SPECIAL FEATURE

Functional trait space and the latitudinal diversity gradient

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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.

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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. 1*A*); 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.

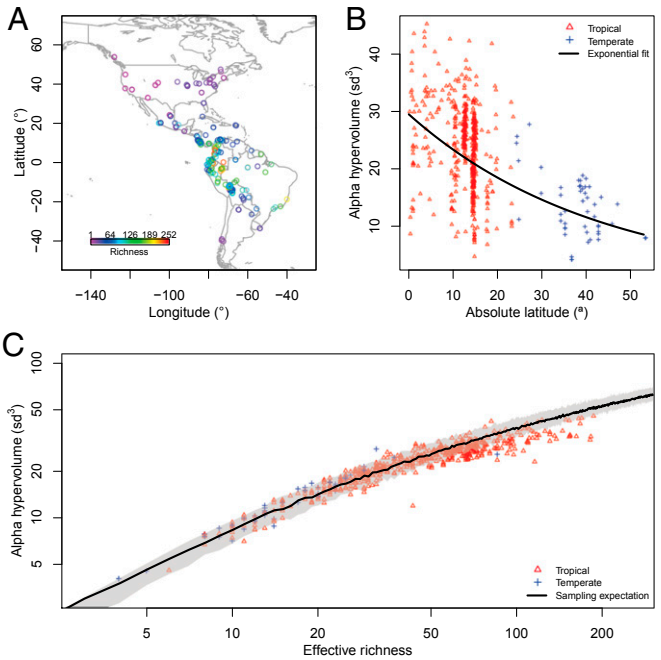


Fig. 1. (*A*) Spatial distribution of the 620 0.1-ha forest plots used in this study. Plots are colored by richness. Plots cover most of the New World forested climate space (Fig. S1). (*B*) Relationship between absolute latitude and alpha hypervolume for tropical (red triangles) and temperate (blue 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).

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

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. 1*C*) (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 4.5×10^{-4} km^{-1} vs. 3.2×10^{-4} 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° 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

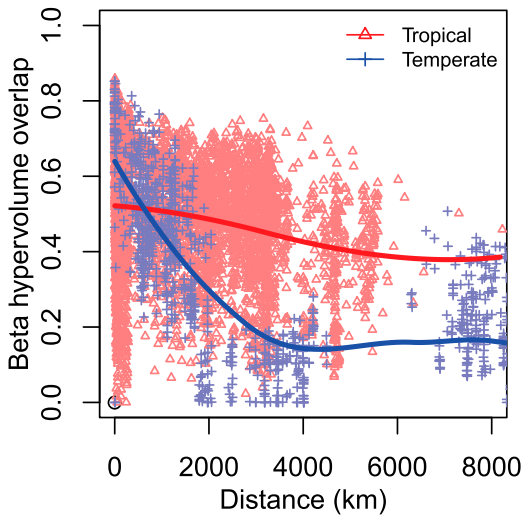


Fig. 2. Beta overlap among forest plots as a function of geographic distance. Comparisons of plot pairs within the tropics are shown in red, and comparisons of plot pairs within the temperate zone are shown in blue. Points show plot pairs, and solid lines show local regressions through each point cloud.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

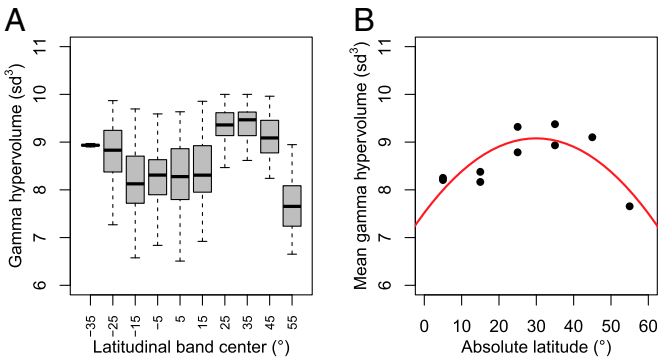


Fig. 3. Gamma trait hypervolumes for species aggregated in latitudinal bands of 10° from 40° S to 60° N. (*A*) Box plots show the distribution of trait hypervolumes when controlling for variation in species pool richness. (*B*) Mean band hypervolume (black points) as a function of absolute latitude.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

temperate trait hypervolumes were larger than tropical hypervolumes (70.8 ± 1.3 SD sd^3 vs. 46.9 ± 2.1 SD sd^3, $t = 69.4$, 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 ± 1.4 SD sd^3 vs. 42.2 ± 2.0 SD sd^3, $t = 42.7$, 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 understorey 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

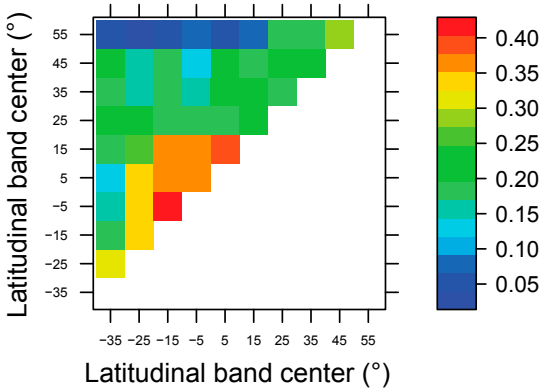


Fig. 4. Fractional overlap (Sørensen index) among gamma hypervolumes for different latitudinal bands.

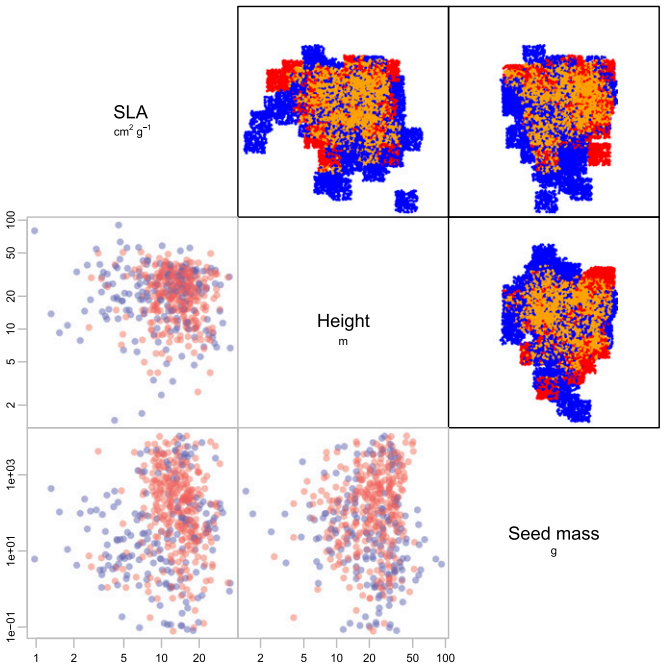


Fig. 5. Gamma temperate and tropical hypervolumes shown as 2D projections for all combinations of trait axes: SLA, plant height, and seed mass. (*Upper* and *Middle Right*) Hypervolumes constructed by resampling 150 species from each species pool. Axes are transformed, with red indicating unique tropical 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 ± 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 × 2-m^2 transects that span a 41° S to 53° N latitudinal range (a map of plot locations is provided in Fig. 1*A*). 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° 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 geovalidated and restricted to noncultivated occurrences, yielding a skewed distribution with n = 388 ± 612 SD records per species. We assigned a species to be present in each latitudinal band of 10° from −40° S to 60° 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° absolute latitude or a tropical species pool (n = 337 species, of which 335 are angiosperms) if its mean latitude was less than 23.5°.

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.

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