Directional changes in the species composition of a tropical forest

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Abstract. Long-term studies have revealed that the structure and dynamics of many tropical forests are changing, but the causes and consequences of these changes remain debated. To learn more about the forces driving changes within tropical forests, we investigated shifts in tree species composition over the past 25 years within the 50-ha Forest Dynamics Plot on Barro Colorado Island (BCI), Panama, and examined how observed patterns relate to predictions of (1) random population fluctuations, (2) carbon fertilization, (3) succession from past disturbance, (4) recovery from an extreme El Niño drought at the start of the study period, and (5) long-term climate change. We found that there have been consistent and directional changes in the tree species composition. These shifts have led to increased relative representations of drought-tolerant species as determined by the species' occurrence both across a gradient of soil moisture within BCI and across a wider precipitation gradient from a dry forest near the Pacific coast of Panama to a wet forest near its Caribbean coast. These nonrandom changes cannot be explained by stochastic fluctuations or carbon fertilization. They may be the legacy of the El Niño drought, or alternatively, potentially reflect increased aridity due to long-term climate change. By investigating compositional changes, we increased not only our understanding of the ecology of tropical forests and their responses to large-scale disturbances, but also our ability to predict how future global change will impact some of the critical services provided by these important ecosystems.

Key words: Barro Colorado Island; carbon fertilization; Center for Tropical Forest Science; climate change; drought; El Niño Southern Oscillation; ENSO; Panama; tropical forest.

Introduction

Tropical forests face many challenges, including both natural climatic events, such as El Niño-associated droughts (Newbery and Lingenfelder 2004, Phillips et al. 2009), and large-scale anthropogenic disturbances, including habitat loss and climate change (Wright 2005, Wright and Muller-Landau 2006, Clark 2007, Bradshaw et al. 2008, Peres et al. 2010). Demographic responses to natural and anthropogenic disturbances will differ among tree species (Körner 2004), potentially resulting in altered interspecific competitive interactions. These changes, in conjunction with the predicted migrations of species as their distributions shift to remain at equilibrium with changing climate (Beaumont et al. 2007, Feeley and Silman 2010*a, b*, Feeley et al. 2011), should manifest as directional shifts in the floristic composition of forest stands (e.g., Condit et al. 1996*a, c*, Condit 1998*a*, Beckage et al. 2008). Changes in species composition will, in turn, have important consequences for ecosystem-level responses to global change (Körner

2004, Bunker et al. 2005). For example, changes in the relative abundance of heavy- vs. light-wooded tree species may result in augmented or reduced carbon stores, respectively (Bunker et al. 2005). Studies of compositional changes are therefore imperative to understanding the impacts of past disturbances and predicting the effects of future global changes on tropical forests and their contributions to the global carbon budget and other ecosystem services.

Recent studies have reported long-term directional changes in the composition of tropical forests (Laurance et al. 2004, Newbery and Lingenfelder 2004, 2009, Chave et al. 2008). However, the causes underlying these changes, and more specifically the contribution of long-term climate change vs. successional recovery from past disturbances, remains debated. For example, a study of forest inventory plots representing lowland rainforests near Manaus, Brazil, indicates directional shifts in tree species composition over the past several decades, with fast-growing, tall-statured genera increasing significantly in relative abundance (Laurance et al. 2004). The explanation for these floristic changes has been attributed to differential responses to increased resource availability, particularly carbon fertilization due to elevated concentrations of atmospheric CO_2 (Laurance

et al. 2004, 2005, Nelson 2005). But other researchers have suggested that the changes may instead reflect the impacts of past fires, floods, or windthrows, or the damage inflicted on some trees during collecting (Nelson 2005). Likewise, evidence of directional shifts in floristic composition have also been observed across a network of 10 large forest dynamics plots located throughout the New and Old World tropics and administered through the Center for Tropical Forest Science (CTFS). Investigating temporal changes in the aboveground biomass of various plant functional groups showed that nearly all of these plots (9 out of 10) had increased representations of heavy-wooded species. These changes were originally attributed primarily to successional recovery from as yet unidentified past large-scale disturbances (Chave et al. 2008), but subsequent reviews have highlighted the possible influence of increasing resource availability and carbon fertilization (e.g., Lewis et al. 2009).

In light of this ongoing debate, we investigated patterns of compositional change at more depth using data from one of the CTFS plots located on Barro Colorado Island (BCI), Panama. The BCI plot covers an area of 50 ha; it was the first plot established by the CTFS (in 1981–1982) and is undoubtedly one of best-studied forests in the world. Within BCI, the dynamics (growth, mortality, and recruitment) of all saplings and trees have been monitored through highly standardized censuses conducted at five-year intervals, providing a detailed record of changes in the structure, dynamics, and composition of this forest over the past three decades (Condit 1998b, Hubbell et al. 1999, 2005).

Weather-monitoring stations located on BCI have recorded climate over the past several decades and have shown changes in temperature and precipitation (Appendix A), with possible implications for plant water availability. Furthermore, there have been several extreme droughts associated with El Niño events since the plot was established (Wright and Calderon 2006). In particular, the El Niño drought of 1982–1983 resulted in elevated tree mortality (Leigh et al. 1990, Condit et al. 1995). The potential effects of changing climate and drought on the BCI tree community composition were previously demonstrated by analyses of the early census data (1981–1990), which showed increased relative abundances of species that were deemed drought tolerant on the basis of their topographic preference (Condit et al. 1996a, b, c, 1998a). At BCI, the hill slopes (Appendix B) are generally more mesic than the flatter areas (Daws et al. 2002), and thus species occurring preferentially on the slopes are classified as being relatively drought intolerant (Condit et al. 1996a, b, c, 1998a, Engelbrecht et al. 2007). Likewise, Hubbell (2004) noted that several drought-intolerant species have declined in abundance rapidly and consistently since the first census, potentially in response to the droughts and/or increasingly xeric conditions.

In order to gain additional insight into the floristic changes at BCI, the underlying mechanisms, and the

potential implications, we tested how ongoing changes in composition relate to species traits using weighted averaging and ordinations. We also analyzed compositional changes at BCI in the context of a well-established regional gradient in floristic composition occurring across the Isthmus of Panama and correlated with a rainfall gradient (Pyke et al. 2001, Engelbrecht et al. 2007) from the wet Caribbean coast in the north to the drier Pacific coast in the south (Appendix C). Using the long-term census data from BCI in conjunction with compositional data from wetter and drier forests, we tested if species composition of the BCI tree community has shifted appreciably since the plot was first established and if the observed changes are consistent with expectations of (1) random fluctuations in species abundances due to stochastic processes, in which case compositional changes would be unrelated to species traits; (2) carbon fertilization, in which case compositional changes would favor faster-growing, light-wooded species; (3) successional recovery from past large-scale disturbance events, in which case there should be increasing abundances of slower-growing and heavier-wooded species, as well as increases in indices of relative forest successional status; (4) recovery from the extreme El Niño drought that occurred at the start of the study period in 1982–1983, which would manifest as increased abundances of drought-tolerant species; and/or (5) altered water availability due to long-term climate change, which likewise would result in increased abundances of drought-tolerant species.

METHODS

We investigated the nature and underlying causes of compositional change in a tropical forest using census data from the 50-ha (1000 m east–west × 500 m north–south) Forest Dynamics Plot located on Barro Colorado Island (BCI), Panama (9.15° N, 79.85° W). BCI's mean annual temperature is ~27°C, and mean annual rainfall is ~2500 mm, but with marked seasonality (dry season is typically January to April with rainfall averaging <60 mm/month). Over the study period (1981–2005) there have been several distinct El Niño events (Wright and Calderon 2006) resulting in decreased rainfall and elevated temperatures, the strongest of which occurred in 1982–1983 (Leigh et al. 1990, Condit et al. 1995).

At BCI, all woody stems ≥10 mm diameter at breast height (dbh), excluding lianas, have been tagged, identified to species, mapped, and measured at approximately five-year intervals. The plot was first censused in 1981–1982 and was recensused in 1985, 1990, 1995, 2000, and 2005. Prior to 1990, all individual palm stems of the genus Bactris were counted as individuals, but in subsequent censuses, conspecific clumps of stems were assumed clones and were not tallied separately, thus reducing abundances independent of changes in actual population sizes. In order to correct for this, we used the number of 5 × 5 m quadrats occupied by each Bactris sp. within each census as our measure of abundance

(maximum possible = 20 000) rather than the raw count of individuals.

Regional differences in forest composition associated with the large-scale rainfall gradient occurring across the Isthmus of Panama (Appendix C) were captured by two complimentary inventory plots located in wet forest at Fort Sherman on the Caribbean coast (2850 mm rain/yr; 9.36° N, 79.95° W) and dry forest at Cocoli on the Pacific coast (1950 mm rain/yr; 8.98° N, 79.59° W). The Fort Sherman plot is 5 ha, and the Cocoli plot is 4 ha (the plot at Fort Sherman is 6 ha but encompasses 1 ha of successional forest, which we excluded from these analyses). Both of these plots have been censused repeatedly using identical methodology as employed at BCI, but for our analyses we characterized composition at the plots using only the data from the 1998 censuses (approximate midpoint of BCI data series).

To test whether there have been changes in community composition at BCI over the past 25 years and if these changes have been random or if they are associated with specific species life history traits, we assembled a database of characters calculated from the census data. The species traits we included were: commonness, sapling and adult growth rates, adult stature, wood specific gravity, and the mean convexity and mean slope of each species' spatial distribution. Commonness is the log number of stems recorded during the initial 1981–1982 census. Sapling growth rate is the mean exponential change in stem diameter over the entire census period for all individuals with an initial dbh of 10–100 mm, and adult growth rate is the mean exponential change in stem diameter for all individuals with an initial dbh $\geq$100 mm. Adult stature is the 95% quantile of a species' diameter measurements. Wood specific gravity (WSG), or wood density, is the ovendry mass of a sample of wood divided by its green volume. WSG values were taken from Chave et al. (2006). Using an elevation map of the BCI plot (Appendix B) we calculated convexity and slope at a scale of 20 × 20 m quadrats. For each species we then calculated the mean convexity and mean slope weighted by the number of individuals within each 20 × 20 m quadrat during the first census in which the species was recorded in the BCI plot. At BCI, water availability increases in areas with greater slope and/or lower convexity (Daws et al. 2002), and thus the location of species in relation to these topographic variables is commonly used as an indicator of relative drought tolerance (Condit et al. 1996a, b, c, 1998a, Engelbrecht et al. 2007). With the exception of sapling and adult growth rates, these species traits are only weakly correlated, and thus we treated them as independent (Pearson correlation coefficient, R, between sapling and adult growth rates = 0.67; for all other pairs of variables R = 0.03–0.39).

We next subdivided the BCI plot into 50 1-ha (100 × 100 m) subplots and calculated the mean trait score across all individuals occurring within each of the subplots at each census by assigning individuals their respective species trait value. For each subplot × trait combination we regressed the mean trait score vs. census year and used the slope of the relationship as a measure of the direction and annual rate of change in the mean species trait due to compositional shifts (Feeley et al. 2007b). To test if the changes in each trait were significantly different from random, we calculated the mean rate of change and the corresponding 95% confidence bounds by bootstrapping across subplots (5000 resamples) and used binomial tests to determine if the changes were directional (i.e., number of subplots increasing or decreasing significantly different from 50%). We tested the relationships between initial trait values and subsequent rates of change using Pearson correlations.

We further investigated patterns of overall compositional change at BCI by calculating the Bray-Curtis (BC) dissimilarity index (Beals 1984, Faith et al. 1987) between the tree communities occurring within each of the 1-ha subplots during each of the six censuses. Based on the BC dissimilarities between all subplot × census compositions (n = 300), we conducted a nonmetric multidimensional scaling (NMDS) ordination with three axes (stress = 0.12; number of axes selected upon visual inspection of a scree plot of stress values; Appendix D). The ordination was conducted in the R statistical package using the MetaMDS function of the vegan library (50 random starts; scaling: centering, PC rotation, halfchange scaling; Oksanen et al. 2009) (program *available online*).[7] By plotting the change in an individual subplot's location in ordinational space through time, it is possible to visually track the shifts in community composition relative to initial composition (Austin 1977, Laurance et al. 2006) as well as relative to the composition of all other subplot communities. If the composition of trees is changing randomly, we would expect that over each census interval the number of subplots increasing in value along an NMDS axis would be equivalent to the number decreasing. We tested this hypothesis using binomial probabilities. We also calculated the mean rate of movement along each axis during each census interval and tested whether it differed significantly from zero based on the 95% confidence interval as estimated through bootstrapping (5000 resamples). To determine how changes in composition potentially relate to species traits we fitted the vectors for subplot convexity, slope, mean adult stature (size), and mean wood density (WSG) onto the ordinations using the Envfit function of the vegan library in R (Oksanen et al. 2009) and the initial census data.

To test how changes in floristic composition at BCI relate to the broader regional-scale gradient in precipitation, we calculated the Bray-Curtis similarity (similarity = 1 − BC distance) between each of the 1-ha subplot communities and the tree communities repre-

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[7] ⟨http://www.R-project.org⟩

sented by the wet-forest plot at Fort Sherman and the dry-forest plot at Cocoli. We also calculated the Bray-Curtis similarity between just the trees that died and just the trees that recruited during each census period at BCI (all subplots combined) vs. Fort Sherman/Cocoli.

We calculated the rate of successional change for each of BCI's 1-ha subplots using the gap phase index GP (Feeley et al. 2007a). GP is based on the relative size distribution of stems per 20×20 m quadrat such that quadrats with a greater proportion of their basal area represented by large trees are estimated to be in later stages of succession or gap recovery than quadrats with greater relative representations of small stems. Specifically, $GP = ln([BA_{300} + 1]/[BA_{100} + 1])$, where BA_{300} is the total basal area of all stems with dbh ≥ 300 mm, and BA_{100} is the total basal area of all stems with dbh ≥ 10 mm and ≤ 100 mm (Feeley et al. 2007a). We calculated the mean GP per subplot and the rate of change in GP from 1985 to 2005 (due to problems with measuring around buttresses, the initial 1981–1982 census was excluded from all analyses using GP).

We do not contend that the 1-ha subplots represent independent sampling units. Rather, this subdivision was performed to help characterize the degree of spatial consistency in magnitude and direction of compositional changes across the plot. The degree of spatial consistency in compositional changes is critical in that it helps to distinguish between small-scale changes driven by stochastic events or local gap phase dynamics vs. larger-scale phenomena such as regional disturbances or changes in regional/global climate and resource availability.

All data on species abundances at the BCI, Fort Sherman, and Cocoli inventory plots are available for public download.[8] Climate data are also available.[9]

RESULTS

There have been directional changes in the species composition of the Barro Colorado Island (BCI) tree community since the plot was initially censused in 1980–1981. Overall, there has been a shift in composition across the 50 1-ha subplots toward significantly greater representations of species with relatively heavy wood, larger adult stature, and greater drought tolerance (greater drought tolerance indicated by both lower mean slope and lower mean convexity scores; Fig. 1). Changes in composition were not significantly related to the other species traits included in our analyses (commonness and sapling and adult tree growth rates; Fig. 1).

The rate at which the subplot tree communities changed in their mean trait scores was inversely related to the subplot's initial mean trait score (Table 1). For example, subplots initially dominated by smaller-statured species experienced significant increases in their

mean adult stature through time, while subplots that initially had greater relative abundances of larger-statured species experienced little or no increase in their mean adult stature over the study period. The negative relationship between initial mean score and subsequent change held true for all of the species traits examined ($R = -0.21$ to -0.79).

These compositional changes are visually apparent as directional shifts in the nonmetric multidimensional scaling ordination scores calculated for each subplot at each of the five-year censuses (Fig. 2). Compositional changes were highly directional (generally negative along all three axes) as indicated by the fact that the distribution of positive vs. negative changes during each census interval differed significantly from random in all but 2 of the 15 possible cases (3 axes × 5 census intervals; Table 2). Subplot slope was significantly positively correlated with axis 1 and negatively correlated with axes 2 and 3. Convexity was significantly negatively correlated with all three axes. As such, the observed changes in composition are generally consistent with shifts toward increasing similarity to the composition that initially occurred in just the drier portions of the plot located on the plateau and hilltops (Fig. 2).

Changes in tree species composition at BCI were also directional when analyzed within the context of the larger isthmus-wide gradient in precipitation; with few exceptions the BCI subplot communities became more similar in composition to the dry forest of Cocoli while at the same time becoming more dissimilar in composition to the wet forest of Fort Sherman (Fig. 3). Accordingly, the mean compositional similarity between BCI and Fort Sherman decreased through time, while the mean compositional similarity between BCI and Cocoli increased monotonically over the 25-year study period (Fig. 3).

The community of trees dying at BCI during the initial census period was less similar in composition to the dry forest at Cocoli than was the community of trees present at BCI in the first census. The disparity in similarity decreased through time as dying trees became increasingly similar to Cocoli at a faster rate than did the standing trees. Accordingly, the trees dying each census period were more similar in composition to the wet forest at Fort Sherman than was the community of trees present at BCI at the start of each period, and this disparity increased marginally through time (Fig. 4).

In contrast to the dying trees, the community of trees recruiting into BCI (i.e., individuals growing to ≥ 1 mm dbh during a five-year census interval) was initially more similar in composition to the dry forest at Cocoli than was the community of trees present at BCI at the start of the period. However, by the final census period, the recruiting tree community was less similar to Cocoli than was the standing tree community. Similarity between recruiting trees and the wet forest of Fort Sherman increased through time despite the concurrent

[8] ⟨http://ctfs.si.edu/datasets/bci⟩
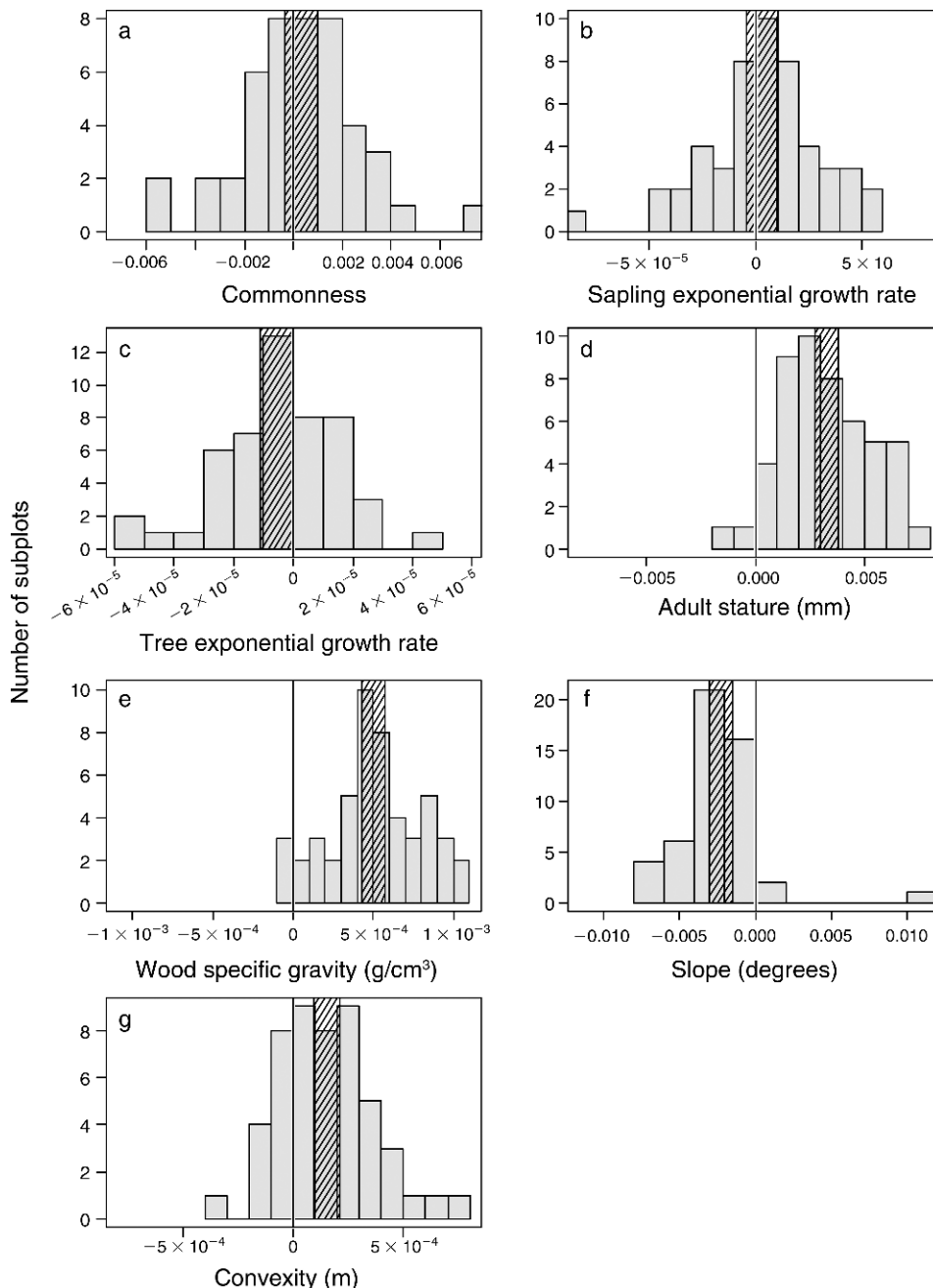[9] ⟨http://striweb.si.edu/esp⟩

Fig. 1. Histograms of the annual rates of change for each of the 1-ha subplot tree communities at Barro Colorado Island, Panama: (a) commonness expressed as log(number of individuals), (b) sapling exponential growth rate expressed as log(dbh2 − dbh1)/time, (c) tree exponential growth rate expressed as log(dbh2 − dbh1)/time, (d) adult stature (mm), (e) wood specific gravity or density (g/cm^3), (f) slope (degrees), and (g) convexity (m). Hatched areas indicate 95% confidence intervals around the mean rate of change for each variable, and thin vertical lines indicate the null hypothesis of zero net change. The mean rates of change were significantly different from zero for (d) adult stature, (e) wood specific gravity, (f) slope, and (g) convexity.

decrease in similarity between Fort Sherman and the standing BCI tree community (Fig. 4).

The mean rate of succession as measured by the change in the subplots' average gap phase (GP) status through time (Feeley et al. 2007a) did not differ significantly from zero, indicating that the size structure

of trees at BCI is not changing consistently, as would be expected if the forest were recovering from a stand-replacing disturbance event (Appendix E). The rate of succession was negatively correlated with initial GP. This is in accord with the general principles of gap phase dynamics and indicates that more mature forest stands

TABLE 1. Annual rates of change in mean species trait values and successional status (gap phase [GP]).

Trait	Mean rate of change	Lower 95% CI	Upper 95% CI	Number of subplots with increasing trait value	Binomial P value	Correlation with initial value
Commonness	3.63×10^{-4}	-2.82×10^{-4}	1.02×10^{-3}	28	0.48	-0.39
Sapling growth rate	5.40×10^{-6}	-2.42×10^{-6}	1.33×10^{-5}	30	0.20	-0.68
Tree growth rate	-4.97×10^{-6}	-1.07×10^{-5}	2.46×10^{-7}	20	0.20	-0.71
Adult stature	3.32×10^{-3}	2.75×10^{-3}	3.88×10^{-3}	48	<0.0001	-0.21
Wood density	5.05×10^{-4}	4.19×10^{-4}	5.85×10^{-4}	48	<0.0001	-0.70
Slope	-2.20×10^{-3}	-2.85×10^{-3}	-1.32×10^{-3}	4	<0.0001	-0.21
Convexity	1.87×10^{-4}	1.20×10^{-4}	2.61×10^{-4}	38	<0.0005	-0.79
GP	-2.33×10^{-4}	-8.68×10^{-3}	4.82×10^{-4}	30	0.20	-0.37

were more likely to experience a disturbance event (i.e., a decrease in GP) than younger forest stands. The mean GP across BCI remained stable through the study period (0.39 in 1985 vs. 0.38 in 2005).

DISCUSSION

Long-term studies have begun to reveal dramatic changes in the structure and dynamics of tropical forests (see reviews in Malhi and Phillips 2004, Wright 2005, Lewis 2006, Clark 2007, Lewis et al. 2009), but the causes of these changes remain heavily debated, being attributed variably to large-scale successional or gap phase processes (Feeley et al. 2007a, Chave et al. 2008), increasing resource availability and specifically carbon fertilization (Baker et al. 2004, Laurance et al. 2004, Lewis et al. 2004, Phillips et al. 2004), extreme climatic events, and/or long-term human-driven climate change (Condit et al. 1996b, 1998a, Clark et al. 2003, Feeley et al. 2007b). Unfortunately, the many logistical difficulties inherent in working with tall, long-lived, complex, species-rich ecosystems have largely prohibited the establishment of large-scale experiments designed to reveal the underlying mechanisms (but see Nepstad et al. 2007). Instead, researchers have, for the most part, been limited to comparing the observed patterns of change with the predictions of the hypothesized mechanisms. Perhaps not surprisingly, this "fingerprinting" approach (Lewis et al. 2004) has proven relatively inconclusive, since most studies are conducted at the stand level, in which case the predicted effects of many potential mechanisms are not mutually exclusive (for examples of ongoing debates see Clark 2004, Laurance et al. 2004, 2005, Nelson 2005, Wright 2005, 2006, Lewis et al. 2006, 2009, Körner 2009). Additional insight may be gained by looking at concurrent patterns of compositional change since at the species level, the hypothesized drivers differ more markedly in some of their predictions. For example, carbon fertilization and succession are both predicted to cause increasing forest biomass at the stand level, but under carbon fertilization, fast-growing, light-wooded species are predicted to increase in relative abundance (Laurance et al. 2004); in contrast, heavy-wooded, slow-growing species are predicted to increase in relative abundance as forests mature and undergo succession (Chave et al. 2008).

Here we used standardized, long-term census data from Barro Colorado Island (BCI) to track changes in forest composition through time. Over the past 25 years there has been high turnover at BCI, with almost 50% of the initial individuals dying and being replaced, resulting in large changes in species composition. These changes have been remarkably directional across the extent of the plot and through time (Fig. 2), leading to increased relative abundances of species with relatively heavy wood, large adult stature, and greater drought tolerance. In addition, species composition shifted such that the forest communities at BCI became more similar to the dry forest on Panama's Pacific coast and less similar to the wet forest on Panama's Caribbean coast. Based on these findings we can now begin to ask what mechanisms may be responsible for the observed changes in composition, specifically examining if the documented patterns are consistent with the expectations of (1) random fluctuations in species abundances, or alternatively, if changes in composition are due to (2) carbon fertilization, (3) successional recovery from past large-scale disturbances, (4) recovery from the 1982–1983 El Niño drought, and/or (5) long-term climate change.

Are compositional changes at BCI random?

The floristic changes at BCI are remarkably constant across both space and time. These highly directional changes cannot be explained by stochastic population fluctuations or neutral processes in the absence of large-scale environmental changes (Laurance et al. 2006). Also, as noted by Hubbell (2004), several tree species at BCI have increased or decreased in abundance much more rapidly and consistently than predicted under stochastic models. Indeed, if compositional change was random, we would expect that the communities of dying and recruiting trees would have approximately the same similarity with the forests at Fort Sherman and Cocoli as the community of trees recorded in BCI at the start of each corresponding census period; this was not the case (Fig. 4).

Are compositional changes at BCI due to increasing CO_2 and carbon fertilization?

According to the predicted responses of forests to carbon fertilization, we expected increased relative
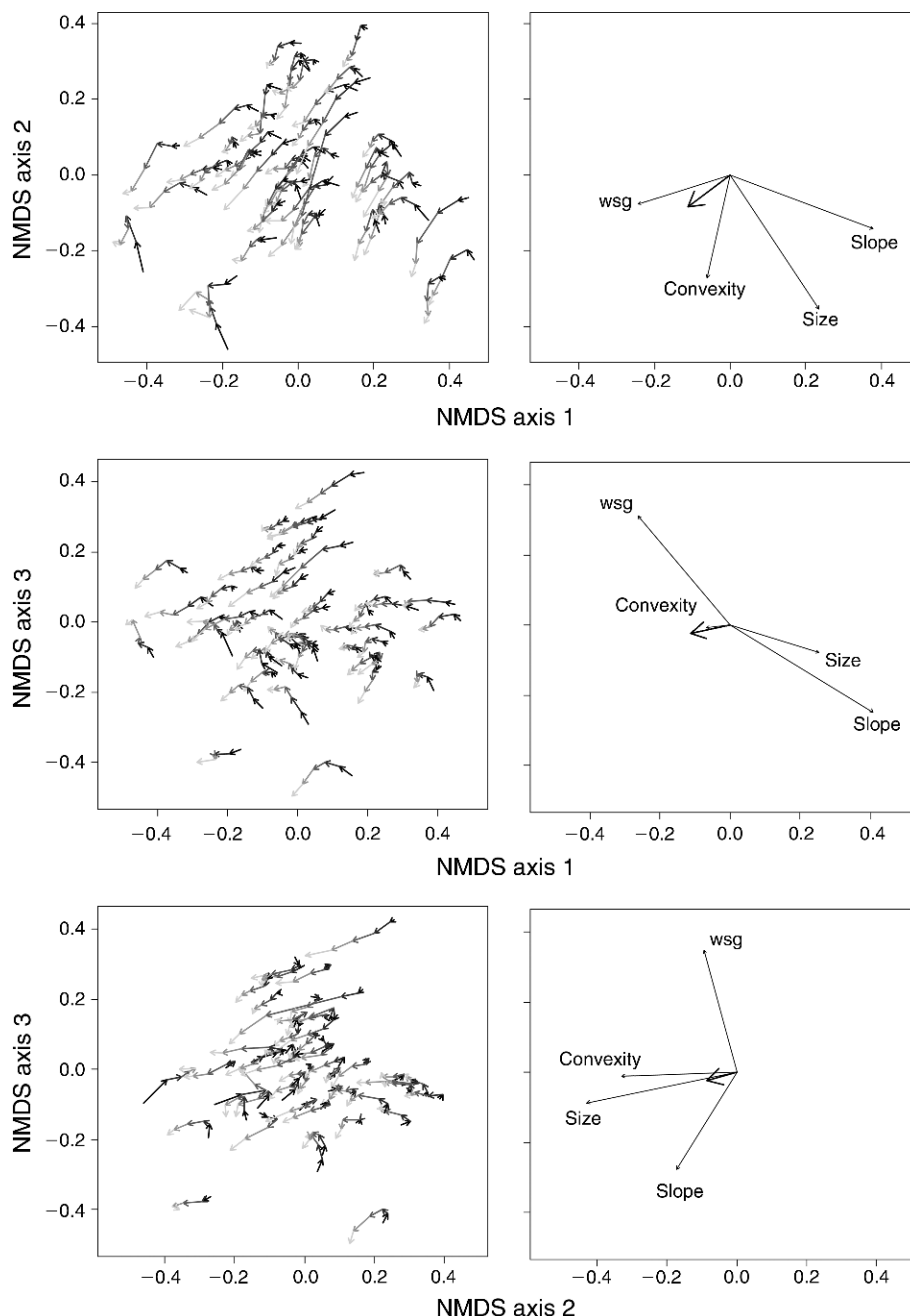
FIG. 2. Left panels show ordination plots (nonmetric multidimensional scaling with three axes built on Bray-Curtis distances) indicating the relative differences in species composition between each of Barro Colorado Island's 50 1-ha subplots and through time (1981–2005; arrows get lighter through time). Right panels show the correlation between the ordination axes and subplot slope, convexity, mean adult stature (size), and mean wood density (wood specific gravity [WSG]), as calculated from the initial census data. The length of the arrows indicates the strength of the correlations. The larger, unlabeled arrows indicate the mean direction and magnitude of change in the subplots' floristic compositions between the initial and final census.

abundances of faster-growing, lighter-wooded species (Laurance et al. 2004). As shown here, as well as by Chave et al. (2008), the compositional changes at BCI do not fit these expectations. Also, contrary to the predictions of increased resource availability, stand-level biomass has remained relatively stable since the

plot was established (Chave et al. 2003, 2008), especially after accounting for gap phase or successional dynamics (Feeley et al. 2007a) and the fact that stand- and species-level tree growth rates (relative basal area growth) have decelerated (Feeley et al. 2007b).

TABLE 2. Patterns of change along axes 1–3 of the nonmetric multidimensional scaling (NMDS) ordination.

Census interval	Number of subplots with negative change	Binomial P value	Mean rate of change	Lower 95% CI	Upper 95% CI
NMDS axis 1					
1981–1985	50	<0.0001	−0.022	−0.020	−0.025
1985–1990	49	<0.0001	−0.024	−0.020	−0.028
1990–1995	46	<0.0001	−0.023	−0.019	−0.027
1995–2000	49	<0.0001	−0.023	−0.020	−0.026
2000–2005	49	<0.0001	−0.020	−0.016	−0.024
NMDS axis 2					
1981–1985	13	<0.0005	0.013	0.018	0.007
1985–1990	33	−0.02	−0.004	0.002	−0.010
1990–1995	49	<0.0001	−0.040	−0.033	−0.050
1995–2000	49	<0.0001	−0.035	−0.030	−0.040
2000–2005	42	<0.0001	−0.018	−0.012	−0.023
NMDS axis 3					
1981–1985	15	<0.005	0.011	0.016	0.007
1985–1990	25	0.56	0.001	0.006	−0.003
1990–1995	38	<0.0005	−0.010	−0.006	−0.015
1995–2000	41	<0.0001	−0.011	−0.007	−0.016
2000–2005	44	<0.0001	−0.014	−0.011	−0.017

Are compositional changes at BCI due to succession from past disturbance?

In accord with expectations of succession, the forest at BCI is, in fact, shifting toward increased relative abundances of heavy-wooded species (Chave et al. 2008). However, we did not find any change in the abundance of species with different sapling growth rates, a species trait that is often used as an indicator of pioneer status. Similarly, the mean rate of change in gap phase (GP; an index of the relative rate of succession) did not differ significantly from zero (Appendix E), and the overall plot-wide mean GP remained stable through the study period (Feeley et al. 2007a). This pattern is more in accord with mature-forest gap phase dynamics than large-scale succession.

Are compositional changes at BCI due to ongoing recovery from the 1983 El Niño drought?

In early 1983, BCI experienced an extreme El Niño drought during which there were only 2 mm of rainfall over a 12-week period, and temperatures were elevated ~2°C above average. Previous studies have shown that this severe drought caused immediate increases in tree mortality (Leigh et al. 1990, Condit et al. 1995) and changes in tree species composition (Condit et al. 1996a, b). Here we document ongoing changes in composition. Specifically, the abundances of species that were initially found more commonly in flat or more convex areas of the plot have increased (Fig. 1). At BCI, soils in these areas are typically drier than along the slopes or in concave areas (Daws et al. 2002), and thus the species specialized on them are considered to be relatively drought tolerant (Condit et al. 1996a, b, c, 1998a, Harms et al. 2001, Engelbrecht et al. 2007). There was also an increase in the abundance of large-statured

tree species. Larger-statured species are potentially more drought resistant than shrubs or tree-let species since their longer roots may reach the water table during dry periods (Condit et al. 1996b). Furthermore, the compositional shifts have resulted in BCI becoming increasingly similar to dry forest and increasingly dissimilar to wet forest. It therefore appears that there has been a persistent directional change in the flora toward an increased abundance of drought-tolerant species (Hubbell 2004). These patterns can potentially be explained by disproportionate mortality and loss of drought-intolerant species in the sapling stems below the measurable size criteria (i.e., ≥10 mm dbh) during the drought, and subsequent long-term changes in plot composition as the altered community "recruits" (Engelbrecht and Kursar 2003, Bunker and Carson 2005, Engelbrecht et al. 2005, 2007, Comita and Engelbrecht 2009). If this is the case, we would expect that, given enough time, the direction of compositional changes will eventually reverse, and the forest will return to its original composition (Condit et al. 1996b).

Consistent with the hypothesis of forest recovery, new recruits recorded at BCI in the second census (1985) were more similar in composition to the dry forest of Cocoli than was the initial BCI tree community, but through time the similarity of recruits to Cocoli decreased to the point that, by final census, the recruiting community was less similar in composition with Cocoli than was the community of trees recorded at BCI at the start of the census period. Also, the recruiting community became increasingly similar to Fort Sherman such that, by the final census, new recruits were more similar to the wet forest than trees recorded at BCI at the start of the census period. In other words, while the measurable tree community has become more
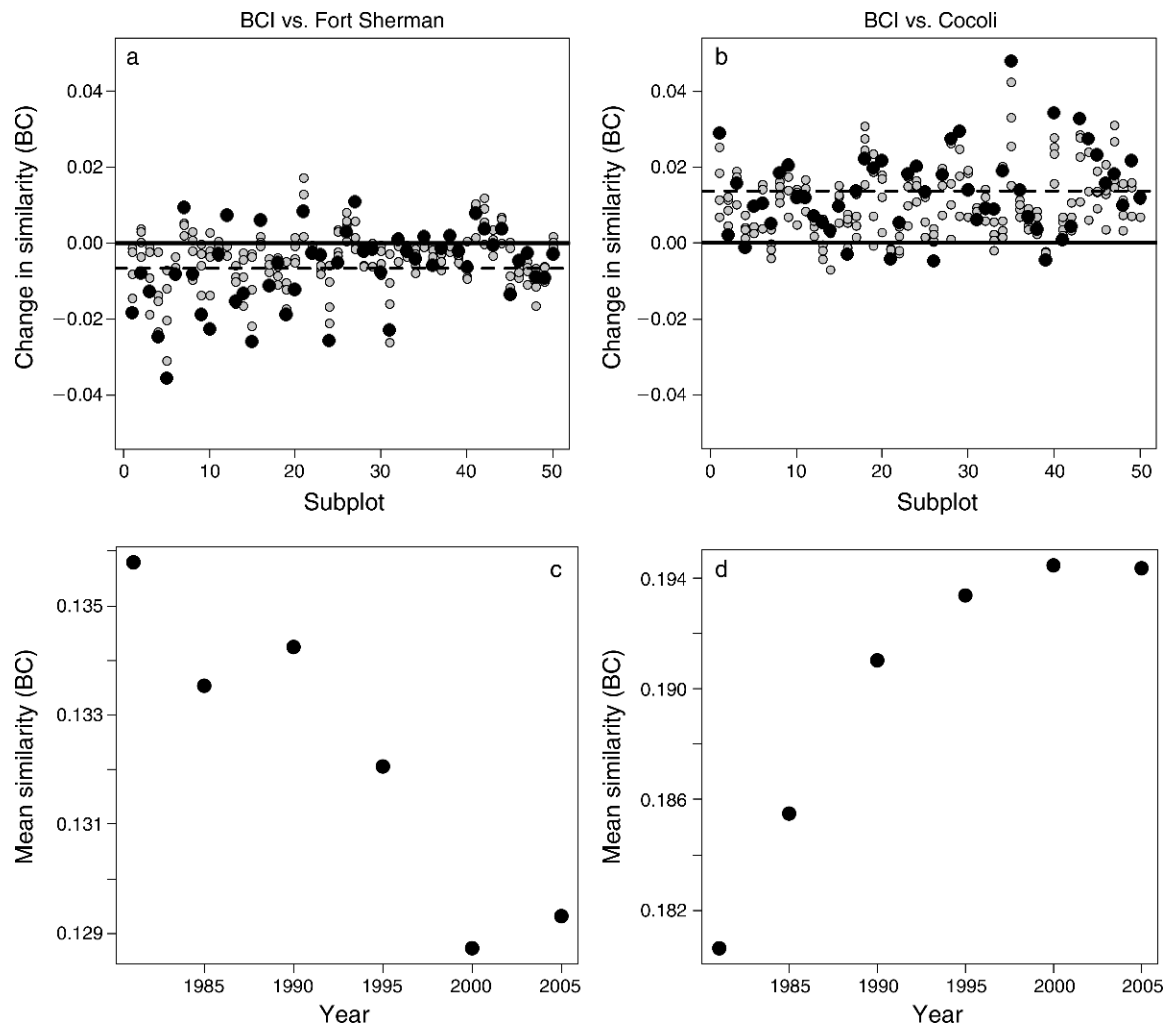
Fig. 3. Change in similarity (similarity = 1 − Bray-Curtis [BC] dissimilarity) between the tree communities at Barro Colorado Island (BCI) and (a, c) the wet forest of Fort Sherman and (b, d) the dry forest of Cocoli. Top panels (a, b) indicate the change in similarity for each of the 1-ha subplots at BCI relative to the similarity as calculated during the initial 1981–1982 census. Change between the initial and final census is highlighted in black, and all intervening censuses are in gray; the mean change for all subplots over the study period is indicated by the dashed line. Bottom panels (c, d) show the mean similarity between BCI and Fort Sherman/Cocoli at each census.

drought tolerant over the 24-year study period, there is decreasing recruitment of dry-forest species and increasing recruitment of wet-forest species. If this continues, it will push BCI to return to a more wet-forest-like composition.

The composition of trees dying during each census period at BCI also show comparable patterns consistent with the hypothesis of forest recovery from drought. Specifically, trees dying over the initial census period were less similar in composition to the dry forest at Cocoli than was the starting BCI community, but through time the similarity of dying trees with Cocoli increased. By the final census period there was no marked difference in the similarity of the dying vs. starting tree communities with Cocoli. In other words, any survivorship advantage enjoyed by dry-forest

species at the start of the study appears to have been lost through time.

Are compositional changes at BCI due to long-term climate change?

Since the 1970s, mean daily temperatures at BCI have increased by almost 2°C (Appendix A). Patterns of rainfall are more complicated, and annual precipitation has actually increased over the study period. However, annual rainfall decreased steadily from the start of monitoring in the 1950s until the early 1980s (Appendix A), potentially favoring the establishment of drought-tolerant species, which is only now becoming apparent in the measurable tree community and explaining the observed compositional shifts toward increased abundances of drought-tolerant, dry-forest species. As
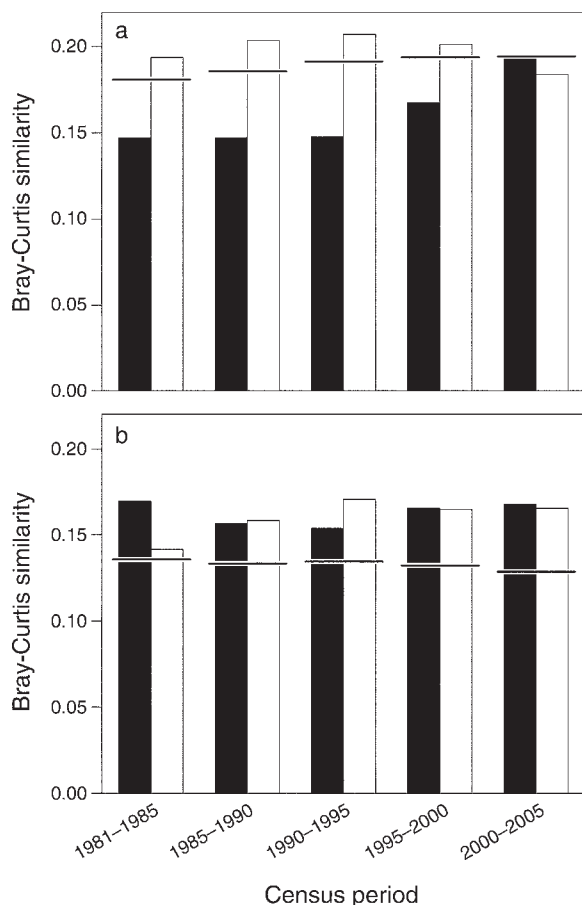
Fig. 4. Similarity (1 − Bray-Curtis dissimilarity) between the community of trees dying (black) and recruiting (white) from/into the Barro Colorado Island (BCI) plot over each census interval vs. (a) the tree community at Fort Sherman and (b) the tree community at Cocoli, and between the tree community recorded at BCI at the start of each census interval vs. tree communities at the other two plots (horizontal lines).

discussed above, if the past decrease in rainfall is responsible for the observed changes, we would expect the composition of recruiting individuals to now be shifting toward increased abundances of drought-intolerant species, as was observed (Fig. 4).

In conclusion, the forest of BCI has exhibited remarkably directional and consistent changes in tree species composition since the early 1980s. These changes cannot be explained through stochastic fluctuations, increasing atmospheric CO_2 concentrations, and carbon fertilization, or through succession from a past large-scale disturbance event. One explanation supported by the observed patterns is that the floristic changes reflect responses to increased aridity in the plot, possibly due to increasing temperatures and/or a past decrease in rainfall. Alternatively, the observed floristic changes may be the result of the extreme drought that occurred early in the census period, causing high mortality of drought-intolerant species, especially in the unmeasured seedling/sapling size classes. Changes in the seedling/

sapling community, due either to past decreases in rainfall or an extreme drought, would in turn lead to differential recruitment and resultant long-term changes in the adult tree community. If this is the case, future censuses may eventually reveal a shift in the floristic community back toward the predisturbance composition. The relative importance of extreme events vs. long-term trends in driving compositional changes at BCI and in other ecosystems is clearly a question that deserves further attention. This is especially true given that some models predict that the frequency and magnitude of extreme events such as El Niño droughts will increase (Timmermann et al. 1999), potentially leading to changes in species composition/structure from which forests have insufficient time to recover.

Whatever the cause(s), changes in forest composition will have important implications for how changes in structure and dynamics translate into changes of important ecosystem services such as carbon storage (Körner 2004, Bunker et al. 2005). For example, at BCI there has been a rapid decrease in relative basal area growth rates since the plot was established (Feeley et al. 2007b). However, over the same period, biomass growth rates have remained relatively stable or have actually increased (Chave et al. 2008). This apparent contradiction can be explained in part by the observed shift in species composition toward heavier-wooded species. In other words, decreased basal area growth is compensated for by increased mean wood density, leading to stable or increasing biomass growth. As this example illustrates, it is critical that we understand how individual species (or at the very least, functional groups) respond to environmental changes if we hope to predict how ecosystem services will be altered by future global changes. Given the importance of tropical forests in the global carbon budget and in regulating global climate, changes in these ecosystem services will have widespread environmental and economic implications. Understanding the effects of global change on natural ecosystems is one of the "grand challenges" to modern ecology (Thuiller 2007), and as such, investigating compositional changes should be a clear research priority.

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APPENDIX A

Plot of annual precipitation and mean daily minimum and maximum temperatures as recorded at Barro Colorado Island, Panama, since 1950 and 1975 (*Ecological Archives* E092-075-A1).

APPENDIX B

Contour map of elevation at Barro Colorado Island, Panama (*Ecological Archives* E092-075-A2).

APPENDIX C

Map of the Isthmus of Panama showing the rainfall gradient from the wet Caribbean coast to the dry Pacific coast and the approximate locations of inventory plots at Barro Colorado Island, Fort Sherman, and Cocoli (*Ecological Archives* E092-075-A3).

APPENDIX D

Scree plot of stress values vs. dimensionality for nonmetric multidimensional scaling ordinations of the tree communities within each of the 50 1-ha subplot tree communities at Barro Colorado Island, Panama, during each census (*Ecological Archives* E092-075-A4).

APPENDIX E

Histogram showing the distribution of succession rates for each of the 50 1-ha subplots at Barro Colorado Island, Panama, for the period 1985–2000 (*Ecological Archives* E092-075-A5).