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Contrasting outcomes of species- and community-level analyses of the temporal consistency of functional composition

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Abstract. Multiple anthropogenic drivers affect every natural community, and there is broad interest in using functional traits to understand and predict the consequences for future biodiversity. There is, however, no consensus regarding the choice of analytical methods. We contrast species- and community-level analyses of change in the functional composition for four traits related to drought tolerance using three decades of repeat censuses of trees in the 50-ha Forest Dynamics Plot on Barro Colorado Island, Panama. Community trait distributions shifted significantly through time, which may indicate a shift toward more drought tolerant species. However, at the species level, changes in abundance were unrelated to trait values. To reconcile these seemingly contrasting results, we evaluated species-specific contributions to the directional shifts observed at the community level. Abundance changes of just one to six of 312 species were responsible for the community-level shifts observed for each trait. Our results demonstrate that directional changes in community-level functional composition can result from idiosyncratic change in a few species rather than widespread community-wide changes associated with functional traits. Future analyses of directional change in natural communities should combine community-, species-, and possibly individual-level analyses to uncover relationships with function that can improve understanding and enable prediction.

Key words: Barro Colorado Island; climate change; cross validation; drought; functional traits; scale dependency; tropical forest; wood density.

Introduction

The composition of natural communities is changing as species respond to multiple anthropogenic drivers (Hautier et al. 2015). Consistent responses are expected among similar species with similar ecologies, which is the basic concept of trait-based ecology (McGill et al. 2006). However, this is not a foregone conclusion. Idiosyncratic responses of species may prevail for many reasons including altered interactions among the responding species, and possible synergisms among anthropogenic drivers and species-specific events (e.g., the outbreak or loss of a host-specific plant pathogen [Gilbert et al. 2001]).

Discriminating between these alternatives is important for our ability to generalize findings and to predict the trajectories of communities into the future. Consistent change across many similar species suggests a common cause and the possibility to predict changes through time or across space once the cause is identified (Lavorel and Garnier 2002). In contrast, directional community-level changes driven by idiosyncratic changes in a handful of species will provide limited insight into causation and future change (Gibson-Reinemer and Rahel 2015). Directional changes in the emergent properties of tropical forest plant communities are widely discussed relative to potential anthropogenic drivers (reviewed by Lewis et al. 2009, Wright 2010); however, the species-level changes that scale up to community-level change are

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rarely evaluated (but see Clark et al. 2003, Wright et al. 2004, Wright and Calderon 2006).

Feeley et al. (2011) and Swenson et al. (2012) independently analyzed temporal changes in the functional composition of trees at the community level for the 50-ha Forest Dynamics Plot (FDP) on Barro Colorado Island (BCI), Panama with seemingly contradictory results. Feeley et al. (2011) documented significant directional changes in functional composition consistent with increases of traits associated with drought tolerance. In contrast, Swenson et al. (2012) documented significant stability of functional composition as trees turned over and little-to-no change in the importance of drought tolerance traits. We return to this problem, address species-level relationships between traits and abundance changes for the first time, and quantify species-specific contributions to directional shifts observed at the community level.

We evaluate community- and species-level changes using seven censuses of the BCI 50-ha plot conducted between 1982 and 2010. If drought-tolerant species are generally increasing in importance (as suggested by Feeley et al. [2011]), then we predict a positive correlation between changes in species' relative abundance and traits associated with drought tolerance. On the other hand, if there is no shift in species composition toward drought tolerant species (as suggested by Swenson et al. [2012]), then any observed community-level trait shifts may be attributable to changes in the abundance of just a few species. We first show that distributions of community-level means appear to shift through time for selected traits. Following on this result, we ask (1) Are there statistically significant shifts of community-level mean trait values? (2) Do traits associated with drought tolerance correlate with species abundance changes? We show that patterns of community and species-level responses do not match, which suggests the importance of idiosyncratic responses of a few species. Finally, to evaluate this possibility, we ask (3) Which species have strong contributions to the directional shifts observed at the community level?

Methods

Study site

We evaluated compositional changes of tree species in the moist lowland forest of the 50-ha FDP on BCI, Panama. All free-standing woody plants with diameter at breast height ≥1 cm were measured in 1982, 1985, 1990, 1995, 2000, 2005, and 2010 (Condit et al. 2012). Annual rainfall averages ~2600 mm, with a four-month dry season between December and April. Mean annual temperature is 27°C.

Trait dataset

We selected one individual-level trait and three population-level traits that are widely hypothesized to be related to drought tolerance. These included wood density, a geographic moisture index, and two topographic indices of soil moisture availability. Wood density is wood dry mass divided by fresh volume and is related to vulnerability to drought-induced xylem cavitation (Hacke et al. 2001). Wood density values are from Wright (2010) and S. J. Wright et al. (*unpublished data*). The geographic moisture index was calculated from species' occurrence probabilities relative to moisture availability across an isthmian rainfall gradient from 1,760 to 3,250 mm annual rainfall (Condit et al. 2013). Larger values indicate species that are more likely to occur in wetter environments. On BCI, soil moisture availability generally increases in areas with greater slope and/or concavity (Becker et al. 1988). Using elevation data for the FDP, we calculated concavity and slope at the scale of 20 × 20 m subplots. For each species we then calculated the mean concavity and mean slope weighted by the number of individuals within each 20 × 20 m subplot for the first census in which the species was recorded following Feeley et al. (2011). Wood density was used by Feeley et al. (2011) and Swenson et al. (2012). Concavity and slope were only used by Feeley et al. (2011). The geographic moisture index was not used in either study; however, Feeley et al. (2011) compared species composition for the FDP and two plots located near the extremes of the isthmian rainfall gradient. We treated population-level traits as species traits in our analysis and hereafter refer to species traits. Wood density, the moisture index, concavity and slope were only very weakly related ($-0.15 <$ Spearman's $\rho < 0.17$; Appendix S1: Table S1).

Data analysis

We used kernel density estimation to visualize trait shifts from 1982 to 2010 at the individual level and at the community level for the 100 × 100 m spatial scale used by Feeley et al. (2011) and for the 20 × 20 m spatial scale used by Swenson et al. (2012). For the individual level, we assigned species mean trait values to all individuals in the FDP. For the community level, we first calculated community-weighted mean (CWM) trait values for each of the 50 100 × 100 m (1 ha) and 1250 20 × 20 m (0.04 ha) subplots weighted by abundance following Feeley et al. (2011). We estimated kernel densities for the individual values or for the CWM values. We used Silverman's rule of thumb to calculate the bandwidth for the CWM values (Silverman 1986). Following Swenson et al. (2012), we made the bandwidth four times larger for the individual-level analysis than for the community-level analyses because many individuals share the same trait values, which makes the individual-level kernel estimates noisy.

To evaluate community mean trait shifts, we modeled temporal changes in CWM trait values across censuses at two spatial scales (0.04 and 1 ha), using a generalized additive mixed model (GAMM) with a normal error distribution. Generalized additive mixed model uses smoothing functions to model nonlinear relationships, providing a flexible, nonparametric regression model (Wood 2006). We fit a continuous autoregressive process of order 1 to account for the temporal autocorrelation structure for each subplot. Error variances were assumed to be increased with the census numbers (i.e., 1–7) to account for heteroscedasticity (unequal variance). We used a 10-fold cross-validation procedure to evaluate model fit. The subplots were randomly split into 10 groups and, for each iteration, nine of the groups were used to estimate model parameters and the remaining group was used to evaluate model fit. A cross-validated r^2 value was calculated (1 − predictive error sum of squares/total sum of squares) and used to assess the strength of model fit. We refer to the cross-validated model fit as r^2_{CV}. Small sample size (seven data points) precluded the GAMM analysis for individual-level traits analyzed at the 50-ha scale.

We fit generalized linear models (GLM) with negative binomial error distributions to evaluate relationships between changes in species-level abundances and trait values. We modeled the abundance of each species in 2010 as a function of the four traits and their interactions, using the logarithm of the 1982 abundance as a baseline intercept (i.e., offset). We used a stepwise variable selection procedure based on the Akaike information criterion to select the best-fit model (Burnham and Anderson 2002). We further used 10-fold cross-validation to evaluate model fit. We modeled species abundance at three spatial scales: 0.04, 1, and 50 ha. We repeated the GLM analysis for each subplot and estimated r^2_{CV} (e.g., once for 50 ha, 50 times for 1 ha, and 1,250 times for 0.04 ha). Finally, to examine response of species with extreme trait values, we repeated the GLM analyses using just those species with trait values in the upper 10%, upper 20%, lower 10% or lower 20% quantiles for each trait. We added one to 1982 and 2010 abundances for every species-subplot combination to eliminate zero values.

To estimate the contribution of each species to community mean trait shifts across the plot, we calculated the following contribution index:

$$\text{contribution index} = (f_{i,2010} - f_{i,1982}) \times (t_{i,j} - \overline{t_j})$$

where $f_{i,A}$ is the relative abundance of species i in the plot at time A, $t_{i,j}$ is the trait j in species i, and $\overline{t_j}$ is the CWM for trait j at the initial census. Thus, the sum of the contribution index across species is approximately equal to CWM change from 1982 to 2010, and the contribution index of each species represents its contribution to CWM change. The contribution index is negative if the abundance of species with small trait values increased or the abundance of species with large trait values decreased. The absolute value of the contribution index is largest for species with large changes in relative abundance and extreme trait values.

Results

Kernel density estimates

Kernel density estimates shift toward larger values through time for wood density and the geographic moisture index, and toward smaller values for the concavity and slope indices for the community-level analysis at the 1-ha scale (Fig. 1e–h). No temporal trends are evident for kernel density estimates at the 0.04-ha scale or for the individual-level analysis conducted at the 50-ha scale (Fig. 1i–l and a–d, respectively).

Generalized additive models for community-level responses

Temporal trends were detected for wood density and concavity and slope indices for 1-ha subplots (Fig. 2he–). Mean wood density for 1-ha subplots increased from 1982 to about 2000 but then declined more recently (Fig. 2a, e). The slope index decreased 1982 to 2000 (Fig. 2d, h), but then increased more recently. The concavity index decreased monotonically (Figs. 2c, g). There were no significant temporal trends for 0.04-ha subplots (Fig. 2i–l) because the 0.04-ha scale subplots average 170 individual trees in a forest with 312 tree species, which produced huge variation in community means (Fig. 2i–l).

Generalized linear models for species-level responses

There were no significant relationships between trait values and species-level changes in abundance from 1982 to 2010 at any of the spatial scales (Fig. 3). At the 50-ha scale, r^2_{CV} equaled −0.095 for the model including all four traits and their interactions (95% confidence interval [CI] of $r^2_{\mathrm{CV}} = -0.247, 0.056$). We obtained similar patterns for other census periods (Appendix S1: Table S2). We repeated the analysis for the 50-ha scale without adding one to every abundance and obtained a similar result ($r^2_{\mathrm{CV}} = -0.093$, 95% CI of $r^2_{\mathrm{CV}} = -0.253, 0.066$). At the 1-ha scale, just three of 50 r^2_{CV} values were positive. At the 0.04-ha scale, just seven of 1250 r^2_{CV} values were positive. The 95% CI of all positive r^2_{CV} values contained zero (Data S1). The r^2_{CV} values for the relationships between trait values and species-level changes in abundance were also negative for species with extreme trait values (Appendix S1: Fig. S1). Negative r^2_{CV} values indicate that these models had almost no predictive ability.

Species-specific contributions to community mean trait shifts

One to six species out of 312 species drove community mean shifts for each trait (Fig. 4). For example, the contribution of *Piper cordulatum* to the moisture index is larger than the total community mean shift (Figs. 2b, 4b). The numbers of positive and negative contributions

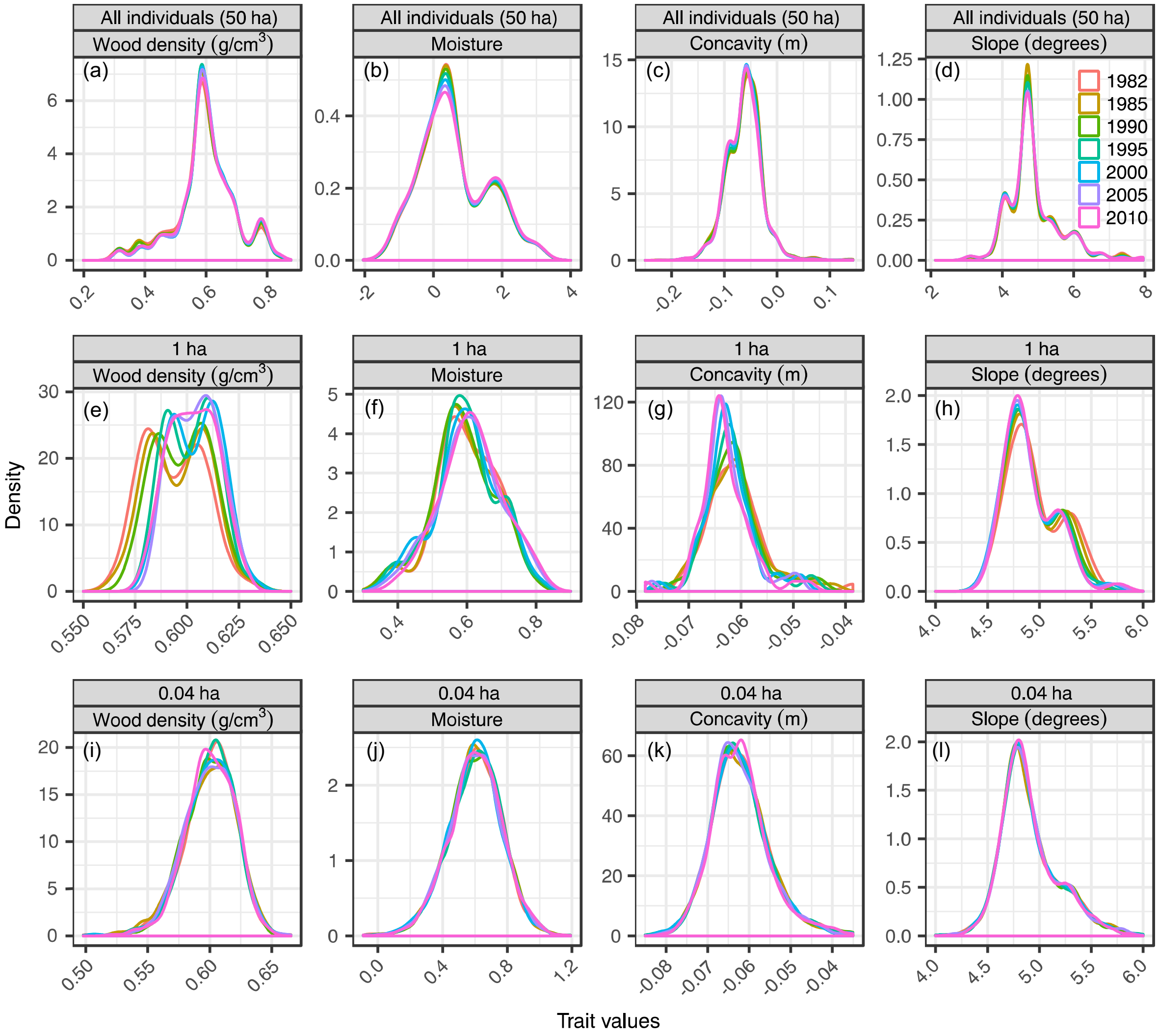

FIG. 1. Kernel density estimates for (a, e, i) wood density and indices of (b, f, j) moisture sensitivity across the Isthmus of Panama and of association with microtopography ([c, g, k] surface concavity, [d, h, l] surface slope) within the Barro Colorado Island 50-ha plot. Kernel density estimates are for trait values for all individuals for the (a–d) 50-ha plot and for (e–h) community weighted mean trait values for 1-ha subplots and (i–l) 0.04-ha subplots. The seven colors represent seven censuses conducted between 1982 and 2010. Note that the horizontal axis scales differ among rows.

are not significantly different for any of the traits (Fig. 4; see Data S2 for abundance changes and contribution indices for each species, binomial $P > 0.05$), confirming that there is little evidence of consistent directional changes associated with trait values across species.

Our contribution index quantifies the contribution of each species to community-level trait shifts. A handful of species were largely responsible for the community mean trait shifts. For example, *Hybanthus prunifolius* and *Faramea occidentalis* were the two most abundant species both in 1982 and 2010 (See Appendix S1: Table S3 for their trait values). Their modest relative abundance changes had large effects for the CWM concavity and slope indices, respectively (Fig. 4c, d). As another example, *Piper cordulatum* and *Poulsenia armata* have very low wood densities (0.36 and 0.32 g/cm^3, respectively) and their abundances in the 50-ha plot dropped precipitously from 3,143 and 3,422 individuals in 1982 to just 87 and 996 individuals in 2010, respectively. These two species accounted for 62.6% of the community mean increase in wood density (Fig. 4a). The most striking pattern is the effect of *Piper cordulatum* on the moisture index (Fig. 4b). The change in the CWM value of the moisture index is smaller than the individual contribution of *Piper cordulatum*. In other words, the significant positive shift observed for the CWM moisture index would become negative without *Piper cordulatum*. The species with the largest contribution indices were either superabundant species with modest proportional change in abundance (e.g., *H. prunifolius* and *F. occidentalis*) or initially abundant

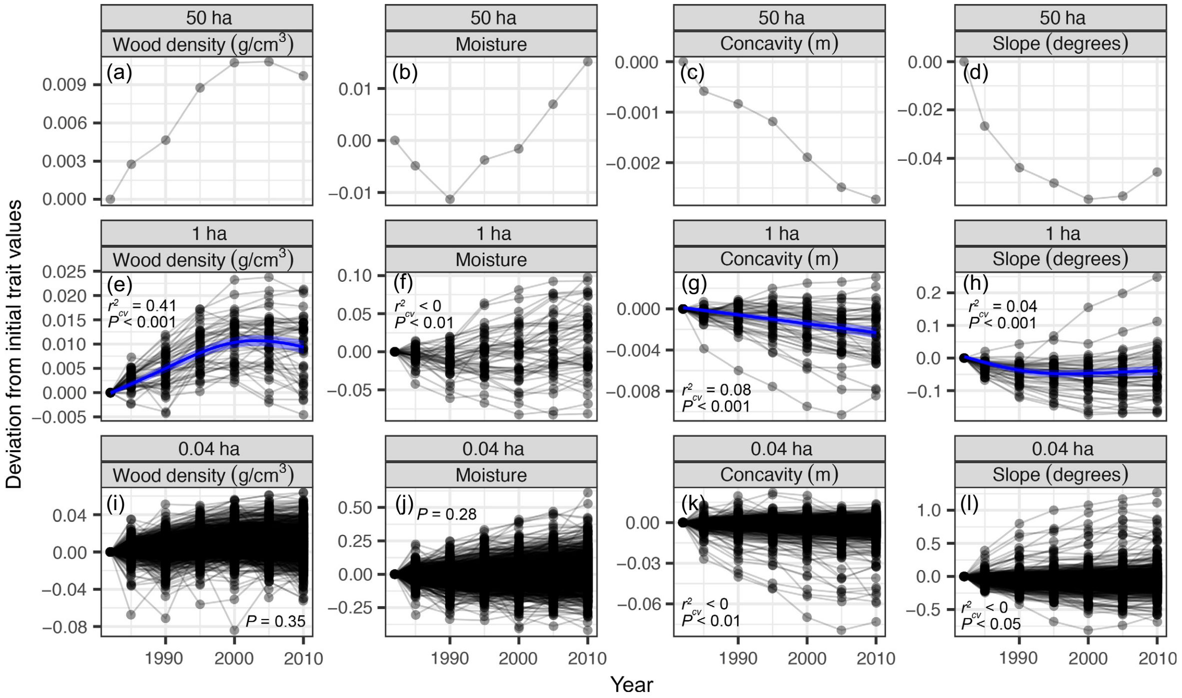

FIG. 2. Temporal trends of community weighted mean traits from 1982 to 2010 for the Barro Colorado Island (a–d) 50-ha plot, (e–h) 1-ha subplot, and (i–l) 0.04-ha subplots. Temporal trends were obtained from a model accounting for temporal autocorrelation and heteroscedasticity. The 95% confidence intervals are shown for relationships with significant ($P < 0.05$) and positive cross-validated r^2 values. Each symbol represents a census by plot or census by subplot combination. Same plots or subplots were connected by lines for readability. Note that statistical models were not applied for the 50-ha plot because of small sample size.

species with extreme trait values that collapsed during the censuses (e.g., *Piper cordulatum* and *Poulsenia armata*).

DISCUSSION

The tree community in the BCI 50-ha plot experienced significant, but weak, community-level changes in functional composition between 1982 and 2010 at the 1-ha scale (Figs. 1e, g, h, 2e, g, h). Temporal trends in CWM values for wood density and the concavity and slope indices appear to suggest a shift toward drought-tolerant species, but these community-level changes were not associated with consistent, trait-dependent, species-level responses (Fig. 3, 4). Additionally, there was no evidence of community-level change for the geographic moisture index (Figs. 1b, 2b, f). A handful of species were largely responsible for the community mean trait shifts (Fig. 4). These idiosyncratic species changes can cause misleading inferences for changes in community level means. We conclude that there is little evidence for shifts in species composition toward drought-adapted tree species on BCI.

Many tree species experience large changes in abundance at decadal time scales in tropical forests, including BCI (Chisholm et al. 2014). Small changes in CWM trait values are unsurprising given these large and still unexplained changes in relative abundances. This is the case on BCI where changes in the abundances of a small number of species (Figs. 3, 4) drove community-level changes in mean trait values (Figs. 1e, g, h, 2e, g, h). Several of those species-specific changes in abundance could represent time-delayed population collapses (Ogle et al. 2015, Blonder et al. 2017) in response to drought. El Niño events bring reduced rainfall and elevated temperatures to BCI (Wright and Calderon 2006), and an extreme El Niño drought in 1983 (Condit et al. 2004) or several decades of declining rainfall from the 1950s through the 1970s (Windsor 1990) might have long-lasting effects leading to population declines in drought sensitive species. It remains unclear, however, why only a handful of species with traits associated with drought intolerance collapsed, while many other species with similar trait values did not (Fig. 3). In addition, BCI rainfall has recovered steadily since 1980, and is now at the highest levels recorded since rainfall records began in 1929 (Appendix S1: Fig. S2). Steadily increasing rainfall from 1980 to the present suggests drought sensitive species should have increased, not decreased in abundance between 1982 and 2010. Alternatively, a handful of species may have experienced population collapses for reasons unrelated to their drought-tolerance. As just one example, species-specific pathogens are known to have caused sharp declines in the abundance of long-lived BCI trees (Gilbert et al. 2001). Additional species-level

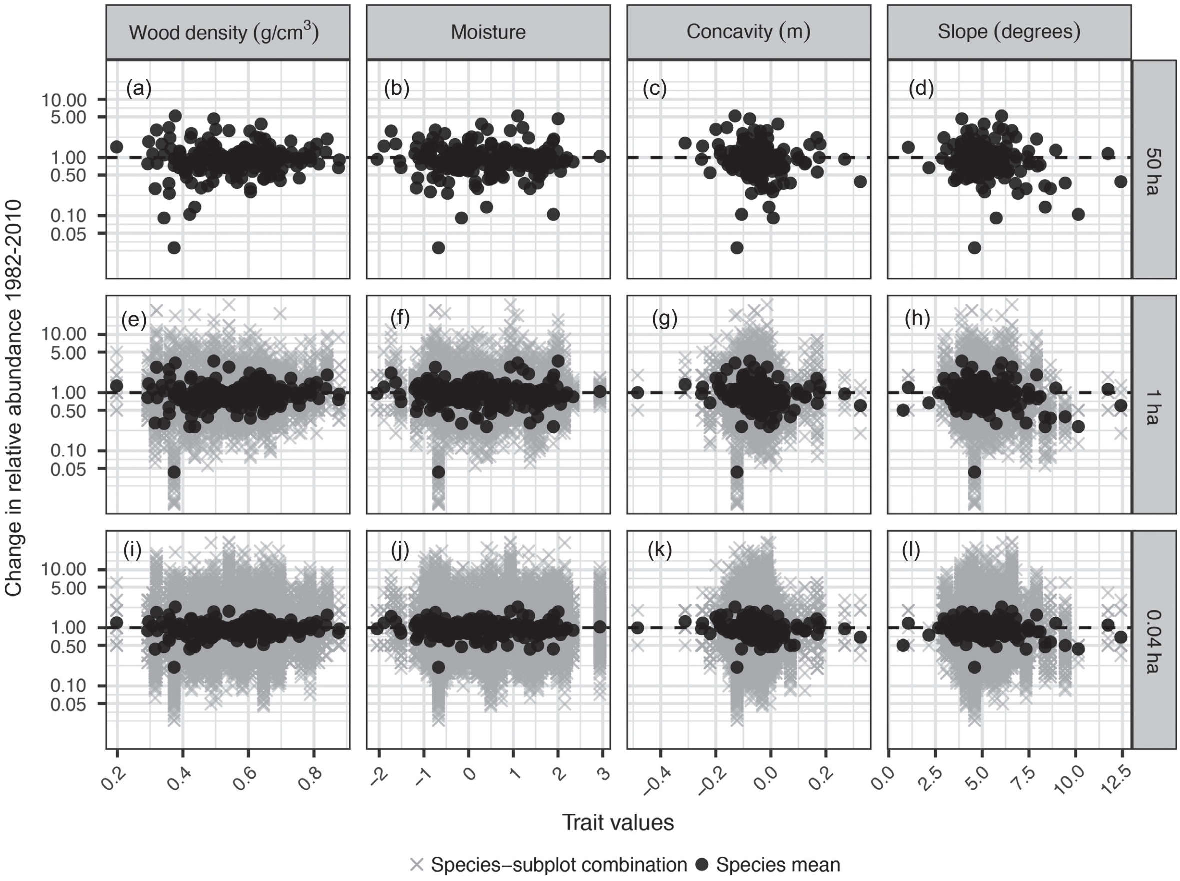

FIG. 3. Scatterplot of relative abundance changes ([no. individuals + 1 for 2010]/ [no. individuals + 1 for 1982]) vs. wood density and geographic moisture, concavity, and slope indices. The relative abundance changes of each species were calculated as the number of individuals in the 2010 census divided by the number of individuals in the 1982 census for the (a–d) 50-ha plot, (e–h) 1-ha subplots, and (i–l) 0.04-ha subplots. In panels e–l, the small gray points represent each species–subplot combination and the large black points represent species mean values. Dashed lines indicate equal abundance in 1982 and 2010.

analyses are needed to gain more mechanistic understanding of changes in species composition.

Future work to link climate change and temporal changes in species composition should explore the mechanisms causing changing abundances directly. A first step will be to explore the changes in mortality and recruitment rates that lead to changes in abundance and species composition (Chave et al. 2008). Mortality and recruitment rates are often well correlated with functional traits (Visser et al. 2016), and these relationships can provide insight into changes in abundance and species composition. Another important step will be to employ harder-to-measure physiological traits, rather than easily measured morphological proxies (Swenson 2013). Although functional traits have potential to explain demographic responses of plants, relationships between such soft functional traits and plant function are often weak. For example, wood density is often used as a surrogate of xylem safety and drought tolerance following Hacke et al. (2001); however, a recent meta-analysis shows that wood density explains just 6% of interspecific variation in xylem safety and 18.9% of interspecific variation in xylem efficiency (capacity to transport water) among angiosperms (Gleason et al. 2015). The large proportion of interspecific variation that is not explained by wood density introduces noise into analyses relating anthropogenic drivers to temporal changes in species functional composition. Future work should also be conducted at other rainforest sites and in other systems to address the generality of the role of idiosyncratic species responses to community level changes. Given that our results are from a single study site, it is premature to be overly pessimistic about the contribution of functional traits toward understanding changing natural communities.

Community-based analysis of functional traits has made great progress in understanding species' distributions and ecosystem function (McGill et al. 2006, Díaz et al. 2007) and is thought to be a promising approach for forecasting biodiversity change (Adler et al. 2013) under future climate scenarios. However, there is no consensus regarding the choice of analytical methods to detect temporal changes in biological communities. We have shown that community- and species-level analyses

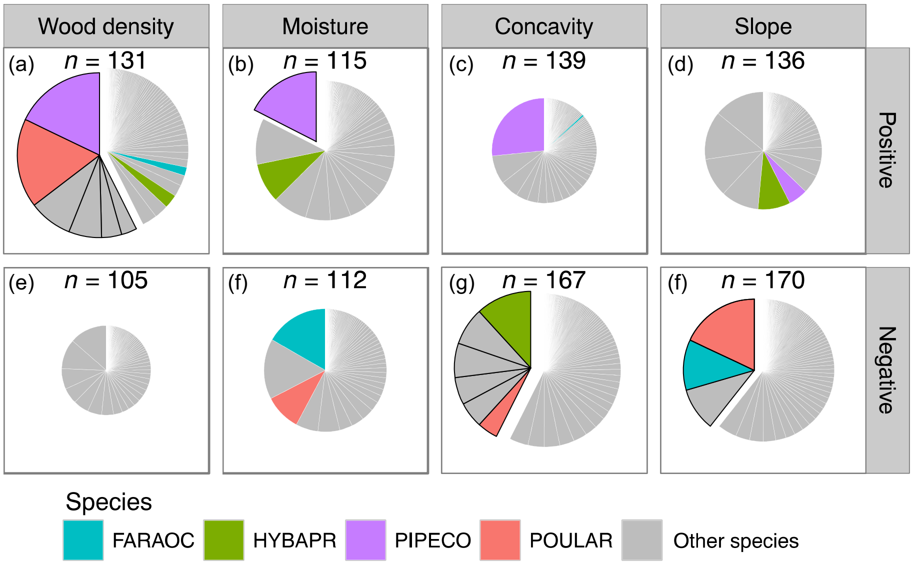

FIG. 4. Species-specific contributions to community mean trait shifts observed from 1982 to 2010 for wood density and moisture, concavity, and slope indices at the 50-ha scale. The pie chart shows the relative contributions of each species to the community mean trait shifts. Positive contributions (top row) indicate species with low trait values decreased in abundance or species with high trait values increased in abundance. Species-level contributions surrounded by black lines are as large as the total community mean shifts. FARAOC, *Faramea occidentalis*; HYBAPR, *Hybanthus prunifolius*; PIPECO, *Piper cordulatum*; POULAR, *Poulsenia armata*; *n*, species number.

can produce opposing outcomes, with just one to six species driving community-level changes in trait distributions in a tree community with 312 species. Predicting future biodiversity will require moving analytical approaches from the community-level to the species-level and possibly to the individual-level. An understanding of why species-level responses to climate change vary with functional traits will be necessary to predict future changes in species composition caused by anthropogenic change, with multiple anthropogenic drivers operating simultaneously (climate change, atmospheric CO_2, N deposition, etc.). We cannot reach this goal without a more mechanistic understanding of species-specific responses.

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