



Climate shapes and shifts functional biodiversity in forests worldwide

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Much ecological research aims to explain how climate impacts biodiversity and ecosystem-level processes through functional traits that link environment with individual performance. However, the specific climatic drivers of functional diversity across space and time remain unclear due largely to limitations in the availability of paired trait and climate data. We compile and analyze a global forest dataset using a method based on abundance-weighted trait moments to assess how climate influences the shapes of whole-community trait distributions. Our approach combines abundance-weighted metrics with diverse climate factors to produce a comprehensive catalog of trait-climate relationships that differ dramatically—27% of significant results change in sign and 71% disagree on sign, significance, or both—from traditional species-weighted methods. We find that (i) functional diversity generally declines with increasing latitude and elevation, (ii) temperature variability and vapor pressure are the strongest drivers of geographic shifts in functional composition and ecological strategies, and (iii) functional composition may currently be shifting over time due to rapid climate warming. Our analysis demonstrates that climate strongly governs functional diversity and provides essential information needed to predict how biodiversity and ecosystem function will respond to climate change.

biodiversity | climate | functional ecology | macroecology | ecosystem function

Determining how the functional composition of communities changes along environmental gradients is the first step toward developing a more mechanistic understanding of climate's role in driving ecosystem structure and function (1–10). Ecologists are working to map relationships between functional composition and environmental conditions (6, 8, 10–15), but this work faces three major challenges. First, due to the difficulty of collecting trait datasets in the field, studies are often restricted to relatively small regions (e.g., a single elevational gradient) and only one or a few functional traits and climatic variables. Second, large-scale functional ecology studies usually do not include location-specific trait measurements (8), relying only on global trait databases that typically have a single, globally averaged value for each species. Third, trait moments and other functional metrics are often weighted according to species rather than to individual abundance or biomass (10), which must more strongly relate to overall ecosystem function and net primary production (16). Specifically, many past studies (e.g., refs. 11–15 and 17) that assess how traits vary across broad climatic gradients typically have not combined species trait values with species abundances to accurately quantify the shapes of whole-community trait distributions (but see refs. 6 and 18 for exceptions). Without overcoming these challenges, it will be difficult to decipher which environmental variables influence different aspects of functional diversity across space and to what extent climate change is causing functional changes within communities over time.

To help overcome these challenges and better assess the variation and drivers of functional biogeography, we compiled a global trait and climate dataset that includes 421 forest plots of 0.1 ha each (tree communities); 2,701 distinct tree species; and 55,983 individual trees over 100° in latitude and 3,351 m in elevation (Fig. 1A and *SI Appendix*, Fig. S1). We assigned trait information to individual trees greater than 2 cm in diameter in all communities. Trait data were collected in situ for 66 communities in our dataset to provide high-fidelity, location-specific trait information. To estimate the multidimensional climatic conditions experienced by each community, we gathered data on multiple environmental variables including temperature, precipitation, vapor pressure, solar radiation, and wind speed using high-resolution global climate raster layers (19–24).

We specifically address four key hypotheses in functional biogeography (14, 25–29): (i) increasingly harsh and variable environments decrease functional diversity, selecting for a narrow range of more conservative growth strategies (14, 25); (ii)

Significance

Functional traits directly link the performance of organisms to the environment and are used to scale up to effects on the overall structure, function, and diversity of ecosystems. Therefore, examining how the community composition of functional traits changes with the environment is key to understanding the role of climate in ecology. We provide a comprehensive assessment of relationships between climate and the functional composition of forests throughout the world. We identify the primary climatic drivers of functional composition/diversity across broad geographic gradients and show that forests may be experiencing functional shifts in response to global warming. These results illuminate important trait-climate relationships that help us understand the distribution of organisms throughout the world and anticipate ecosystem responses to future climate change.

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Data deposition: All data used in this study have been deposited on figshare (<https://doi.org/10.6084/m9.figshare.7436951.v1>). All custom R codes used in this study are available on GitHub at https://github.com/DanWieczynski/PNAS_201813723.git.

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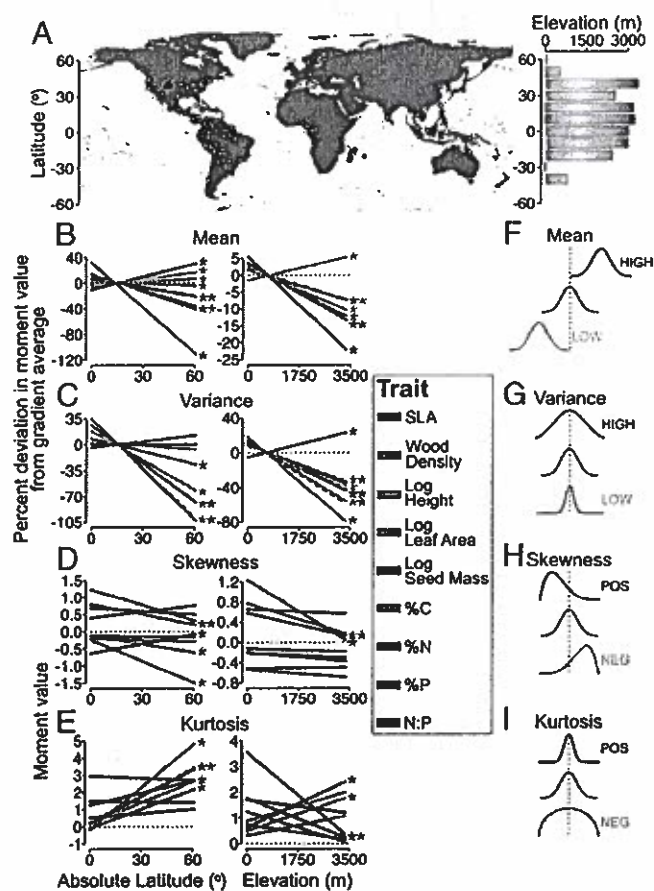


Fig. 1. Shifts in the community-weighted moments of several key functional plant traits along latitudinal and elevational gradients. (A) Geographic distribution of the 421 forest communities in this study (triangles designate the 66 locally sampled communities). (B–E) Abundance-weighted moments of whole-community trait distributions across (absolute) latitude and elevation. For mean and variance (B and C), lines represent linear regressions on the percent deviation between individual community values and the average moment value for a given trait and geographic gradient. For skewness and kurtosis (D and E), lines are regressions on raw moment values and absolute values of latitude and elevation to enable comparison with normality (skewness/kurtosis = 0). Stars signify significant regressions, and dashes are used to visualize overlapping lines. (F–I) Cartoons illustrating how variation in trait distribution shape is captured by each of the respective moments.

these functional shifts are primarily driven by changes in mean annual temperature and precipitation (26); (iii) community and biogeographic shifts in functional diversity across broad gradients reflect directional shifts in ecological strategies (27, 28); and (iv) climate change is currently driving shifts in functional composition over time (29). We find solid support for hypotheses (i), (iii), and (iv) but reject hypothesis (ii), instead finding temperature variability and vapor pressure to be the primary drivers.

For this study, we analyzed a suite of key functional traits that are known to influence plant performance (27, 28, 30), including specific leaf area (SLA), wood density, tree height, seed mass, leaf area, leaf carbon (%C), nitrogen (%N), and phosphorus (%P) content, as well as the ratio of leaf nitrogen to phosphorus (N:P). We characterized the functional composition of each tree community by calculating the first four central moments—mean, variance, skewness, and kurtosis—of abundance-weighted trait distributions for each trait across the whole community. These moments and distributions are weighted based on the total abundance of individuals within each species with a specific trait value (9, 31–33)

rather than weighting trait values equally across species (species weighting). Here we use abundance to weight species trait values within communities. We note that other forms of biomass weighting could produce different results and could be more appropriate depending on the study. Thus, we also analyzed our data using basal area weighting, finding that only 2% of significant trait–environment correlations exhibit changes in sign compared with abundance weighting (*SI Appendix*, Fig. S2C).

Analyses based on abundance-weighted trait moments often differ substantially from those using species-weighted metrics, with 27% (166/612) differing in sign while maintaining significance and 71% (433/612) differing in sign, significance, or both (*SI Appendix*, Fig. S2). Additionally, weighted metrics more accurately connect with whole-ecosystem function and net primary productivity, which arise from sums across all individuals and total biomass (16). We quantify the shapes of whole-community trait distributions by accounting for the relative abundance and rarity of trait values that are driven by unequal species abundances, thus capturing key features of functional diversity (34, 35) and reflecting the dynamics of community assembly that result from differences in individual performance (9, 35). Abundance-weighted mean trait values represent the average location of a community in trait space. Comparing means across communities provides a measure of functional diversity at regional or global scales (36, 37). Together, the higher-order trait moments describe important and nuanced aspects of local functional diversity by characterizing the range or richness (variance), asymmetry (skewness), and evenness (kurtosis) of trait values within communities.

We compared abundance-weighted trait moments across forests throughout the world and associated shifts in functional composition and diversity with shifts in climate. Although previous studies have explored multiple traits or environmental drivers separately, few studies have combined abundance-weighted metrics with a wide range of traits and environmental drivers simultaneously. Indeed, to our knowledge this has never been performed at large (multicontinental) geographic/climatic scales as is done in the present study. Hence, our study creates a crucial catalog of trait–climate relationships in forests that provides a more comprehensive and detailed understanding of the complex role of climate in functional biogeography.

Across the globe we found that forests exhibit significant and substantial shifts in trait moments across latitude and elevation (Fig. 1 B–E and *SI Appendix*, Fig. S3). These shifts represent changes in the shapes of community trait distributions that directly correspond to distinct aspects of functional composition and diversity (Fig. 1 F–I). All traits (except seed mass) exhibit significant relationships between mean trait values for communities and both absolute latitude and elevation (Fig. 1B). As latitude and elevation increase, community mean values of many leaf traits related to growth demonstrate coordinated shifts toward more conservative growth strategies (27, 30)—lower SLA, leaf area, leaf N and P content (elevation only for %P), and higher leaf C content. In addition, most traits decline in variance (Fig. 1C), skewness tends toward zero (Fig. 1D), and kurtosis tends to increase away from zero (Fig. 1E) with increases in latitude and elevation. These trends in higher community moments collectively suggest that rare phenotypes at the edges of trait space are selected against in harsher environments, consistent with the “favorability hypothesis” (14, 25) stating that environmental filtering becomes more pronounced as environmental conditions become less favorable. Taken together, these results demonstrate community-wide shifts in growth strategies and sweeping declines in functional diversity—richness, asymmetry, and evenness—within forest communities along these geographic gradients.

That most trait moments exhibit the same trends across latitude and elevation is consistent with the hypothesis that there is widespread convergence in how functional composition changes along these major geographic gradients. Despite this convergence, two key realizations are: (i) latitudinal shifts in trait moments are generally larger in magnitude than elevational shifts, and

(ii) notable examples of divergent trends appear in mean tree height, mean %P, and variance in seed mass. Consequently, these two geographic gradients are not completely interchangeable proxies for measuring changes in functional biodiversity in response to climatic variation across space. Our findings allow us to accurately calculate shifts in biodiversity with changes in latitude and elevation. These results also indicate that more detailed analyses using individual environmental variables may be necessary to fully evaluate spatial shifts in functional composition.

Pairwise correlations between individual environmental variables and trait moments reveal more nuanced influences of climate on functional diversity (Fig. 2 and *SI Appendix*, Fig. S2). Several different climate variables—not just mean annual temperature and precipitation—exhibit significant correlations with trait moments (Fig. 2A). Indeed, vapor air pressure (VAP) and temperature seasonality (TS) exhibit the strongest correlations on average across all trait moments (Fig. 2B). More specifically, measures of temperature and vapor pressure are among the strongest predictors of mean and variance in all traits, signifying the influence of these two climatic factors on functional richness both among (comparing means) and within (variance) communities. SLA, leaf area, seed mass, %N, and N:P exhibit very similar trends between community mean values and climate, with values that are strongly positively related to measures of mean annual temperature (MAT), isothermality (ISO), and mean vapor pressure [VAP, vapor pressure deficit (VPD), potential evapotranspiration (PET)] yet negatively related to measures of temperature variability [temperature diurnal range (TDR), temperature annual range (TAR), and TS]. Likewise, mean height, %C, and %P are strongly positively related to temperature variability (TDR, TAR, TS) and negatively related to MAT, ISO,

and vapor pressure (VAP, VPD, PET, although height is only significantly related to VPD). Variance in SLA, wood density, height, leaf area, %C, %N, and N:P is positively related to measures of vapor pressure and negatively related to measures of temperature variability (except SLA with temperature variability), suggesting that higher VAP, VPD, and PET promote functional richness while temperature variability actually limits functional richness. Measures of skewness in height, %C, %P, and N:P all exhibit negative relationships with temperature variability and positive relationships with vapor pressure, implying that these environmental variables also control functional asymmetry in forests. Interestingly, trait variance and kurtosis have divergent relationships (opposite signs) with environmental variables in 85% (51 of 60) of the cases in which both variance and kurtosis are significantly correlated with a single environmental variable. This suggests that functional richness and evenness are positively related and coordinated along environmental gradients.

These analyses demonstrate striking similarities in how different climatic variables influence variation in functional composition/diversity in forests, highlighting temperature and vapor pressure as potentially the primary drivers of this variation. Although our analysis identifies temperature variability and vapor pressure as the most important predictors of trait–environment relationships, it is important to note that other environmental drivers—such as mean annual temperature—do exhibit strong and meaningful correlations with trait moments. Indeed, the strongest individual environmental driver of each moment varies widely among traits, showing that a variety of different climatic factors influence functional composition across different trait axes (Fig. 2A). The divergence between latitude and elevation relationships observed in mean height, mean %P, and variance

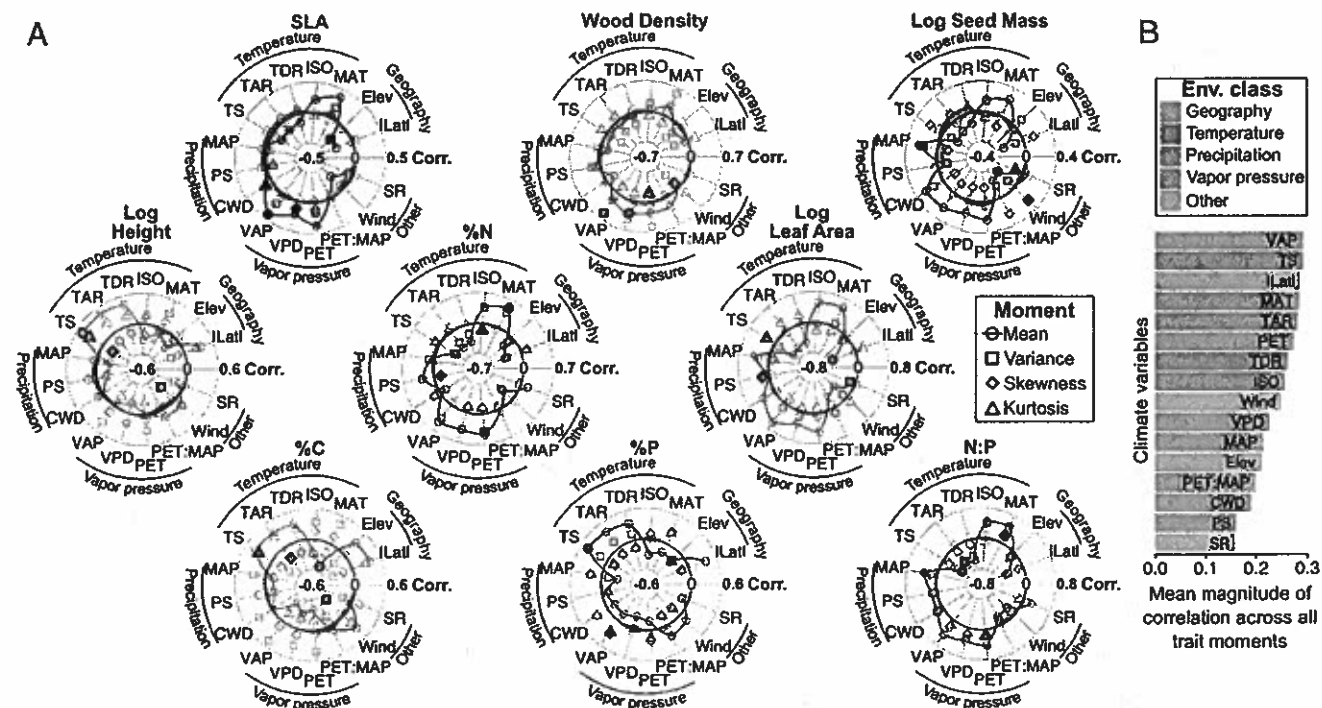


Fig. 2. Relationships between the community-weighted moments of individual traits and all environmental variables across all forests. (A) Radar plots showing all trait moment–environment correlations. Each symbol represents a different trait moment, and its position along the radial axis indicates the strength of correlation between that moment and a given environmental variable. The solid black line represents zero correlation, the region inside (outside) this line represents negative (positive) correlations. Gray shading represents nonsignificant correlations. Filled shapes highlight the environmental variables that are most strongly correlated with each of the four trait moments. (B) Mean magnitudes (absolute values) of all significant correlations between all trait moments and each environmental variable. Environmental variables are abbreviated as follows: absolute value of latitude (Lat), elevation (Elev), mean annual temperature/precipitation (MAT/MAP), isothermality (ISO), temperature diurnal range (TDR), temperature annual range (TAR), temperature/precipitation seasonality (TS/PS), climate water deficit (CWD), vapor air pressure (VAP), vapor pressure deficit (VPD), potential evapotranspiration (PET), wind velocity (Wind), and solar radiation (SR).

in seed mass—representing the exception and not the rule—can be explained by relationships between individual environmental variables with latitude and elevation (*SI Appendix*, Fig. S1B). For example, both mean height and %P are most strongly related to temperature seasonality, which is strongly positively correlated with latitude but only weakly correlated with elevation. Likewise, variance in seed mass is most strongly related to mean annual precipitation, which is strongly negatively correlated with latitude but not significantly correlated with elevation. Relationships between temperature seasonality, latitude, and mean and skewness in tree height distributions reflect shifts in canopy structure from communities dominated by understory trees in the tropics toward those dominated by canopy trees in the temperate region (Fig. 24). Seed mass is also a notable exception in these analyses because it is driven most strongly by wind velocity—seed mass distributions become dominated by smaller seeds under windier conditions—suggesting that wind dispersal plays a principal role in driving seed mass distributions.

Next, we identify the primary climatic drivers of multidimensional trait variation—as opposed to each trait individually—among forests by conducting a principal component analysis (PCA) on the combined community mean values of *all* traits across tree communities. This allows us to reduce a multidimensional community mean trait space to its first two principal trait axes (traits PC1 and PC2; Fig. 3A). To examine as many traits as possible, we included only the subset of communities for which we had data for all nine traits [323 communities with trait values filled using the Botanical Information and Ecology Network (BIEN) trait database (38), as opposed to in situ-sampled plots (*Materials and Methods*)]. Trait PC1 aligns most strongly with variation in N:P (0.54), %P (−0.52), leaf area (0.37), height (−0.36), and seed mass (0.33), and trait PC2 aligns with %N (0.62), SLA (0.55), and %C (−0.39) (eigenvalues shown in parentheses) (Fig. 3A).

Together, these principal trait axes account for 48.4% (PC1 = 28.9%, PC2 = 19.5%) of total variation in mean trait values across all forests and encapsulate fundamental trade-offs in growth strategies operating at the community level (Fig. 3A). Covariation in mean values of SLA, %N, leaf area, and seed mass at the community level closely matches previously published results for global trait covariation at the species level (28) (Fig. 3A and *SI Appendix*, Fig. S44). Because these traits are major axes in plant economics and ecological strategies (27, 28, 30), this result demonstrates that constraints on plant growth operate similarly at the species and community levels.

We identified the strongest potential climatic drivers of trait covariation by calculating correlations between individual climatic variables and traits PC1 and PC2 (Fig. 3B and C). Trait PC1 is most strongly related to measures of temperature variability and absolute latitude (Fig. 3B) while trait PC2 is most strongly related to measures of vapor pressure, MAT, and elevation (Fig. 3C). Notably, our pairwise analysis (Fig. 2 and *SI Appendix*, Fig. S2) identifies the same environmental correlates as identified via alignment with traits PC1 and PC2. These findings demonstrate that geography, temperature variability, and vapor pressure are potentially more important than mean annual temperature and precipitation for driving patterns in functional diversity. Furthermore, these different types of environmental factors somewhat independently drive functional composition along distinct dimensions of trait space.

Finally, to examine whether climate is also driving changes in functional composition over time, we tested for signatures of whole-community trait distribution shifts in response to global warming (Fig. 4). Recent theory (9) suggests that climate change (e.g., rapid warming or rapid fluctuations in temperature or precipitation) should cause whole-community trait distributions to track the environment by decreasing fitness and growth of existing dominant phenotypes while increasing fitness of some currently rare phenotypes. As warming occurs and phenotypes shift, the expectation is that a one-sided tail in the distribution (skewness) will be created due to time lags caused by individuals

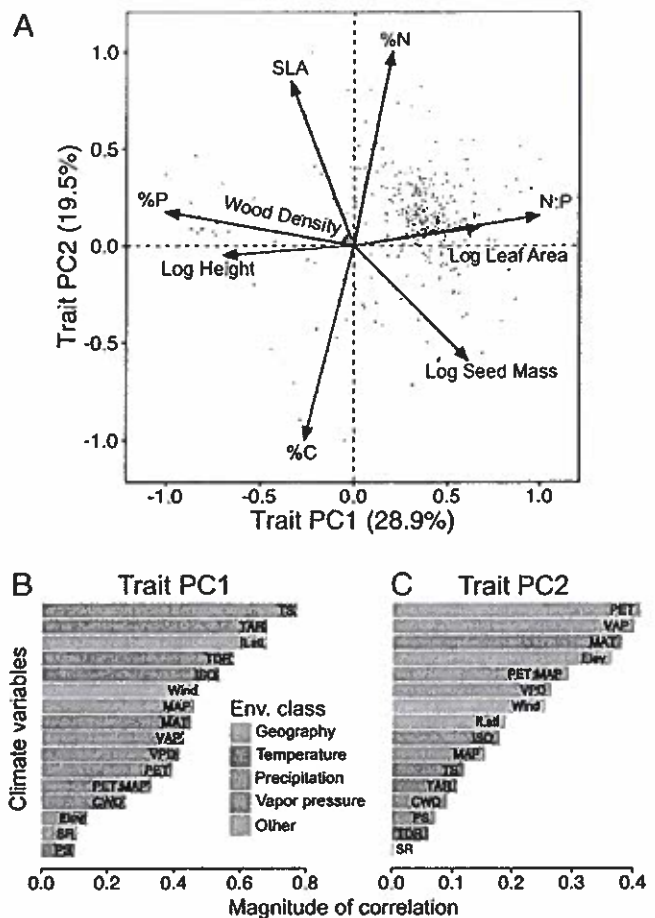


Fig. 3. The first two principal component axes of community-weighted mean trait space (traits PC1 and PC2) across all traits and communities and the strength of their correlations with each environmental variable. (A) The first two principal trait axes (traits PC1 and PC2). Gray points show the principal coordinates for each community, and colored lines represent loadings (eigenvalues) for individual traits, which indicate the relative contribution of each trait to variation in each PC axis. Both the coordinates and loadings have been rescaled to the interval $[-1, 1]$. (B and C) Correlations between the first two principal trait axes and individual environmental variables.

with newly maladaptive traits that are slowly declining in frequency (9) (Fig. 4A). If environmental change (e.g., climate warming) causes a trait distribution to shift upward or downward in trait space, the mean trait value also shifts upward or downward, and the lagging tail will exhibit negative or positive skewness, respectively, relative to the initial distribution.

We calculated “relative” moments for several traits in response to climate warming and compared these values to the null expectation that trait distributions are not currently shifting (relative mean and skewness = 0). Because there are no direct measurements of these community trait distributions before climate change, we use the current global (all plots combined) mean and skewness of each trait as the initial values within each community (*SI Appendix*, *Supplementary Methods*). These values represent a well-mixed average baseline that is not biased toward current environmental conditions in each individual forest community. If warming is currently shifting community-level trait distributions over time, then trait moments of communities are expected to deviate from global values in a direction that is dictated by the underlying relationships with temperature (demonstrated in Fig. 4A). To isolate location-specific trait values and account for potential variation within species across plots, only in situ-sampled communities [66 communities,

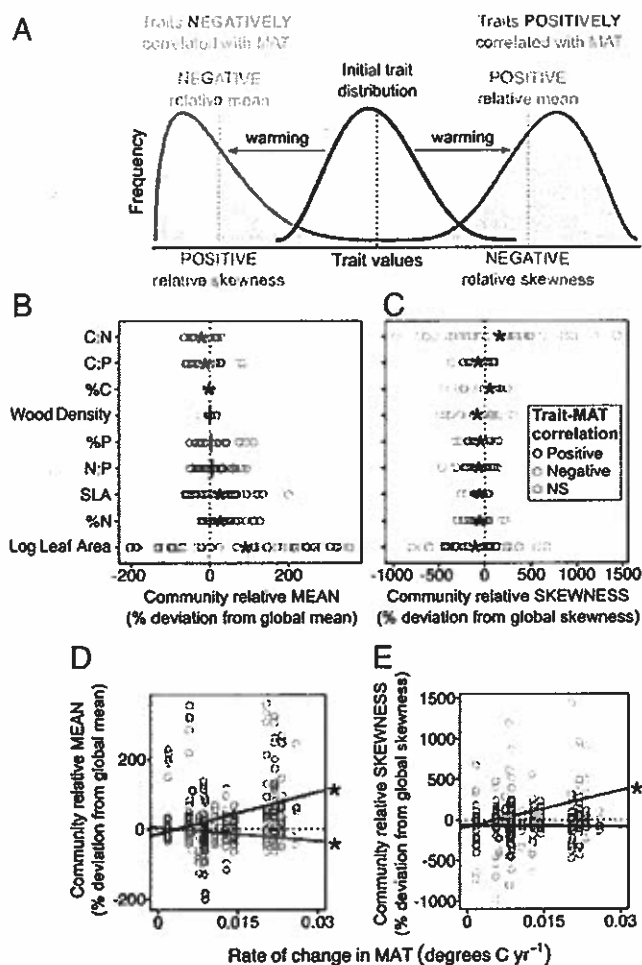


Fig. 4. Signatures of community trait shifts in response to rapid climate warming. (**A**) Expected shifts in mean and skewness relative to an initial distribution. (**B** and **C**) Community relative mean (**B**) and skewness (**C**) values for all communities shown as deviations between local and global (a proxy for initial) moment values (*SI Appendix, Supplementary Methods*). Circles indicate individual communities, and colors designate underlying relationships (correlations) between traits and temperature (MAT). Stars indicate significantly nonzero averages. Bars are nonsignificant. (**D** and **E**) Regressions of relative mean (**D**) and skewness (**E**) for all traits combined against the historical rate of change in MAT. Stars indicate significant trends.

excluding all plots in which trait values were filled using the BIEN trait database (38)) were considered for this analysis.

Several traits do indeed exhibit patterns of relative mean and skewness that are consistent with trait distributions tracking recent climate warming (Fig. 4 *B* and *C*). This striking result is consistent with the hypothesis that recent climate change is currently causing forests to shift their entire trait distributions in the direction of shifting climates. Additionally, the magnitudes of these shifts correspond to the rate of warming experienced by each individual community (Fig. 4 *D* and *E*). These results suggest that climate is already changing the functional composition of forests at large spatial scales in measurable, predictable, and pervasive ways that will affect ecosystem productivity and function.

Our analyses demonstrate how current trait–climate relationships and trait moments can be combined to provide potential metrics for predicting climate-driven shifts in functional biodiversity in the future. The observed trait mean and skewness values are consistent with expected community shifts under climate change, but direct evidence of such shifts will require a time

series of trait distributions across several time points and will be bolstered by including larger forest plots enabling more accurate trait moment estimates. Furthermore, in future studies it will also be important to explore trait shifts in response to changes in other climate variables—including temperature variability and vapor pressure—for which data are currently too limited both geographically and temporally to conduct such analyses.

Using abundance-weighted metrics across the whole community allows us to provide a more complete representation of functional composition within communities, potentially increasing the accuracy of resulting trait–climate relationships. Indeed, we note important deviations between abundance-weighted and species-weighted results within our study (Fig. 2 and *SI Appendix, Fig. S2*). Our results also contrast with previous work using species-weighted trait values (15), specifically in relationships between height, SLA, phosphorus content, and wood density [mean annual precipitation (MAP), precipitation seasonality (PS)]. Understanding why species- and abundance-weighted analyses often produce different trait–climate relationships will require disentangling the relative impacts of trait richness (inherently related to species richness in this study) and the relative abundance of unique trait values (determined by species evenness) on functional diversity–climate relationships. As a first step to address this, we examine shifts in species abundance distributions across latitude and elevation and find that both species richness and evenness change along these geographic gradients (*SI Appendix, Fig. S5*). This result means (*i*) that both unique trait values and trait relative abundances (weighting) likely contribute to climatic shifts in functional diversity and (*ii*) that differences between species- and abundance-weighted analyses are likely due to geographic variation in species evenness. Therefore, we expect that both of these aspects of functional diversity—trait richness and evenness—will be important for future studies.

Increasing the coverage and quality of community-wide datasets will strengthen analyses of trait–climate relationships by including other types of traits (e.g., physiological and phenological traits), a wider range of environmental factors (e.g., soil condition/nutrient composition, microclimate, disturbance), greater geographic coverage, and larger plots with more trait samples. In addition to the climatic conditions examined in this study, functional diversity could also be influenced by the history of local land use, management, or other forms of disturbance (39). Therefore, including information about site history may help increase the accuracy of trait–climate analyses. Although our study covers a wide range in latitude, elevation, and climate space (*SI Appendix, Fig. S1*), we are restricted to predominantly New World sites and lack representation at higher absolute latitudes. Future work will benefit from including both trait and abundance/biomass data at more sites in these underrepresented regions of the world. Finally, most studies (including ours) rely on a small sample representing the greater forest community, which is a potential source of error when calculating functional diversity metrics. In this study, we find that removing trait moment estimates with high uncertainty has no significant effect on our results (*SI Appendix, Fig. S6*). However, including larger forest plots with more individual trait samples will help reduce such issues of uncertainty in future work.

Discovering and quantifying relationships between climate and functional composition is necessary to anticipate community and ecosystem responses to future environmental change (4, 10, 29). Earth system models are increasingly incorporating trait–environment relationships to improve estimates of how past and future changes in climate influence ecosystem functioning (40). Our results expose many relationships between functional composition and climate that are crucial for developing more accurate mechanistic models to make predictions about climate-driven shifts in community structure and ecosystem productivity. Nonetheless, further insights will likely arise as more location-specific trait data become available that better capture the functional variation expressed within and among communities (41), thus increasing the ability to accurately detect trait–environment relationships (*SI Appendix, Fig. S7*). Such data limitations may be

overcome by leveraging remote-sensing techniques (42) that obtain comprehensive trait data while reducing the logistical difficulties and time constraints of traditional field campaigns.

By more fully accounting for individual-level trait variation within communities, our insights will help future studies successfully bridge plant economics theory (12, 27, 28, 30) and functional biogeography (7, 8, 10, 11) to better evaluate and predict relationships between climate, ecosystem structure, and productivity. Therefore, our analysis not only strengthens our understanding of broad ecological patterns across space and time, but also represents a vital step toward predicting changes in ecosystem function and stability in the future.

Materials and Methods

Forest Trait and Climate Data. Species identities and abundances were determined for all individuals ≥ 2 cm in diameter within each forest plot (421 0.1-ha plots total). Trait data were collected locally in 66 forest plots (in situ plots). For the 355 forest plots (BIEN plots) that lack locally collected trait data, we paired local community composition with trait data gathered from BIEN [accessed using the BIEN package (38) in R (43)]. Species mean trait values were assigned by taking the mean value across all available samples (one or more individuals) within each species for each plot. In BIEN plots, if species-level trait values were unavailable, then either genus or family values were used. We log-transformed all size-dependent traits—height, leaf area, and seed mass—to eliminate size-dependent trait biases before analysis (44). Site-specific climate data were gathered using climate raster layers available online (19–24).

Trait Moment Analyses. Species mean trait values were weighted by species abundances within each forest plot to calculate abundance-weighted trait

moments (9)—mean, variance, skewness, and (excess) kurtosis (see *SI Appendix, Supplementary Methods* for equations). Outliers were removed by dropping the outer 1% (0.5% highest and 0.5% lowest) of species mean and community moment values for each trait. To standardize scale across traits in the latitude and elevation analysis, community mean and variance are given as the percent of deviations from the average community value across each gradient (i.e., individual community values that are X% higher or lower than the average trait value for a given gradient, with the sign denoting the direction of the percent of deviation). Linear regressions between trait moments and latitude and elevation were calculated using the `lm` function in R (43). Relationships between trait moments and individual environmental variables were determined using Pearson product-moment correlations. PCA was conducted on community-weighted means across all traits using the `prcomp` function in R (43). Only BIEN plots were used in the PCA analysis because there are no data for tree height or seed mass for the in situ plots. Community relative moments were calculated as the percent deviation between local community values (m_{local}) and global values (m_{global}) for each moment (% deviation = $(m_{local} - m_{global})/m_{global} \times 100$). We used two-sided *t* tests to determine whether community relative moments were significantly different from 0—the null expectation given no shift in trait-distribution shape. Only in situ data were used in the relative moment analysis to ensure that trait estimates were specific to each location rather than being taken from a trait database. All data (45) and custom code (46) used in this study have been made publicly available online.

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- Chapin FS, III, et al. (2000) Consequences of changing biodiversity. *Nature* 405:234–242.
- Lavelle S, Garnier E (2002) Predicting changes in community composition and ecosystem functioning from plant traits: Revisiting the Holy Grail. *Funct Ecol* 16:545–556.
- McGill BJ, Enquist BJ, Weiher E, Westoby M (2006) Rebuilding community ecology from functional traits. *Trends Ecol Evol* 21:178–185.
- Westoby M, Wright IJ (2006) Land-plant ecology on the basis of functional traits. *Trends Ecol Evol* 21:261–268.
- Cadotte MW, Carscadden K, Mirotchnick N (2011) Beyond species: Functional diversity and the maintenance of ecological processes and services. *J Appl Ecol* 48:1079–1087.
- Newbold T, Butchart SHM, Sekercioglu CH, Purves DW, Scharlemann JPW (2012) Mapping functional traits: Comparing abundance and presence-absence estimates at large spatial scales. *PLoS One* 7:e44019.
- Reichstein M, Bahn M, Mahecha MD, Kattge J, Baldocchi DD (2014) Linking plant and ecosystem functional biogeography. *Proc Natl Acad Sci USA* 111:13697–13702.
- Violle C, Reich PB, Pacala SW, Enquist BJ, Kattge J (2014) The emergence and promise of functional biogeography. *Proc Natl Acad Sci USA* 111:13690–13696.
- Enquist BJ, et al. (2015) Scaling from traits to ecosystems. *Adv Ecol Res* 52:249–318.
- Funk JL, et al. (2017) Revisiting the Holy Grail: Using plant functional traits to understand ecological processes. *Biol Rev Camb Philos Soc* 92:1156–1173.
- Reich PB, Oleksyn J (2004) Global patterns of plant leaf N and P in relation to temperature and latitude. *Proc Natl Acad Sci USA* 101:11001–11006.
- Wright IJ, et al. (2005) Modulation of leaf economic traits and trait relationships by climate. *Glob Ecol Biogeogr* 14:411–421.
- Swenson NG, Enquist BJ (2007) Ecological and evolutionary determinants of a key plant functional trait: Wood density and its community-wide variation across latitude and elevation. *Am J Bot* 94:451–459.
- Swenson NG, et al. (2011) The biogeography and filtering of woody plant functional diversity in North and South America. *Glob Ecol Biogeogr* 21:798–808.
- Šimová I, et al. (2018) Spatial patterns and climate relationships of major plant traits in the New World differ between woody and herbaceous species. *J Biogeogr* 45:895–916.
- Grime JP (1998) Benefits of plant diversity to ecosystems: Immediate, filter and founder effects. *J Ecol* 86:902–910.
- Butler EE, et al. (2017) Mapping local and global variability in plant trait distributions. *Proc Natl Acad Sci USA* 114:E10937–E10946.
- Gross N, et al. (2017) Functional trait diversity maximizes ecosystem multifunctionality. *Nat Ecol Evol* 1:132.
- Arora VK (2002) The use of the aridity index to assess climate change effect on annual runoff. *J Hydrol (Amst)* 265:164–177.
- Zomer RJ, Trabucco A, Bossio DA, Verchot LV (2008) Climate change mitigation: A spatial analysis of global land suitability for clean development mechanism afforestation and reforestation. *Agric Ecosyst Environ* 126:67–80.
- Hansen J, Ruedy R, Sato M, Lo K (2010) Global surface temperature change. *Rev Geophys* 48:RG4004.
- Chave J, et al. (2014) Improved allometric models to estimate the aboveground biomass of tropical trees. *Glob Change Biol* 20:3177–3190.
- Harris I, Jones PD, Osborn TJ, Lister DH (2014) Updated high-resolution grids of monthly climatic observations: The CRU TS3.10 dataset. *Int J Climatol* 34:623–642.
- Karger DN, et al. (2017) Climatologies at high resolution for the earth's land surface areas. *Sci Data* 4:170122.
- Fischer AG (1960) Latitudinal variations in organic diversity. *Evolution* 14:64–81.
- Moles AT, et al. (2014) Which is a better predictor of plant traits: Temperature or precipitation? *J Veg Sci* 25:1167–1180.
- Wright IJ, et al. (2004) The worldwide leaf economics spectrum. *Nature* 428:821–827.
- Diaz S, et al. (2016) The global spectrum of plant form and function. *Nature* 529:167–171.
- Madani N, et al. (2018) Future global productivity will be affected by plant trait response to climate. *Sci Rep* 8:2870.
- Reich PB (2004) The world-wide 'fast-slow' plant economics spectrum: A traits manifesto. *J Ecol* 102:275–301.
- Norberg J, et al. (2001) Phenotypic diversity and ecosystem functioning in changing environments: A theoretical framework. *Proc Natl Acad Sci USA* 98:11376–11381.
- Savage VM, Webb CT, Norberg J (2007) A general multi-trait-based framework for studying the effects of biodiversity on ecosystem functioning. *J Theor Biol* 247:213–229.
- Webb CT, Hoeting JA, Ames GM, Pyne MI, LeRoy Poff N (2010) A structured and dynamic framework to advance traits-based theory and prediction in ecology. *Ecol Lett* 13:267–283.
- Mason NWH, Moullot D, Lee WG, Wilson JB (2005) Functional richness, functional evenness and functional divergence: The primary components of functional diversity. *Oikos* 111:112–118.
- Violle C, et al. (2007) Let the concept of trait be functional! *Oikos* 116:882–892.
- Ackerly DD, Cornwell WK (2007) A trait-based approach to community assembly: Partitioning of species trait values into within- and among-community components. *Ecol Lett* 10:135–145.
- De Bello F, et al. (2009) Partitioning of functional diversity reveals the scale and extent of trait convergence and divergence. *J Veg Sci* 20:475–486.
- Maltner BS, et al. (2018) The bien r package: A tool to access the Botanical Information and Ecology Network (BIEN) database. *Methods Ecol Evol* 9:373–379.
- Krishnadas M, et al. (2018) Environment and past land use together predict functional diversity in a temperate forest. *Ecol Appl*, 10.1002/ea.1802.
- Wulfschlegel SD, et al. (2014) Plant functional types in earth system models: Past experiences and future directions for application of dynamic vegetation models in high-latitude ecosystems. *Ann Bot* 114:1–16.
- Baraloto C, et al. (2010) Functional trait variation and sampling strategies in species-rich plant communities. *Funct Ecol* 24:208–216.
- Asner GP, Martin RE (2009) Airborne spectrometry: Mapping canopy chemical and taxonomic diversity in tropical forests. *Front Ecol Environ* 7:269–276.
- R Core Team (2016) R: A Language and Environment for Statistical Computing (R Foundation for Statistical Computing, Vienna). Available at <https://www.R-project.org/>. Accessed June 21, 2016.
- Kerkhoff AJ, Enquist BJ (2009) Multiplicative by nature: Why logarithmic transformation is necessary in allometry. *J Theor Biol* 257:519–521.
- Wieczynski DJ, et al. (2018) Data from "Climate shapes and shifts functional biodiversity in forests worldwide." Figshare. Available at <https://doi.org/10.6084/m9.figshare.7436951.v1>. Deposited December 7, 2018.
- Wieczynski DJ, et al. (2018) Code from "Climate shapes and shifts functional biodiversity in forests worldwide." GitHub. Available at https://github.com/DanWieczynski/PNAS_201813723. Deposited December 7, 2018.