

# Functional trait space and the latitudinal diversity gradient

Christine Lamanna<sup>a,1</sup>, Benjamin Blonder<sup>b,c,1</sup>, Cyrille Violle<sup>d,1,2</sup>, Nathan J. B. Kraft<sup>e</sup>, Brody Sandel<sup>f,g</sup>, Irena Šimová<sup>h</sup>, John C. Donoghue<sup>l,b,i</sup>, Jens-Christian Svenning<sup>f</sup>, Brian J. McGill<sup>a,j</sup>, Brad Boyle<sup>b,i</sup>, Vanessa Buzzard<sup>b</sup>, Steven Dolins<sup>k</sup>, Peter M. Jørgensen<sup>l</sup>, Aaron Marcuse-Kubitzka<sup>i,m</sup>, Naia Morueta-Holme<sup>f</sup>, Robert K. Peet<sup>n</sup>, William H. Piel<sup>o</sup>, James Regetz<sup>m</sup>, Mark Schildhauer<sup>m</sup>, Nick Spencer<sup>p</sup>, Barbara Thiers<sup>q</sup>, Susan K. Wiser<sup>p</sup>, and Brian J. Enquist<sup>b,i,r</sup>

<sup>a</sup>Sustainability Solutions Initiative and <sup>j</sup>School of Biology and Ecology, University of Maine, Orono, ME 04469; <sup>b</sup>Department of Ecology and Evolutionary Biology, University of Arizona, Tucson, AZ 85721; <sup>c</sup>Center for Macroecology, Evolution, and Climate, Copenhagen University, 2100 Copenhagen, Denmark; <sup>d</sup>Centre d'Ecologie Fonctionnelle et Evolutive, Unité Mixte de Recherche 5175, Centre National de la Recherche Scientifique–Université de Montpellier–Université Paul-Valéry Montpellier–École Pratique des Hautes Études, 34293 Montpellier, France; <sup>e</sup>Department of Biology, University of Maryland, College Park, MD 20742; <sup>f</sup>Section for Ecoinformatics and Biodiversity, Department of Bioscience and <sup>g</sup>Center for Massive Data Algorithmics, Department of Computer Science, Aarhus University, DK-8000 Aarhus, Denmark; <sup>h</sup>Center for Theoretical Study, Charles University in Prague and Academy of Sciences of the Czech Republic, 110 00 Praha, Czech Republic; <sup>i</sup>Plant Collaborative, Tucson, AZ 85721; <sup>k</sup>Department of Computer Science and Information Systems, Bradley University, Peoria, IL 61625; <sup>l</sup>Missouri Botanical Garden, St. Louis, MO 63166; <sup>m</sup>National Center for Ecological Analysis and Synthesis, University of California, Santa Barbara, CA 93106; <sup>n</sup>Department of Biology, University of North Carolina at Chapel Hill, Chapel Hill, NC 27599; <sup>o</sup>Yale–NUS College, Republic of Singapore 138614; <sup>p</sup>Landcare Research, Lincoln 7640, New Zealand; <sup>q</sup>New York Botanical Garden, Bronx, NY 10458; and <sup>r</sup>Santa Fe Institute, Santa Fe, NM 87501

Edited by Peter B. Reich, University of Minnesota, St. Paul, MN, and accepted by the Editorial Board May 23, 2014 (received for review September 25, 2013)

The processes causing the latitudinal gradient in species richness remain elusive. Ecological theories for the origin of biodiversity gradients, such as competitive exclusion, neutral dynamics, and environmental filtering, make predictions for how functional diversity should vary at the alpha (within local assemblages), beta (among assemblages), and gamma (regional pool) scales. We test these predictions by quantifying hypervolumes constructed from functional traits representing major axes of plant strategy variation (specific leaf area, plant height, and seed mass) in tree assemblages spanning the temperate and tropical New World. Alpha-scale trait volume decreases with absolute latitude and is often lower than sampling expectation, consistent with environmental filtering theory. Beta-scale overlap decays with geographic distance fastest in the temperate zone, again consistent with environmental filtering theory. In contrast, gamma-scale trait space shows a hump-shaped relationship with absolute latitude, consistent with no theory. Furthermore, the overall temperate trait hypervolume was larger than the overall tropical hypervolume, indicating that the temperate zone permits a wider range of trait combinations or that niche packing is stronger in the tropical zone. Although there are limitations in the data, our analyses suggest that multiple processes have shaped trait diversity in trees, reflecting no consistent support for any one theory.

Species richness increases toward the equator (1, 2) in major clades of both extant and extinct species of plants and animals (3, 4). The generality of the pattern hints at a correspondingly general explanation, yet the latitudinal gradient in species richness remains one of ecology's greatest unsolved puzzles. Long-running debates over the causes of the latitudinal gradient of species richness have focused on ecological, evolutionary, and geographic explanations (5–10). Although there has been some progress (11), it is also increasingly clear that there are numerous obstacles to understanding the primary drivers of the latitudinal gradient, including an ever-increasing number of hypotheses (12, 13), challenges in clearly separating their interdependencies (14, 15), and difficulties in rigorously falsifying their assumptions and predictions (16).

More powerful tests of biodiversity theories need to move beyond species richness and instead explicitly focus on the mechanisms generating the gradient, by recasting the theories in terms of other measures of diversity, such as functional diversity (17–19). For example, explanations that assume species richness is limited by resource availability have often focused on the strength of species interactions, life history differences, and environmental constraints on how species pack into niche space (20). Evolutionary hypotheses have focused on differences in

diversification rates, as well as the influence of species interactions on diversification rates (9). These interaction-based explanations implicitly refer to the degree of ecological differentiation among species, and therefore to trait dispersion within clades and assemblages, suggesting that patterns of functional diversity may provide a more powerful test of theory than taxonomic richness (21).

A particularly important concept that unifies many ecological and evolutionary theories is the concept of the Hutchinsonian multidimensional niche (22). Hutchinsonian niches can be quantified by assessing the functional trait hypervolumes that characterize phenotypic space occupied by a set of species. Quantifying the volume, overlap, and packing of functional trait space at different spatial scales enables inferences about how differing ecological and evolutionary processes structure functional diversity and ecological strategies (23, 24).

Here, we recast several contrasting hypotheses for the latitudinal gradient in terms of functional trait space. We focus on the proximate ecological mechanisms that ultimately can influence evolutionary processes. We quantify tree functional trait

## Significance

We present a conceptual framework for testing theories for the latitudinal gradient of species richness in terms of variation in functional diversity at the alpha, beta, and gamma scales. We compared ecological community theory with large-scale observational data of tree species richness and functional diversity. We found that the patterns of functional trait diversity are not consistent with any one theory of species diversity. These conflicting results indicate that none of the broad classes of biodiversity theory considered here is alone able to explain the latitudinal gradient of species diversity in terms of functional trait space.

Author contributions: C.L., B. Blonder, C.V., and B.J.E. designed research; C.L., B. Blonder, C.V., and V.B. performed research; C.L., B. Blonder, C.V., N.J.B.K., B.S., I.S., J.C.D., J.-C.S., B.J.M., B. Boyle, S.D., P.M.J., A.M.-K., N.M.-H., R.K.P., W.H.P., J.R., M.S., N.S., B.T., S.K.W., and B.J.E. contributed new reagents/analytic tools; C.L., B. Blonder, and C.V. analyzed data; and C.L., B. Blonder, C.V., N.J.B.K., B.S., I.S., J.-C.S., B.J.M., N.M.-H., and B.J.E. wrote the paper.

The authors declare no conflict of interest.

This article is a PNAS Direct Submission. P.B.R. is a guest editor invited by the Editorial Board.

<sup>1</sup>C.L., B. Blonder, and C.V. contributed equally to this work.

<sup>2</sup>To whom correspondence should be addressed. Email: cyrille.violle@cefe.cnrs.fr.

This article contains supporting information online at [www.pnas.org/lookup/suppl/doi:10.1073/pnas.1317722111/-DCSupplemental](http://www.pnas.org/lookup/suppl/doi:10.1073/pnas.1317722111/-DCSupplemental).

space across latitude at three spatial scales: (i) within assemblages (alpha), (ii) among assemblages (beta), and (iii) among biomes (gamma). For alpha and beta analyses, we use tree species assemblage data from 620 standardized 0.1-ha forest plots (Fig. 1A); for gamma analyses, we calculated the latitudinal range distributions for 520 New World tree species where we had sufficient data on geographic distribution and functional traits. In total, across all analyses, we used paired geographic occurrence data with trait data for 6,839 tree species.

We primarily measured hypervolumes for three central traits hypothesized to characterize major axes of ecological strategy variation (25): specific leaf area (SLA), maximum height, and seed mass. SLA represents the tradeoff between leaf longevity and maximum photosynthetic rate (26); height is important for light competition and dispersal (27); and seed mass represents tradeoffs between fecundity, dispersal, and seedling survival (27). Although whole-plant resource strategies can be more fully assessed in higher dimensions (28, 29), we focus on these traits because of data availability (*Materials and Methods*). We use a hypervolume algorithm for calculating the volume and overlap of trait space (30) (*Materials and Methods*). All hypervolumes are reported in units of SDs of centered and scaled log-transformed trait values, raised to the power of the number of trait dimensions used.

At all scales, our overall results and conclusions are similar (i) with and without gap-filling missing data, (ii) if we use convex hulls instead of hypervolumes to calculate trait spaces, and (iii) if we include additional trait axes. Additional details are given in Figs. S2–S7.

### Recasting Hypotheses for the Species Richness Latitudinal Gradient in Terms of Functional Trait Space

We assess multiple theories for the latitudinal gradient of species richness by recasting several of their predictions for the alpha, beta, and gamma components of functional diversity. Not all biodiversity

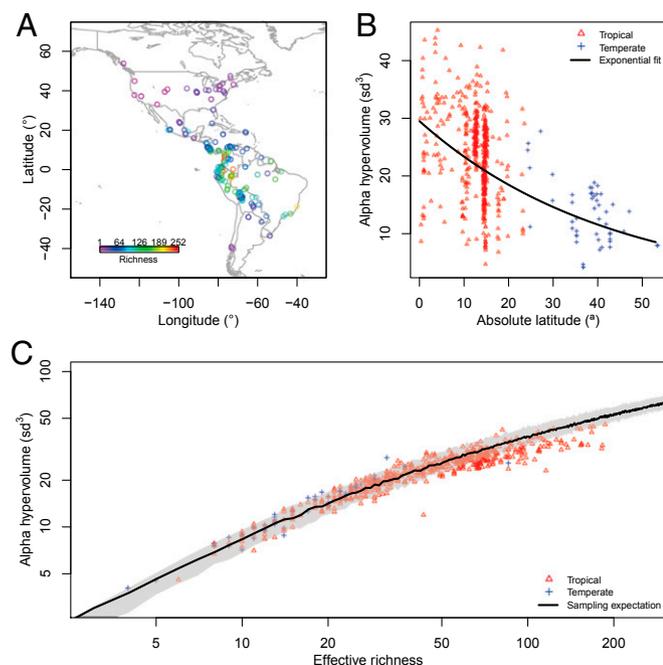
theories make clear predictions for patterns of trait diversity at different scales. Further, our approach assumes that functional trait diversity captures major niche axes (31). Nonetheless, we can focus on the predictions of three major groups of theories that can be directly related to functional similarities and differences among species:

- i) Competitive exclusion and niche theory predicts that the strength of species interactions is reflected in differences in the total volume of trait space. The packing of species in niche space (i.e., volume overlap) may either decrease or increase, depending on niche packing vs. displacement of functional trait values over evolutionary time (20, 32, 33). Nonetheless, a common expectation is that the niche volume occupied by the assemblage will increase as species are added to an assemblage (34).
- ii) Environmental filtering theory states that abiotic factors, such as climatic stress and seasonality, increasingly constrain the types of traits and ecological functions expressed in more stressful environments (35–37), and thus reduce hypervolumes. Niche conservatism, which describes the pattern of retention of ecological similarity over time (38), may contribute to this effect by limiting evolution of the functional hypervolume outside of ancestral environments (i.e., often warmer, less seasonal climates) (39).
- iii) Neutral dynamics theory predicts that richness gradients reflect differences in speciation rates and metacommunity size rather than trait differences. Neutral theory assumes demographic equivalence of species (40) so that there is no immediate mapping between traits and performance (31, 41). However, assuming a Brownian motion model of trait evolution, increases in net speciation rate, and/or more time for neutral speciation would then lead to increases in niche space via sampling effects (42–44).

Each theory leads to predictions for functional diversity at alpha, beta, and gamma scales. We describe these predictions below and summarize them in Table 1.

**Alpha Functional Diversity.** In the absence of niche-based processes [i.e., in neutral dynamics theory (45)] we predict that the trait composition of a local assemblage will be a random subset of a shared regional species pool. As a result, variation in trait alpha diversity should increase with richness but at the same rate as a random sample from the species pool (i.e., new species are not preferentially added in unfilled portions of trait space) (46). In competitive exclusion theory (47), new species are most likely to be added to unfilled portions of niche space; thus, hypervolumes should always be larger than a sampling expectation. In contrast, although environmental filtering theory predicts that in more stressful environments, the trait hypervolume will also increase with richness, the hypervolume will be smaller than the null expectation because some trait combinations are not viable.

**Beta Functional Diversity.** Average trait values within communities (and therefore the location of the hypervolume in trait space) can also shift across geographic space. Each theory predicts different relationships for the overlap among trait hypervolumes across tropical and temperate biomes. We define overlap as the hypervolume in common divided by the mean volume of the two hypervolumes. Based on neutral dynamics theory, we predict a constant relationship between trait hypervolume overlap and geographic distance. Although species compositional similarity decreases with distance, all species assemblages' traits are a random sample from a functionally equivalent species pool, and the metric used to calculate fractional overlap corrects for mean trait hypervolume. As a result, no distance decline in beta diversity is expected. In contrast, environmental filtering theory predicts a decline in trait hypervolume overlap with increased distance, because different regions should be associated with



**Fig. 1.** (A) Spatial distribution of the 620 0.1-ha forest plots used in this study. Plots are colored by richness. Plots cover most of the New World forested climate space (Fig. S1). (B) Relationship between absolute latitude and alpha hypervolume for tropical (red triangles) and temperate (blue pluses) plots. (C) Alpha hypervolume as a function of effective species richness (number of species with full trait coverage). We compare this hypervolume with a null expectation based on sampling the same number of species from the regional pool (median, dark gray line; 90% quantile range, light gray envelope).

**Table 1. Predictions of three classes of diversity theory regarding different aspects of trait hypervolume geometry at alpha, beta, and gamma scales**

Pattern	Predictions			Observed results
	Competitive exclusion	Environmental filtering	Neutral	
Alpha scale: assemblage hypervolume vs. richness, deviation from sampling expectation	Higher	Lower	Zero	Lower
Beta scale: biome in which decline in hypervolume overlap with distance is steepest	Unclear	Temperate	Neither	Temperate
Gamma scale: sign of species pool hypervolume vs. latitude relationship	Unclear	Negative	Zero	Midlatitude hump

Our results are not consistent with all of the predictions of any single class of theory.

different viable combinations of traits. However, comparisons within temperate areas should show the steepest decay with distance because of higher levels of climatic turnover within the temperate zone (48). Predictions for distance decline for trait hypervolume overlap from competitive exclusion theory depend on variation in the strength of species interactions. Latitudes with more competition (i.e., more competitive exclusion) should show the steepest decay of similarity with distance because of higher levels of trait divergence. Evidence suggests the tropics have stronger species interactions [see ref. 49, but refer to Schleuning et al. (50)] but not necessarily stronger resource competition. Additionally, many growth-rate tradeoffs related to light competition appear similar in the temperate and tropical zones (51–53).

**Gamma Functional Diversity.** Constraints on local community diversity may reflect not only intrinsic local processes but also extrinsic biogeographic processes operating on large scales (54). For example, species pools from different latitudinal bands may differ in their functional trait space because of differences in their biogeography and evolutionary history. Neutral theory makes no predictions for the trait composition of a sample from a species pool, potentially suggesting no relationship between hypervolume and latitude once differences in species richness are accounted for. In contrast, competitive exclusion theory predicts that latitudes with more competition will have larger trait hypervolumes once differences in species richness are accounted for because of reduced similarity among species due to alpha-scale competition. However, uncertainties with the geographical distribution of the relative importance of resource competition (alpha scale) prevent a clear predictive linkage for the functional relationship between niche volume and latitude. Alternatively, environmental filtering assumes that increasing environmental stress restricts the subset of traits that are viable in a given species pool (38, 55). Because cold tolerance is thought to be one of the most limiting physiological challenges for plants (56), we predict a negative relationship between hypervolume and latitude as well.

## Results

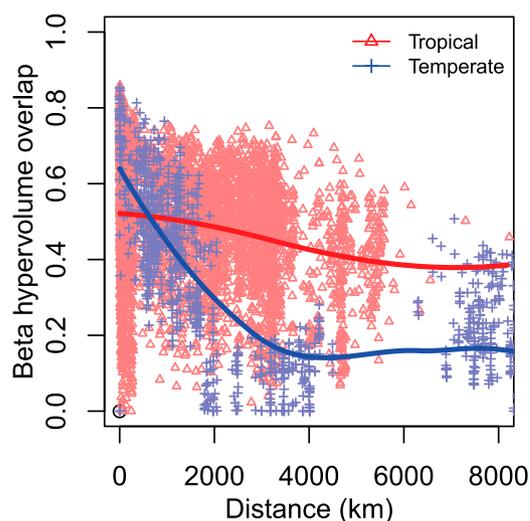
**Alpha Functional Diversity.** Tree assemblage trait hypervolumes increase at lower absolute latitude (exponential fit;  $P < 10^{-15}$ ,  $r^2 = 0.22$ ), mirroring the absolute latitudinal gradient in tree species richness ( $P < 10^{-15}$ ,  $r^2 = 0.26$ ) (Fig. 1). Trait hypervolumes for tree assemblages increase as effective species richness increases ( $P < 10^{-15}$ ,  $r^2 = 0.76$ ), but at a lower rate than expected by sampling from the species pool (Fig. 1C) (one-sided  $t$  test, 329 of 620  $P$  values  $< 0.05$ ). Filtering was inferred more often for tropical sites (71% significant  $t$  tests) compared with temperate sites (40% significant  $t$  tests) (proportion test,  $\chi^2 = 17.37$ ,  $df = 1$ ,  $P < 10^{-4}$ ).

**Beta Functional Diversity.** The geographic distance decay was steepest within the temperate biome (multiple regression on distance matrix; slope of  $4.5 \times 10^{-4} \text{ km}^{-1}$  vs.  $3.2 \times 10^{-4} \text{ km}^{-1}$ ,  $P = 0.002$ ,  $r^2 = 0.70$ ) (Fig. 2).

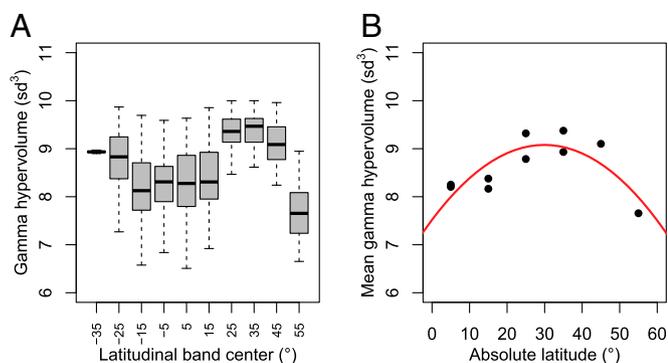
**Gamma Functional Diversity.** Opposite to expectations, trait hypervolumes created from species pools with range centers in latitudinal bands of  $10^\circ$  were smallest at the highest and lowest latitudes when controlling for species richness. The largest trait hypervolumes were found at middle latitudinal bands (linear regression with quadratic term;  $P = 0.02$ ,  $r^2 = 0.65$ ) (Fig. 3).

Overlap in trait hypervolumes among differing latitudinal bands was variable, ranging from 4 to 40% (Fig. 4). The overlap was highest between adjacent latitudinal bands and lowest when comparing temperate bands from opposite hemispheres. Interestingly, comparisons among tropical latitudinal bands generally had higher overlaps than other types of comparisons, indicating that trait space occupation of different species pools in temperate latitudes is much more variable than in the tropics.

We also measured the relative functional diversity of the temperate and tropical biomes by constructing hypervolumes for all species in the temperate and tropical pools and determining their overlap after standardizing for richness by resampling 150 species per biome (Fig. 4 and animated in [Movie S1](#)). Resampled



**Fig. 2.** Beta overlap among forest plots as a function of geographic distance. Comparisons of plot pairs within the tropics are shown in red, and comparisons of plot pairs within the temperate zone are shown in blue. Points show plot pairs, and solid lines show local regressions through each point cloud. A random subset of pairwise comparisons is plotted to improve clarity.



**Fig. 3.** Gamma trait hypervolumes for species aggregated in latitudinal bands of 10° from 40° S to 60° N. (A) Box plots show the distribution of trait hypervolumes when controlling for variation in species pool richness. (B) Mean band hypervolume (black points) as a function of absolute latitude. Red line, quadratic regression.

temperate trait hypervolumes were larger than tropical hypervolumes ( $70.8 \pm 1.3$  SD  $\text{sd}^3$  vs.  $46.9 \pm 2.1$  SD  $\text{sd}^3$ ,  $t = 69.4$ ,  $\text{df} = 82$ ,  $P < 10^{-15}$ ) (Fig. 5). The temperate space is primarily defined by low SLA, whereas the unique tropical space is defined by high seed mass. We repeated this analysis removing all gymnosperms from the dataset, resampling 100 species per biome. The temperate hypervolume was still larger ( $57.2 \pm 1.4$  SD  $\text{sd}^3$  vs.  $42.2 \pm 2.0$  SD  $\text{sd}^3$ ,  $t = 42.7$ ,  $\text{df} = 89$ ,  $P < 10^{-15}$ ). The angiosperm temperate space was differentiated by its inclusion of species with low SLA, short height, and intermediate seed mass (Fig. S8).

## Discussion

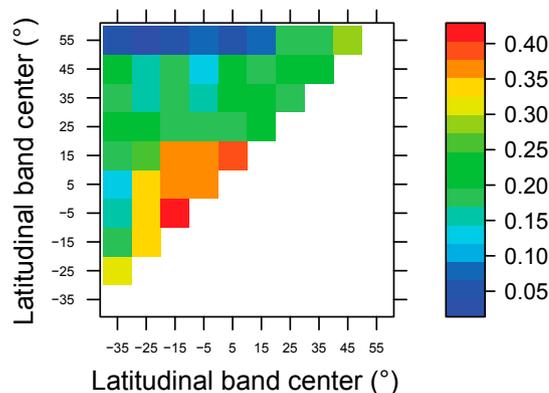
We have presented a conceptual framework for testing theories for the latitudinal gradient of functional diversity at the alpha, beta, and gamma scales. There are several other theories for the origin of diversity gradients where the relationships between taxonomic and functional diversity are not clear. Nevertheless, our approach offers a foundation that can be further refined and extended, and it should be applicable to a wide range of organisms, species assemblages, traits, and functional diversity metrics.

We found that the patterns of functional trait diversity that characterize species assemblages at different geographic scales were not consistent with any one theory of species diversity. For example, tropical alpha trait hypervolumes were often smaller than the sampling expectation, opposite to the prediction from environmental filtering theory that temperate alpha volumes should be smaller and suggesting that alpha trait filtering may be more important in tropical communities. Beta hypervolume overlap decayed most strongly among temperate communities, consistent with environmental filtering theory. However, at the gamma scale, we found that trait hypervolumes, in general, were larger in the temperate zone, rejecting all of the theories examined here. The high overall temperate gamma hypervolumes may be a result of combining species from many environments that differ greatly in the kind of environmental filtering they present (e.g., drought, freezing, heat stress). The faster decay in overlap of beta temperate hypervolumes with climatic and geographic distance supports the idea that the temperate zone contains a larger range and higher turnover of viable functional strategies, including the needle-like leaves of conifers. Indeed, intriguingly, our findings are similar to those of the recently reported increase in high-latitude trait space seen in mammals (57). Our results suggest that trait gamma diversity may show a hump-shaped relationship with latitude. These results contrast with the lack of a latitudinal trait space gradient (58, 59) and recent claims, based on single trait analysis, that the functional diversity of tropical woody assemblages is greater than that expected given their species richness (17).

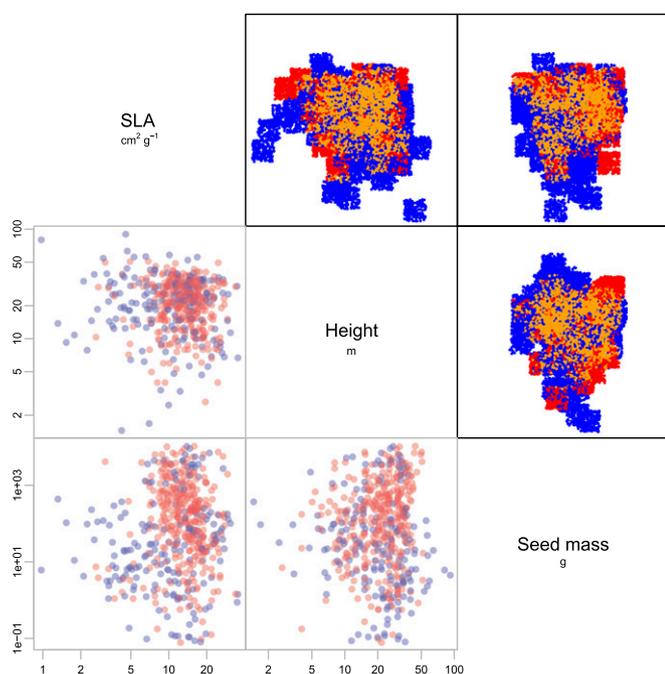
Variation in niche packing may help explain our conflicting results of high alpha trait hypervolumes in species-rich assemblages and a peak in gamma trait hypervolume in midlatitude temperate regions (24, 35, 60, 61). Species' intraspecific trait volumes may either completely fill up or overlap in the larger assemblage volume (complete niche packing), or leave holes (displacement) instead. These two possibilities may be more or less common at the alpha or gamma scale, and they may also vary relative to different environmental factors. At the alpha scale, greater competition (62) may select for closer niche packing and smaller hypervolumes. Our fixed-bandwidth hypervolume analysis cannot directly measure niche packing (because we assume each species can occupy a fixed maximum volume of trait space), but intraspecific trait data would make it possible to address this question (24). If there is an upper bound on the amount of niche space occupied by any species, our alpha results do indicate greater niche packing (more species per unit trait hypervolume) for high-richness sites (exponential fit,  $P < 10^{-15}$ ,  $r^2 = 0.23$ ; Fig. S4).

An open challenge is to obtain better data for testing the functional predictions of diversity theories. The generality of our conclusions were necessarily limited by the availability and quality of trait data. For example, wood density (53) and dark respiration rate (63) may play important roles in competitive exclusion theories, but we did not have sufficient data to include these traits here (except at the gamma scale; Fig. S7). Inclusion of reproductive traits would also be necessary to measure plant ecological strategies fully (64). Traits such as floral morphology and pollination syndrome may also structure assemblages (65), particularly in the tropics, where animal pollination is more prevalent than wind pollination (66). However, such analyses remain limited by a lack of simultaneous trait measurements for these species. Extending tests beyond trees to groups, such as epiphytes or understory herbs, could also assess the generality of these conclusions (67). More complete observational and plot data could also reduce biases. Our hypervolumes may be underestimated in high-richness species pools, because functional traits are more likely to be measured on abundant species than on rare species. Finally, increased plot coverage at high absolute latitudes would increase the robustness of the gamma analysis.

In conclusion, a more robust empirical assessment of the latitudinal diversity gradient will become possible as data improve. New trait databases (68–70) are beginning to emerge. Furthermore, standardized measurements across taxonomic groups and biomes, as well as new statistical methods, are being developed for inferring missing values in high-dimensional datasets [e.g., multiple imputation, hierarchical probabilistic matrix factorization (71)]. Our hypervolume approach can work with functional niche space in higher dimensions as these data become available, enabling more robust testing of the functional



**Fig. 4.** Fractional overlap (Sørensen index) among gamma hypervolumes for different latitudinal bands.



**Fig. 5.** Gamma temperate and tropical hypervolumes shown as 2D projections for all combinations of trait axes: SLA, plant height, and seed mass. (Upper and Middle Right) Hypervolumes constructed by resampling 150 species from each species pool. Axes are transformed, with red indicating unique tropical trait space, blue indicating unique temperate trait space, and orange indicating shared trait space. (Middle Left and Lower) All untransformed trait data available for each species pool, with light red indicating tropical species and light blue indicating temperate species. This figure is animated as [Movie S1](#).

predictions that stem from diversity theories in a much wider range of contexts.

## Materials and Methods

**Trait Data.** We assembled trait data from literature sources, our respective research groups, and publicly available trait databases (*SI Materials and Methods*). These data are available in the Botanical Information and Ecology Network (BIEN) database (<http://bien.nceas.ucsb.edu/bien/>). We used three traits to characterize functional diversity: SLA, maximum height, and seed mass. When multiple measurements per species were available, we averaged observations to create a species mean trait value. For alpha and beta analyses, we used genus-level means when species-level data were not available (SLA, 37% of species; maximum height, 49% of species; and seed mass, 46% of species), yielding a dataset of 4,460 species in plots and with SLA, height, and seed mass data. To test the effect of using genus-level mean traits, we also repeated all alpha and beta analyses using a dataset of only species-level data, comprising 495 species in plots and with SLA, height, and seed mass data (Figs. S2 and S5). Analyses use an “effective” species richness corresponding to the number of species with full trait coverage ( $74 \pm 16\%$  SD of true richness across plots). For gamma analyses, we used only complete species-level data ( $n = 520$  species with range data available). We were able to extend the gamma analysis to four dimensions (including wood density as a trait), but results were qualitatively similar to the 3D main text analysis (Fig. S7). Each trait value was  $\log_{10}$ -transformed (except wood density) and then scaled to have a mean of 0 and SD of 1 relative to the New World species pool (i.e., the full set of trait values for each analysis). This transformation was performed to make Euclidean distances and volumes in functional trait space comparable within and across analyses. The trait data are used to calculate hypervolumes (see below) and are not analyzed directly.

**Assemblage Data.** For alpha and beta analyses, we obtained tree species assemblage data from a set of 620 0.1-ha plots from the BIEN database, each composed of ten  $50 \times 2\text{-m}^2$  transects that span a  $41^\circ$  S to  $53^\circ$  N latitudinal range (a map of plot locations is provided in Fig. 1A). Methods follow the system of Gentry (72). Morphospecies were assigned for every individual with

a diameter at breast height  $>10$  cm within each plot, and species identity was assigned where possible. All observations were assigned standardized taxon names using the Taxonomic Name Resolution Service, version 3.0 (73). Each assemblage was designated as tropical if its absolute latitude was less than  $23.5^\circ$  or as temperate otherwise. Plots covered nearly all of the New World forested climate space (Fig. S1), although geographic coverage was somewhat more limited in the temperate regions of the Southern Hemisphere as well as in the boreal forests of the Northern Hemisphere.

**Occurrence Data.** For gamma analyses, we generated species pools by assigning latitudinal bands to each species with complete trait coverage ( $n = 520$ ). We first obtained georeferenced occurrence records from the BIEN database (<http://bien.nceas.ucsb.edu/bien/>) (74) for each species, including records outside plots. Occurrence records were geolocated and restricted to noncultivated occurrences, yielding a skewed distribution with  $n = 388 \pm 612$  SD records per species. We assigned a species to be present in each latitudinal band of  $10^\circ$  from  $-40^\circ$  S to  $60^\circ$  N if the band overlapped the species’ maximum and minimum latitudinal ranges. The species pool for each latitudinal band was then the set of species inferred to be present in each band. We also assigned species to either a temperate species pool ( $n = 183$  species, of which 133 are angiosperms) if its mean latitude was greater than  $23.5^\circ$  absolute latitude or a tropical species pool ( $n = 337$  species, of which 335 are angiosperms) if its mean latitude was less than  $23.5^\circ$ .

**Hypervolume Measurement.** All analyses were conducted with the “hypervolume” R package (30). These algorithms infer the shape and volume of high-dimensional objects via a thresholded kernel density estimate. A full description of the algorithms and a test of the method’s statistical properties (e.g., scaling of accuracy with dimensionality and sample size) can be found in a study by Blonder et al. (30). Hypervolumes are reported in units of SDs to the power of the number of trait dimensions used. Additional details of computational parameters are available in *SI Materials and Methods*.

For alpha analyses, we reported the inferred hypervolume for each assemblage or species pool relative to a null expectation constructed by sampling the same number of species from a regional species pool defined by all species in the New World for which traits were available. For beta analyses, we reported the Sørensen index (intersection hypervolume divided by mean hypervolume) for each pair of assemblages. We then transformed these similarities to distances ( $1 - x$  transform) and performed a multiple regression on distance matrices, including a term for geographic distance interacting with each of the temperate-temperate, tropical-tropical, and temperate-tropical categories. For gamma analyses, we reported the distribution of hypervolumes in latitudinal bands, inferred using a resampling procedure to correct for variation in species pool size (i.e., trait coverage) across latitudes. From each latitudinal species pool, we randomly sampled 10 species without replacement and constructed a hypervolume using these data; we then repeated the process 100 times. We also calculated hypervolume overlap between each pair of latitudinal bands, for 20 random samples of 10 species from each species pool, and report the mean overlap for each combination of latitudinal bands. Finally, we calculated temperate and tropical hypervolumes by resampling 150 species from each species pool, or by resampling 100 species from each species pool for an angiosperm-only analysis.

**ACKNOWLEDGMENTS.** This study was conducted as a part of the BIEN Working Group (Principal Investigators: B.J.E., Richard Condit, B. Boyle, S.D., and R.K.P.) supported by the National Centre for Ecological Analysis and Synthesis, a center funded by the National Science Foundation (NSF) (Grant EF-0553768); the University of California, Santa Barbara; and the State of California. The BIEN Working Group was also supported by iPlant (NSF Grant DBI-0735191). We thank all the contributors for the invaluable data provided to the BIEN (<http://bien.nceas.ucsb.edu/bien/people/data-contributors/>). C.L. was supported by NSF Award EPS-0904155 to the Maine EPSCoR at the University of Maine and the Senator George J. Mitchell Center. B. Blonder was supported by an NSF predoctoral fellowship, a Nordic Research Opportunity cosponsored by the NSF, and the Danish National Research Foundation. C.V. was supported by a Marie Curie International Outgoing Fellowship within the Seventh European Community Framework Program (DiversiTraits Project, Grant 221060). J.-C.S. was supported by the European Research Council (ERC) Starting Grant Project “Macroecological studies of long-term historical constraints on functional diversity and ecosystem functioning across continents” (Grant ERC-2012-StG-310886-HISTFUNC). B.J.E. was supported by a fellowship from the Aspen Center for Environmental Studies and NSF Macrosystems Award DBI-1065861. I.S. was supported by Grant P505/11/2387 from the Grant Agency of the Czech Republic.

- Wallace AR (1878) *Tropical Nature and Other Essays* (Macmillan, New York).
- Dobzhansky T (1950) Evolution in the tropics. *Am Sci* 38:209–221.
- Brown JH, Lomolino MV (1998) *Biogeography* (Sinauer, Sunderland, MA).
- Hillebrand H (2004) On the generality of the latitudinal diversity gradient. *Am Nat* 163(2):192–211.
- Stephens PR, Wiens JJ (2003) Explaining species richness from continents to communities: The time-for-speciation effect in emydid turtles. *Am Nat* 161(1):112–128.
- Buckley LB, et al. (2010) Phylogeny, niche conservatism and the latitudinal diversity gradient in mammals. *Proc Biol Sci* 277(1691):2131–2138.
- Stevens GC (1989) The latitudinal gradient in geographic range: How so many species coexist in the tropics. *Am Nat* 133:240–256.
- Allen AP, Brown JH, Gillooly JF (2002) Global biodiversity, biochemical kinetics, and the energetic-equivalence rule. *Science* 297(5586):1545–1548.
- Mittelbach GG, et al. (2007) Evolution and the latitudinal diversity gradient: Speciation, extinction and biogeography. *Ecol Lett* 10(4):315–331.
- Mannion PD, Upchurch P, Benson RB, Goswami A (2014) The latitudinal biodiversity gradient through deep time. *Trends Ecol Evol* 29(1):42–50.
- Simova I, et al. (2011) Global species-energy relationship in forest plots: Role of abundance, temperature and species climatic tolerances. *Glob Ecol Biogeogr* 20: 842–856.
- Rohde K (1992) Latitudinal gradients in species diversity: The search for the primary cause. *Oikos* 65:514–527.
- Pianka E (1966) Latitudinal gradients in species diversity: A review of concepts. *Am Nat* 100:33–46.
- Currie DJ (1991) Energy and large-scale patterns of animal and plant species richness. *Am Nat* 137:27–49.
- Currie DJ, et al. (2004) Predictions and tests of climate-based hypotheses of broad-scale variation in taxonomic richness. *Ecol Lett* 7:1121–1134.
- Currie DJ, Francis AP, Kerr JT (1999) Some general propositions about the study of spatial patterns of species richness. *Ecoscience* 6:392–399.
- Swenson NG, et al. (2012) The biogeography and filtering of woody plant functional diversity in North and South America. *Glob Ecol Biogeogr* 21:798–808.
- Ricklefs RE (2012) Species richness and morphological diversity of passerine birds. *Proc Natl Acad Sci USA* 109(36):14482–14487.
- Roy K, Jablonski D, Valentine JW (2004) *Frontiers of Biogeography: New Directions in the Geography of Nature*, eds Lomolino MV, Heaney LR (Sinauer, Sunderland, MA), pp 151–170.
- Ricklefs RE, O'Rourke K (1975) Aspect diversity in moths: A temperate-tropical comparison. *Evolution* 29:313–324.
- McGill BJ, Enquist BJ, Weiher E, Westoby M (2006) Rebuilding community ecology from functional traits. *Trends Ecol Evol* 21(4):178–185.
- Hutchinson GE (1957) Concluding remarks. *Cold Spring Harb Symp Quant Biol* 22: 415–427.
- Moullot D, et al. (2005) Niche overlap estimates based on quantitative functional traits: A new family of non-parametric indices. *Oecologia* 145(3):345–353.
- Violle C, et al. (2012) The return of the variance: Intraspecific variability in community ecology. *Trends Ecol Evol* 27(4):244–252.
- Westoby M (1998) A leaf-height-seed (LHS) plant ecology strategy scheme. *Plant Soil* 199:213–227.
- Wright IJ, et al. (2004) The worldwide leaf economics spectrum. *Nature* 428(6985): 821–827.
- Thompson F, Moles AT, Auld T, Kingsford R (2011) Seed dispersal distance is more strongly correlated with plant height than with seed mass. *J Ecol* 99:1299–1307.
- Stahl U, et al. (2013) Whole-plant trait spectra of North American woody plant species reflect fundamental ecological strategies. *Ecosphere* 4:1–28.
- Laughlin D (2014) The intrinsic dimensionality of plant traits and its relevance to community assembly. *J Ecol* 102:186–193.
- Blonder B, Lamanna C, Violle C, Enquist BJ (2014) The n-dimensional hypervolume. *Glob Ecol Biogeogr* 23:595–609.
- Violle C, Jiang L (2009) Towards a trait-based quantification of species niche. *J Plant Ecol* 2:87–93.
- Schemske DW (2009) *Speciation and Patterns of Diversity*, eds Butlin RK, Bridle JR, Schluter D (Cambridge Univ Press, Cambridge, UK), pp 220–239.
- MacArthur RH, Levins R (1967) The limiting similarity, convergence and divergence of coexisting species. *Am Nat* 101:377–385.
- Tilman D, Lehman CL, Thomson KT (1997) Plant diversity and ecosystem productivity: Theoretical considerations. *Proc Natl Acad Sci USA* 94(5):1857–1861.
- Janzen D (1967) Why mountain passes are higher in the tropics. *Am Nat* 101:233–249.
- Klopfner P, MacArthur R (1961) On the causes of tropical species diversity: Niche overlap. *Am Nat* 95:223–226.
- Kerkhoff AJ, Moriarty PE, Weiser MD (2014) The latitudinal species richness gradient in New World woody angiosperms is consistent with the tropical conservatism hypothesis. *Proc Natl Acad Sci USA* 111(22):8125–8130.
- Kleidon A, Mooney HA (2000) A global distribution of biodiversity inferred from climatic constraints: Results from a process-based modelling study. *Glob Change Biol* 6:507–523.
- Wiens JJ, Donoghue MJ (2004) Historical biogeography, ecology and species richness. *Trends Ecol Evol* 19(12):639–644.
- Hubbell SP (2001) *The Unified Neutral Theory of Biodiversity and Biogeography* (Princeton Univ Press, Princeton).
- Violle C, et al. (2007) Let the concept of trait be functional! *Oikos* 116:882–892.
- Cardillo M (1999) Latitude and rates of diversification in birds and butterflies. *Proc Biol Sci* 266:1221–1225.
- Rosenzweig ML (1995) *Species Diversity in Space and Time* (Cambridge Univ Press, Cambridge, UK).
- Jablonski D, Roy K, Valentine JW (2006) Out of the tropics: Evolutionary dynamics of the latitudinal diversity gradient. *Science* 314(5796):102–106.
- Kraft NJB, Valencia R, Ackerly DD (2008) Functional traits and niche-based tree community assembly in an Amazonian forest. *Science* 322(5901):580–582.
- Mouchet M, Vilàger S, Mason N, Moullot D (2010) Functional diversity measures: An overview of their redundancy and their ability to discriminate community assembly rules. *Funct Ecol* 24:867–876.
- Hardin G (1960) The competitive exclusion principle. *Science* 131(3409):1292–1297.
- Terborgh J (1973) On the notion of favorableness in plant ecology. *Am Nat* 107: 481–501.
- Schemske D, Mittelbach G, Cornell H, Sobel J, Roy K (2009) Is there a latitudinal gradient in the importance of biotic interactions? *Annu Rev Ecol Syst* 40:245–269.
- Schleuning M, et al. (2012) Specialization of mutualistic interaction networks decreases toward tropical latitudes. *Curr Biol* 22(20):1925–1931.
- Kobe R, Pacala S, Silander J (1995) Juvenile tree survivorship as a component of shade tolerance. *Ecol Appl* 5:517–532.
- Pacala S, et al. (1996) Forest models defined by field measurements: Estimation, error analysis and dynamics. *Ecol Monogr* 44:1–43.
- Wright SJ, et al. (2010) Functional traits and the growth-mortality trade-off in tropical trees. *Ecology* 91(12):3664–3674.
- Cornell H, Lawton J (1992) Species interactions, local and regional processes, and limits to the richness of ecological communities: A theoretical perspective. *J Ecol* 61: 1–12.
- Woodward FI (1988) *Climate and Plant Distribution* (Cambridge Univ Press, Cambridge, UK).
- Zanne A, et al. (2014) Three keys to the radiation of angiosperms into freezing environments. *Nature* 506(7486):89–92.
- Safi K, et al. (2011) Understanding global patterns of mammalian functional and phylogenetic diversity. *Philos Trans R Soc Lond B Biol Sci* 366:2536–2544.
- Ricklefs RE (2009) Aspect diversity in moths revisited. *Am Nat* 173(3):411–416.
- Ricklefs RE, Marquis RJ (2012) Species richness and niche space for temperate and tropical folivores. *Oecologia* 168(1):213–220.
- Laughlin DC, Joshi C, van Bodegom PM, Bastow ZA, Fulé PZ (2012) A predictive model of community assembly that incorporates intraspecific trait variation. *Ecol Lett* 15(11): 1291–1299.
- May RM, MacArthur RH (1972) Niche overlap as a function of environmental variability. *Proc Natl Acad Sci USA* 69(5):1109–1113.
- Mayfield MM, Levine JM (2010) Opposing effects of competitive exclusion on the phylogenetic structure of communities. *Ecol Lett* 13(9):1085–1093.
- Baltzer J, Thomas S (2007) Determinants of whole-plant light requirements in Bornean rain forest tree saplings. *J Ecol* 95:1208–1221.
- Armbruster W (1995) The origins and detection of plant community structure: Reproductive versus vegetative processes. *Folia Geobot* 30:483–497.
- Sargent RD, Ackerly DD (2008) Plant-pollinator interactions and the assembly of plant communities. *Trends Ecol Evol* 23(3):123–130.
- Ollerton J, Winfree R, Tarrant S (2011) How many flowering plants are pollinated by animals? *Oikos* 120:321–326.
- King DA, Wright SJ, Connell JH (2006) The contribution of interspecific variation in maximum tree height to tropical and temperate diversity. *J Trop Ecol* 22:11–24.
- Kattge J, et al. (2011) TRY—A global database of plant traits. *Glob Change Biol* 17: 2905–2935.
- Homburg K, Homburg N, Schäfer F, Schuldt A, Assmann T (2013) Carabids.org—A dynamic online database of ground beetle species traits (Coleoptera, Carabidae). *Insect Conserv Divers* 7:195–205.
- Baldrige E, Myrholvd N, Ernest SM (2012) Macroecological life-history trait database for birds, mammals, and reptiles. *Mammalia* 153:5416.
- Shan H, et al. (2012) Gap filling in the plant kingdom—trait prediction using hierarchical probabilistic matrix factorization. *Proceedings of the 29th International Conference of Machine Learning*. Available at <http://icml.cc/2012/papers/652.pdf>.
- Gentry A (1982) Patterns of neotropical plant species diversity. *Evol Biol* 15:1–84.
- Boyle B, et al. (2013) The taxonomic name resolution service: an online tool for automated standardization of plant names. *BMC Bioinformatics* 14:1471–2105.
- Morúeta-Holme N, et al. (2013) Habitat area and climate stability determine geographical variation in plant species range sizes. *Ecol Lett* 16:1446–1454.

# Supporting Information

Lamanna et al. 10.1073/pnas.1317722111

## SI Materials and Methods

Here, we provide additional information about the materials and methods used in this study.

**Assemblage Data.** We assembled a network of 620 communities that used a consistent methodology in sampling. The majority of the plots come from the Synthesis and Analysis of Local Vegetation Inventories Across Scales (SALVIAS) tree plot network. The SALVIAS tree plot network contains the original “Alwyn H. Gentry Forest Transect Dataset” (1, 2) ([www.mobot.org/MOBOT/research/gentry/transect.shtml](http://www.mobot.org/MOBOT/research/gentry/transect.shtml)) plus numerous additional “Gentry-style” plots. Information about the SALVIAS project and methodology of selected plots is available at [www.salvias.net/pages/database\\_info.php](http://www.salvias.net/pages/database_info.php). The selected plots for our study are as follows: Brad Boyle altitudinal gradient dataset transects (37 plots), Organization for Tropical Studies transects (15 plots), RAINFOR 0.1-ha Madre de Dios, Peru (102 plots), DeWalt Bolivia Forest Plots (2 plots), La Selva Secondary Forest Transects (3 plots), Bonifacio Forest Transects (4 plots), Alwin H. Gentry Forest Transect Dataset (152 plots), and Madidi Transects (222 plots). In addition, we included 62 Enquist Lab forest plot inventories from Costa Rica, Mexico, Puerto Rico, Panama, Canada, Colorado, California, Oregon, North Carolina, Massachusetts, and Arizona. All plots follow a Gentry-style sampling methodology (2), are 0.1 ha in area, and contain counts and stem measurements of individual trees with a 2.5-cm or greater diameter at breast height.

1. Gentry A (1988) Changes in plant community diversity and floristic composition on environmental and geographic gradients. *Ann Mo Bot Gard* 75:1–34.
2. Phillips O, Miller J (2002) *Global Patterns of Plant Diversity: Alwyn H. Gentry's Forest Transect Data Set* (Missouri Botanical Garden Press, St. Louis).
3. Hijmans R, Cameron S, Parra J, Jones P, Jarvis A (2005) Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology* 25:1965–1978.

## References Used for the Compilation of Trait Data

- Ackerly DD (2004) Functional traits of chaparral shrubs in relation to seasonal water deficit and disturbance. *Ecol Monogr* 74:25–44.
- American Forests (2005) The National Register of Big Trees. Available at [www.americanforests.org/resources/bigtrees/search\\_register.php](http://www.americanforests.org/resources/bigtrees/search_register.php). Accessed December 19, 2012.
- Brodribb TJ, Holbrook NM, Zwieniecki MA, Palma B (2005) Leaf hydraulic capacity in ferns, conifers and angiosperms: Impacts on photosynthetic maxima. *New Phytol* 165(3): 839–846.
- Bucci SJ, et al. (2004) Functional convergence in hydraulic architecture and water relations of tropical savanna trees: From leaf to whole plant. *Tree Physiol* 24(8): 891–899.
- Cavender-Bares J, Kitajima K, Bazzaz FA (2004) Multiple trait associations in relation to habitat differentiation among 17 Floridian oak species. *Ecol Monogr* 74:635–661.
- Database of Brazilian Woods (2006). Available at [www.ibama.gov.br/lpf/madeira/default.htm](http://www.ibama.gov.br/lpf/madeira/default.htm). Accessed November 14, 2011.
- Franco AC, et al. (2005) Leaf functional traits of Neotropical savanna trees in relation to seasonal water deficit. *Trees (Berl West)* 19:326–335.
- He JS, et al. (2006) A test of the generality of leaf trait relationships on the Tibetan Plateau. *New Phytol* 170(4):835–848.
- Henderson A, Galeano G, Bernal R (1995) *Field Guide to the Palms of the Americas* (Princeton Univ Press, Princeton).
- Huante P, Rincon E, Acosta I (1995) Nutrient availability and growth rate of 34 woody species from a tropical deciduous forest in Mexico. *Funct Ecol* 9:849–858.
- Jepson Flora Project (2006) Ecological Flora of California. Available at <http://ucjeps.berkeley.edu/efc/core-traits.html>. Accessed May 10, 2009.

**Climate Space.** To verify that plots were a good representation of the New World climate space, we compared climate values from plots with the entire climate space of the New World, as well as with the climate space of forested regions. We obtained mean annual temperature [Bioclim variable 1 (BIO1)] and precipitation (BIO12) climate variables from the WorldClim database (3) at a resolution of 10 arcminutes, and we extracted climate values for the New World (North America and South America, excluding Greenland), as well as for each plot. New World climate values were assigned to be forested if mean tree height was greater than zero in a global tree height database (4). We found that plots covered nearly all of the forested climate space (Fig. S1).

**Hypervolume Measurement.** We constructed each hypervolume using a quantile threshold of 0.05 (so that each hypervolume includes 95% of the total probability density), 1,000 Monte Carlo samples per data point, and a fixed kernel bandwidth for all axes (0.5 SD for traits and 0.1 SD for gamma climate analyses). These values lead to conservative estimates of hypervolumes (i.e., low padding of sparsely sampled datasets) and to strong correlations of hypervolume with convex hull volume. We also compared hypervolume estimates with convex hulls constructed from the same data for alpha and gamma analyses. Overlap analyses using convex hulls were not performed because algorithms were not available to compute intersections of *n*-dimensional convex hulls (but refer to ref. 5). Except where noted in the main text, results were qualitatively similar regardless of method or bandwidth choice.

4. Lefsky MA (2010) A global forest canopy height map from the moderate resolution imaging spectroradiometer and the Geoscience Laser Altimeter System. *Geophys Res Lett* 37:L15401.
5. Villéger S, Novack-Gottshall PM, Moullot D (2011) The multidimensionality of the niche reveals functional diversity changes in benthic marine biotas across geological time. *Ecol Lett* 14(6):561–568.

- Kalácska M, Calvo-Alvarado JC, Sánchez-Azofeifa GA (2005) Calibration and assessment of seasonal changes in leaf area index of a tropical dry forest in different stages of succession. *Tree Physiol* 25(6):733–744.
- King DA, Wright SJ, Connell JH (2006) The contribution of interspecific variation in maximum tree height to tropical and temperate diversity. *J Trop Ecol* 22:11–24.
- Kleyer M, et al. (2008) The LEDA Trait database: A database of life-history traits of the Northwest European flora. *J Ecol* 96:1266–1274.
- Kolb KJ, Davis SD (1994) Drought tolerance and xylem embolism in co-occurring species of coastal sage and chaparral. *Ecology* 75:648–659.
- Kraft NJB, Valencia R, Ackerly DD (2008) Functional traits and niche-based tree community assembly in an Amazonian forest. *Science* 322(5901):580–582.
- Liu K, Eastwood RJ, Flynn S, Turner RM, Stuppy WH (2008) Seed Information Database (release 7.1, May 2008). Available at [www.kev.org/data/sid](http://www.kev.org/data/sid). Accessed June 14, 2010.
- Poorter L, Bongers F (2006) Leaf traits are good predictors of plant performance across 53 rain forest species. *Ecology* 87(7):1733–1743.
- Royer DL, Wilf P, Janesko DA, Kowalski EA, Dilcher DL (2005) Correlations of climate and plant ecology to leaf size and shape: Potential proxies for the fossil record. *Am J Bot* 92(7):1141–1151.
- Rozendaal DMA, Hurtado VH, Poorter L (2006) Plasticity in leaf traits of 38 tropical tree species in response to light is only weakly related to light demand and adult stature. *Funct Ecol* 20:207–216.
- USDA (2008) PLANTS database. Available at <http://plants.usda.gov>. Accessed September 22, 2010.
- Wright IJ, et al. (2004) The worldwide leaf economics spectrum. *Nature* 428(6985): 821–827.







