest size classes. SEFDP, San Emilio Forest Dynamics Plot.

candidisimum, Exostema mexicana, Macura tinctora, and *Tababueia ochracea.* Reflecting the patterns shown in Fig. 4., the most common shade-tolerant evergreen species characteristic of mid- to late succession *Annona reticulata, O. veraguensis,* and *Hirtella racemosa* (Arroyo-Mora *et al.*, 2005), have all decreased in abundance and biomass. In addition, *A. deppeana* an understory shrub to treelet species typical of more evergreen forest experienced a dramatic reduction of individuals (from 151 in 1976 to 1 in 1996).

Lianas. Summing the total number of lianas surveyed in 1976 and 1996 reveals that there was a slight increase in the total number of lianas. A total of 1774 liana stems were recorded in 1976 and 1891 lianas in 1996 (see Fig. S4 and Supplement 2). As a proportion of all stems within the forest, lianas significantly increased from 7.02% to 10.16%.

Forest community multivariate differences trajectories

DCA axis correlations and trajectories. We observed a significant relationship between quadrat DCA scores, for both species abundance (N-DCA), and species biomass (M-DCA) scores, and local plot environmental attributes (provided in Table 1 and Tables S1 and S4; see Appendix S1). Figures 6 and 7 plot the mean 1976 and 1996 site scores for each habitat type and relative age class, respectively. The temporal difference between mean quadrat scores indicates a directional shift in forest community dominance. First, for the N-DCA scores, for each of the habitats and relative forest ages, despite temporal changes in their multivariate scores between 1976 and 1996, the relative spacing between the forest habitats and forest ages was maintained. This result means that the absolute differences in the change of community composition and dominance *between* both the forest habitats and the different aged areas of the forest were maintained across time. Second, across habitats and ages, there has been a uniform and directional change in N-DCA scores in the floristic composition and abundance. In contrast to the N-DCA results, analysis of the temporal trajectories of mean habitat and age M-DCA scores did not reveal these patterns and there were not strong uniform directional changes across habitats and forest ages (see Fig. S6). The difference for N-DCA and M-DCA trajectories likely reflects that most of the observed change in the total number of individuals within the SEFDP was associated with the smallest size classes (Fig. 5) that together comprise a very small proportion of forest biomass (Chave *et al.*, 2003; Enquist *et al.*, 2009).

Discussion

Over the past century, several studies have reported a gradual decrease in mean annual rainfall in lowland Guanacaste. This observed drying trend is similar to findings from other studies reporting longer-term decreases in precipitation in Central America (Windsor & Rand, 1985; Fleming, 1986; Vargas & Trejos, 1994; Borchert, 1998; Pounds *et al.*, 1999; New *et al.*, 2001; Neelin *et al.*, 2006). These changes can be visualized spatially for this region utilizing the Climate Wizard tool (Girvetz *et al.*, 2009) (results from http://www.climatewizard.org/, accessed April 1, 2010), and appear to correspond with the 'warm' Pacific Decadal Oscillation period (Mantua & Hare, 2002). The trend is also consistent with predictions from global change models showing increased probabilities of decreased precipitation in this region of Central America (Christensen *et al.*, 2007; IPCC, 2007; Meehl *et al.*, 2007; Girvetz *et al.*, 2009).
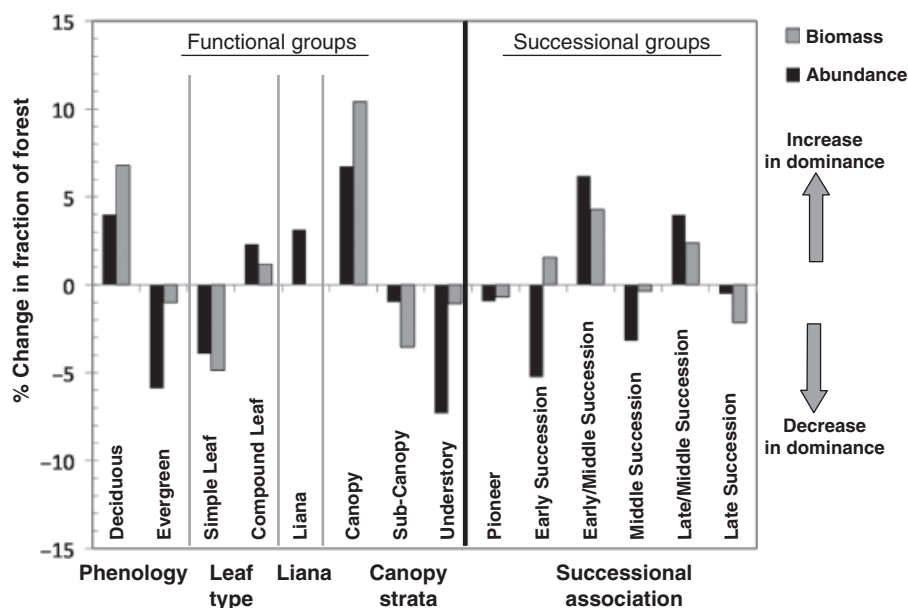
Fig. 6 Proportional change in functional and successionary groups within the SEFDP between the 1976 and 1996 survey. Each bar is the proportional change in trees within each functional group measured in abundance (black) and biomass (grey). Each of the functional groups and successionary groups experienced significant changes in proportion between the two surveys (see the main text). Summary data for each species are given in Data Supplement 2. SEFDP, San Emilio Forest Dynamics Plot.

As the trees originally recorded in the SEFDP in 1976 were established during the period after 1921, which consisted of numerous wet years (Malhi & Wright, 2004) and based on previous findings on the role of ENSO driven drought on tropical forest soil water reserves (Nepstad *et al.*, 1994; Borchert, 1998) it is reasonable to expect that the increase of dry years between 1976 and 1996 might differentially influence the species and functional composition of the forest in between census periods of 1976 and 1996. However, to date there has been a limited number of studies on the degree of differential functional responses of tropical forests to drought.

Overall, our findings highlight five changes in the SEFDP that are consistent with the hypothesis that decreasing water availability between the two surveys has primary influenced the dynamics and functional composition of the SEFDP between 1976 and 1996 via differential species responses:

First, our density-based DCA analyses showed unidirectional temporal shifts in species composition and/ or species dominance along soil moisture and topographic gradients (Fig. 8). This pattern was observed across all habitat types and relative age classes. The observed correlations between each DCA axis and soil moisture and elevation is consistent with the expectation that differential species responses to soil moisture availability is a significant component of species separation

along mesotopographic gradients within the San Emilio forest as well as the response of the forest to drought.

Second, the uniform shift in species composition and dominance is reflected in a shift in the functional attributes of specific taxa across the forest (Fig. 6). We observed a *decrease* in the total number of smaller sized stems (between 3 and 4 cm dbh) (Fig. 5). Further, we observe a significant change in the proportional representation in the forest including a reduction in the trees that were understory, simple-leaved, and evergreen (Fig. 6). While the decrease in the total number of stems was observed throughout the forest (Fig. S5), the wettest and more evergreen areas of the plot have experienced the greatest decreases (Fig. 4) and (Table S1). This is also reflected by the fact that in 1976 we observed weak to no correlation between stem density per $20\,m^2$ plot and soil moisture (Table S1), however, in 1996 a significant *negative* correlation was observed. The functional changes observed in Fig. 6 and the change in the more dominant species (see Fig. 7) are consistent with past findings on the response of functional types to drought stress (Condit, 1998) but opposite to the expected functional change in the forest due to successionary changes (Arroyo-Mora *et al.*, 2005). Condit *et al.* (1996a) found that drought lead to a reduction in abundance of the small statured subcanopy trees and shrub species which tend to be found in the wetter areas of the forest. Drought deciduous species tend to be more able to
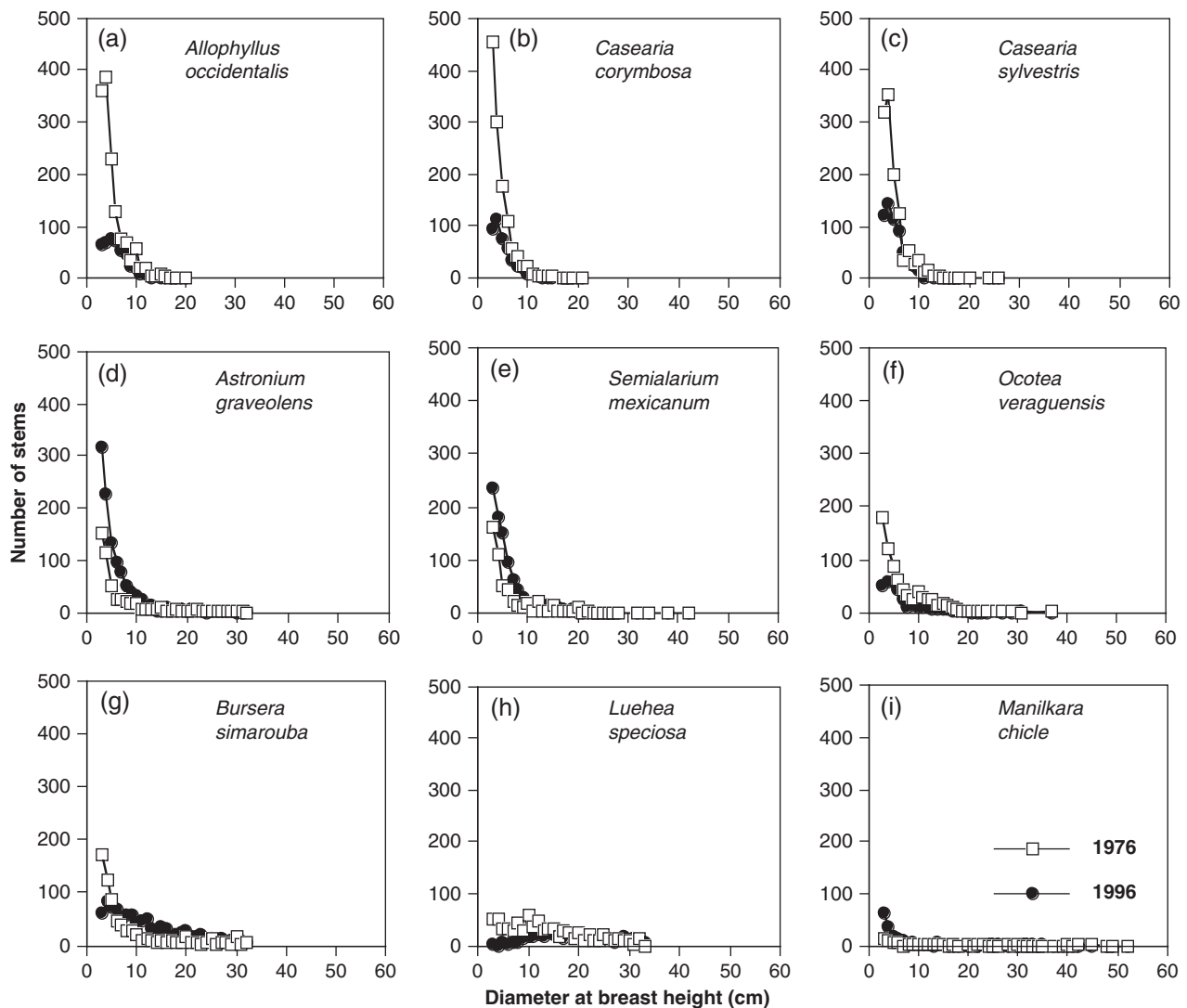
Fig. 7 Comparisons of stem size class distributions between 1976 and 1996 for nine focal species that differ in the functional characteristics. (a) *Allophyllus occidentalis* (partially evergreen, midsuccession stage, and understory to subcanopy); (b) *Casearia corymbosa* (evergreen, simple leaved, mid-to-late succession stage, understory); (c) *Casearia sylvestris* (evergreen, simple leaved, mid-to-late succession stage, understory); (d) *Astronium graveolens* (deciduous, compound leaf, mid- to late succession stage, and canopy); (e) *Semialarium mexicanum* (deciduous, simple leaved, early succession stage, understory); (f) *Ocotea veraguensis* (evergreen, simple leaved, late succession stage, understory); (g) *Busera simarouba* (deciduous, compound leaf, early to mid- succession, and canopy); (h) *Luehea speciosa* (deciduous, simple leafed, early succession stage, canopy); and (i) *Manilkara chicle* (evergreen, late succession stage, canopy). Note, many of the understory and evergreen species have experienced a large decrease in numbers – especially in the smallest size classes. In contrast, many of the deciduous, canopy species have increased in abundance.

withstand periods of increased water stress than more evergreen species (Borchert, 1994; Condit, 1998). Further, understory species and species associated with wetter slope habitats have been noted to be more sensitive to variation in edaphic conditions than canopy species (Gentry & Emmons, 1987) most likely due to more shallow rooting depths (Condit, 1998; Poorter, 2005).

Third, many of the changes in abundances of the focal species appear to match expectations from differential susceptibility to drought based on leafing habit and their geographic distribution across rainfall and rainfall seasonality gradients (Fig. 7). Many of the dominant species that have *decreased* in abundance, *C. corymbosa*, *C. sylvestris*, *O. veraguensis*, *A. occidentalis*, have geographic distributions that extend into more mesic
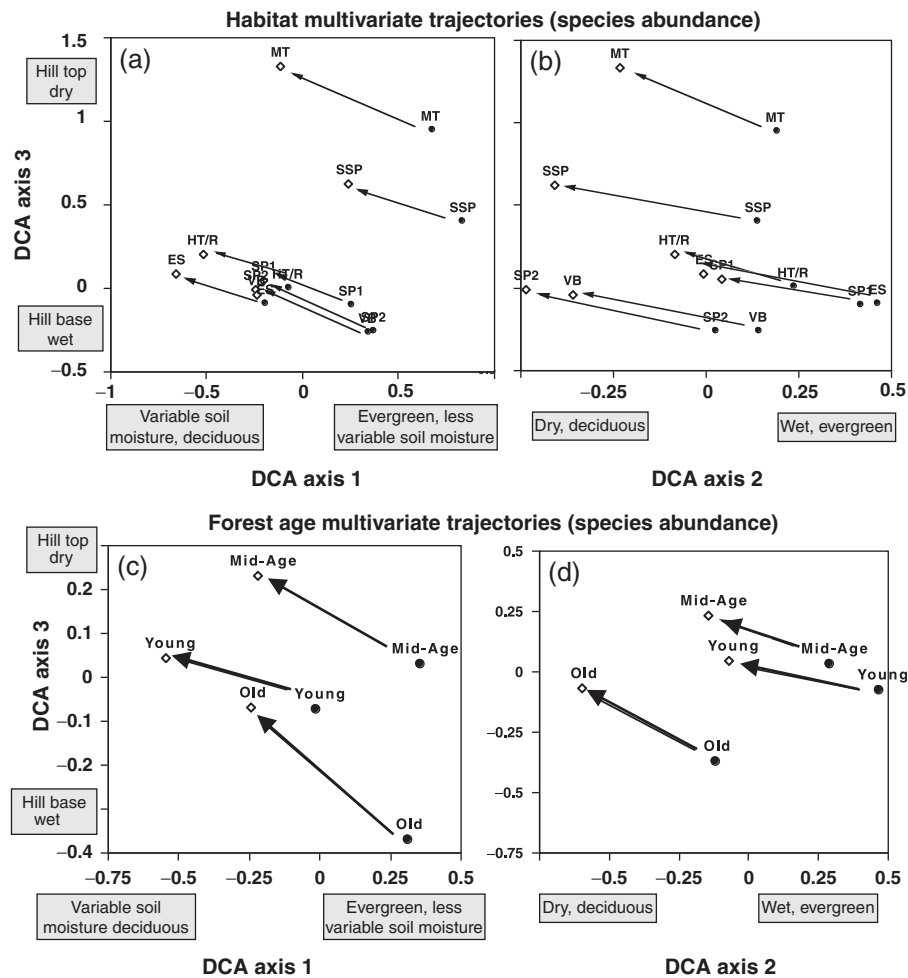
Fig. 8 Mean detrended canonical analysis (DCA) site scores, in units of stem density, across habitat types. (a) Plot of N-DCA axis 1 on the x-axis vs. DCA axis 3 on the y-axis; (b) depicts DCA axis 2 on the x-axis, vs. DCA axis 3 on the y-axis. The specific habitats labeled are ES = ravine/ephemeral stream, VB, valley bottom; SP1, gentle slope; SP2, slope; HT/R, hill top/ridge; SSP, steep slope; MT, mesa top. Arrows indicate direction of temporal change from 1976 to 1996. Also plotted are the mean DCA site scores, in units of density, across the three relative forest age classes – young forest, middle-aged forest, and oldest forest. (c) Plot shows DCA axis 1 on the x-axis; (d) depicts DCA axis 2 on the x-axis vs. DCA axis 3 on the y-axis. Each DCA axis is significantly correlated with either measures of soil moisture, annual variation in soil moisture, the degree of deciduousness of the canopy, or the elevation of the plot (see Table 1). Arrows indicate direction of temporal change from 1976 to 1996. Across all habitats and ages the floristic composition shifted from a more wet, evergreen forest to a deciduous forest typical of a more variable and drier soil moisture regime.

regions and are characterized by shorter duration of the dry season (see discussion Appendix S1). Further, many of the dominant species that have *increased* in abundance, *Semialarium mexicanum*, *Astronium graveolens*, *Bursera simarouba*, tend to have geographic distributions that extend into either more xeric regions with lower mean annual precipitation and/or experience a longer dry season. These species may be more broad climatic generalists (see Appendix S1).

Fourth, additional evidence of an observed compositional/dominance shift in the SEFDP comes from a reduction in the evergreen understory species. Perhaps the best example of this decline come from *Piper amalago*

L. In general, *P. amalago* is more typical of wet, dark understory of both secondary and old growth wet tropical forests in Mesoamerica (Chazdon & Field, 1987; Condit, 1998) (http://www.fs.fed.us/global/iitf/pdf/shrubs/Piper%20amalago.pdf). Consistent with the fourth point above, *P. amalago* has a geographic distribution that extends into wet forest and rainforest including Ecuador, Peru, and Bolivia. *P. amalago* rarely attains stem sizes >3 cm dbh, the minimal size cutoff of the SEFDP survey, and so was sporadically covered in the SEFDP forest survey. However, in 1976 many of the original survey maps included notes of understory species composition and cover. In particular, these maps

Table 1 Summary of the main environmental and physical correlations generating variability in multivariate space as marked by detrended correspondence analysis (DCA) conducted on species abundances (N) within each of the 386 continuous $20\,m^2$ subplots within the SEFDP

	N-DCA axis 1	N-DCA axis 2	N-DCA axis 3
Soil moisture mean			−0.43074***
Soil moisture dry season			−0.35291***
Elevation		−0.38464***	0.58950***
Soil moisture wet season	−0.1323*	0.30408***	
Percent cover dry season	0.3517***	0.30956***	
Range in soil moisture	−0.2900***		

Pearson's product moment correlation coefficient, r, for the top three correlates with each of the N-DCA axes. Note, here, the reported correlations are on DCA transformed on logarithmic axes. ***Significant at the 0.0001 level, *Significant at the 0.01 level.

show that multiple locations throughout the forest were dominated by *P. amalago*. In resurveying the forest in 1996 we paid attention to these notes of understory composition and in particular the presence of *P. amalago* clones. In 1996 *P. amalago* was reduced to one small clone within the SEFDP (that later died after the 1996 survey) indicating that this evergreen understory species typical of more evergreen forest has experienced a local population crash between the 1976 and 1996 survey. A similar precipitous decrease in the genus *Piper* occurred in response to El Niño driven drought in Panama (Condit *et al.*, 1996b).

Fifth, in contrast with expectations based on successional chronosequences (Letcher & Chazdon, 2009) we find that the proportion of liana stems has significantly increased (Fig. 6), even though the total number of stems in the forest as a whole has decreased. This functional shift in forest structure supports past statements that increases in drought conditions will favor lianas due to their superior drought resistance (Schnitzer, 2005; Swaine & Grace, 2007). Importantly, these findings also point to the need to take into account of *proportional changes* in forest composition and not just changes in absolute numbers.

Lack of a recovery from disturbance/successionary signal within the forest?

Overall, the observed temporal trends in forest dynamics and overall reduction in biomass, do not follow

expectations based on recovery primarily responding to recovery from disturbance (Gerhardt & Hytteborn, 1992; Gillespie *et al.*, 2000) (see Appendix S1). The different aged areas of the forest do not follow the expected trajectory from classical successionary theory where the species composition and dominance of younger forests shifts over time to gradually resemble the dominance and species composition of older forest (Austin, 1977; Bakker *et al.*, 1996; Franklin *et al.*, 1999). Further, the observed functional shift in the SEFDP is not expected from recovery from disturbance. For example, with tropical succession, the proportion of trees with compound, deciduous leaves decrease while those with simple, evergreen leaf types increase (Budowski, 1970; Givinsh, 1978; Opler, 1978; Janzen, 1986). The observed reduction in evergreen species and increase in deciduous species is *opposite* to the observed functional changes observed when studying chronosequences from forests nearby to the SEFDP of different ages (Arroyo-Mora *et al.*, 2005).

Even given the above findings we do find support for a *secondary signal* within the SEFDP that reflects successionary dynamics. For example, (*i*) our DCA multivariate analyses does show convergence in composition on one of the multivariate axis (see Fig. S6 where we observe that on Axis 3 and Axis 1 the 'mid-age' area of the SEFDP converged on the 'old' areas of the forest); (*ii*) the biomass of early (ES) succession stage species did decrease forest-wide; and (*iii*) there has been relative increases in the density and biomass of species associated with early-to-mid (EM) and mid-to-late (ML) succession stages. For example, we have observed declines in the abundance of early successional species: *Enterolobium cyclocarpum* (Fabaceae), *Cecropia peltata* (Cecropiaceae) and *Apeiba tibourbou* (Tiliaceae). These species have been noted as early successional species in Guanacaste (Janzen 1988). Nonetheless, despite these changes, as discussed below, the weight of evidence indicates that changes in precipitation has had more of a role is shaping the species and functional changes in the forest.

Forest dynamics driven by drift?

Lastly, we note that our results are also not consistent with forest dynamics being primarily driven by 'neutral' drift (Bell, 2001; Hubbell, 2001). According to neutral theory – demographic neutrality and stochastic drift across species would result in each of the different habitats (see Fig. 6) following idiosyncratic multivariate trajectories. Instead, across all habitats within the forest, we observe uniform and directional trajectories in forest composition and dominance and a consistent multivariate distances between habitats and differing ages of the forest.

Conclusions

Understanding how changing climate, in particular drought, influences the growth and survivorship of trees (McDowell *et al.*, 2008; Allen *et al.*, 2010), as well as forest dynamics, and terrestrial carbon budgets (Saleska *et al.*, 2007; Phillips *et al.*, 2009) is currently the focus of much study. Overall, our results are similar to observed past changes in the BCI 50 ha forest dynamics plot to the severe 1982–1983 El Niño drought (Condit *et al.*, 1996a, b; Condit, 1998; Poorter, 2005) and recent claims by Allen *et al.* (2010) who stated that *some of the world's forested ecosystems are already responding to climate change and . . . forests may be increasingly vulnerable to higher background mortality rates . . . in response to amplified drought and heat stress.*

Our findings are consistent with the expectation that increased prevalence of drought-like conditions in-between the census period as well as a potential longer-term drying trend has likely influenced the SEFDP via differential responses of tree species. We have found that the there has been a directional shift in the floristic composition and dominance throughout the forest but that some forest locations are more susceptible to change. A mechanistic basis to these observed changes may be found in several studies that have linked differential variation in phenology, physiology, and life history of dry forest trees to annual and interannual variation in precipitation (Reich & Borchert, 1984; Sobrado, 1986; Holbrook *et al.*, 1995; Enquist & Leffler, 2001).

Our findings intersect with two additional prominent findings on the role of drought on forest biomass, functional composition, dynamics, and carbon:

First, recent experimental and observational drought studies have emphasized that extreme droughts in tropical forest result in elevated water deficits and lead to increased tree mortality and decreases in the number of individuals (Nepstad *et al.*, 2007; Brando *et al.*, 2008; Phillips *et al.*, 2009). Our results are consistent with two findings from Nepstad and colleagues (see Fig. 5 and S4). Nepstad and colleagues found that experimental drought resulted in a larger *absolute* decline in abundance for trees in the *smallest* size classes (see their Fig. 3a) indicating that small trees may be more susceptible to drought than large trees. They also found that the annualized community-wide mortality rate for trees in the experimental drought plot increased to 3.77% from the nondrought mortality rate of 2.72%. This 'drought' mortality rate is similar to our observed rate of mortality in the SEFDP during the time period of several dry years. Together, these two similarities are consistent with the expectation that decreases in rainfall have primarily influenced the observed dynamics in the SEFDP. However, Nepstad *et al.* (2007) observed a decline in liana density in response to drought. The SEFDP did not apparently witness any dramatic change in liana density [although most of the lianas recorded within the SEFDP maybe smaller than the size cutoff in Nepstad *et al.* (2007)] indicating potential differences in how lianas respond to heightened drought between more seasonally dry forests (such as the SEFDP) and the more wet Amazonian forests.

Second, our work, in accordance with Phillips *et al.* (2009), shows a decrease in forest biomass in response to drought. It is important to note, however, that this decrease appears to be mainly driven by a one or a few large biomass quadrats (see Fig. 2b). When forest biomass was examined on a per unit quadrat basis (biomass per $20\,m^2$ quadrat), we find that the average biomass per quadrat did not significantly change between the two sample periods indicating that assessing changes in biomass is sensitive to the spatial scale of sampling and to the biomass estimates of the largest trees (Chave *et al.*, 2003). While we see a reduction in biomass in the subcanopy and understory components we also observe an increase in biomass within the canopy trees. Previous work by Phillips *et al.* (2009) found an immediate decrease in total forest biomass in response to a single severe drought year. We note that our findings are for a much larger temporal scale (20 years) than the Phillips and colleagues study. Further, most of the reduction in the number of individuals within the SEFDP has been in the smallest size classes, which contribute relatively little in terms of forest biomass (see Enquist *et al.*, 2009).

Our results also build upon a large literature that shows that variation in soil moisture and topography influence the species composition and dominance of tropical tree species (Gonzalez & Zak, 1994; Oliveira-Filho *et al.*, 1998; Clark *et al.*, 1999; Webb & Peart, 2000; Harms *et al.*, 2001). Together, the observation of maintained multivariate segregation across habitats but yet differential species and functional responses during a period of heightened drought conditions, are consistent with niche differentiation theories of species coexistence across environmental gradients (Chesson, 2000; Swenson *et al.*, 2007; Kraft *et al.*, 2008) as opposed to models of demographic drift or neutrality/ecological equivalence (Bell, 2001; Hubbell, 2001).

Our results support past conclusions that water stress can shape the species functional composition of tropical forests. (Woods, 1989; Leigh *et al.*, 1990; Hartshorn, 1992; Condit, 1998; Yavitt & Wright, 2008). Based on observed directional shifts in species composition and abundance patterns, in 20 years the San Emilio forest became a more deciduous and canopy species dominated forest. Evidence presented here suggests that this is primarily the result of differential species-level responses to

several drought years in-between surveys as well as a longer-term mean change in precipitation. However, while a recovery from past disturbance signal is present it is secondary in importance. Additional long-term data including further censuses and the collection of functional traits across the species within the SEFDP will help elucidate the mechanistic basis to observed patterns observed here as well as to assess the relative importance of these patterns into the future. Furthermore, disentangling the functional nature of which species have increased in dominance and how the predicted future decreases in precipitation and increases in temperature combine to influence the water balance of tropical forests will be of central importance (Engelbrecht *et al.*, 2007).

Acknowledgements

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