The adaptive challenge of extreme conditions shapes evolutionary diversity of plant assemblages at continental scales

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The tropical conservatism hypothesis (TCH) posits that the latitudinal gradient in biological diversity arises because most extant clades of animals and plants originated when tropical environments were more widespread and because the colonization of colder and more seasonal temperate environments is limited by the phylogenetically conserved environmental tolerances of these tropical clades. Recent studies have claimed support of the TCH, indicating that temperate plant diversity stems from a few more recently derived lineages that are nested within tropical clades, with the colonization of the temperate zone being associated with key adaptations to survive colder temperatures and regular freezing. Drought, however, is an additional physiological stress that could shape diversity gradients. Here, we evaluate patterns of evolutionary diversity in plant assemblages spanning the full extent of climatic gradients in North and South America. We find that in both hemispheres, extratropical dry biomes house the lowest evolutionary diversity, while tropical moist forests and many temperate mixed forests harbor the highest. Together, our results support a more nuanced view of the TCH, with environments that are radically different from the ancestral niche of angiosperms having limited, phylogenetically clustered diversity relative to environments that show lower levels of deviation from this niche. Thus, we argue that ongoing expansion of arid environments is likely to entail higher loss of evolutionary diversity not just in the wet tropics but in many extratropical moist regions as well.

angiosperms | drought | evolutionary diversity | latitudinal diversity gradient | phylogenetic clustering

Earth's most studied biodiversity pattern is the latitudinal diversity gradient (LDG): species richness and evolutionary diversity decrease from the warm, moist, aseasonal tropics toward the colder, more seasonal poles (1–5). Many hypotheses have been proposed to explain the LDG (6), but the tropical conservatism hypothesis (TCH) has garnered much attention due to its focus on interacting ecological and evolutionary mechanisms (1, 2, 7–9) (Fig. 1*A*).

The TCH makes two key assumptions: 1) that most clades of animals and plants have a tropical origin (3, 10, 11) and 2) that after the global cooling initiated at the end of the Eocene (34 Mya), the trait innovations necessary to persist and thrive in temperate regions (e.g., freezing tolerance) (12) are phylogenetically conserved within a small subset of more recently derived lineages (7, 12–14). Hence, the TCH predicts that relative to tropical regions, species richness in the temperate zone will be lower because temperate biodiversity stems from these few, more recently derived lineages that are phylogenetically nested within clades of tropical origin, and thus have had less time for diversification.

While the inability of most plant lineages to survive regular freezing conditions clearly contributes to the LDG for flowering plants (2, 12), temperature may not be the sole stressor associated with the LDG. In particular, drought stress from either low precipitation (relative to evapotranspiration) or precipitation seasonality may have also disproportionately shaped diversity gradients (15, 16). Nonetheless, recent studies testing the validity of the TCH have ignored gradients of water availability in full (2) or have not included regions of extreme cold and drought in their analyses (17). Here, we evaluate an extended view of the TCH (8) (Fig. 1*B*). This view still assumes a tropical origin for most clades of extant species but generalizes the conservatism assumption such that the key innovations needed to thrive in any harsh or seasonal conditions, not just freezing temperatures, are limited to a few lineages.

Under assumptions of the extended TCH, we would predict that any seasonally cold or dry environment will be made up of clusters of taxa within a few evolutionarily nested lineages of tropical origin. In these seasonal environments, we thus expect lower evolutionary diversity relative to regions that are aseasonal, warm, and wet year-round (henceforth, "tropical moist").

Although we make no assumptions regarding the age of extratropical dry environments, besides the TCH assumption of tropical

Significance

We explore an extended view of the tropical conservatism hypothesis to account for two often-neglected components of climatic stress: drought and the combined effect of seasonal cold and drought—the latter being a common feature of extratropical dry environments. We show that evolutionary diversity of angiosperm assemblages in extratropical dry biomes is even lower than in biomes subject to only one type of climatic stress. We further show that evolutionary diversity in many assemblages from eastern North America is higher or comparable to that of tropical moist forests, suggesting that some extratropical moist biomes have accumulated angiosperm lineages over deep evolutionary timescales with their flora assembled from lineages that represent the entirety of the angiosperm tree of life.

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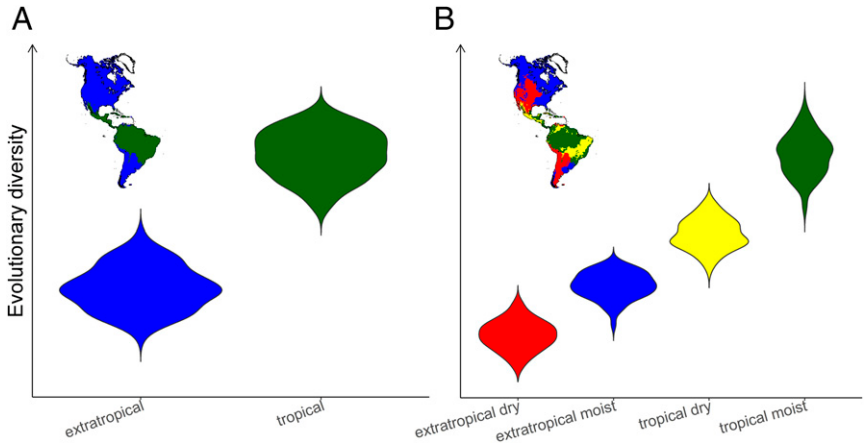

Fig. 1. A conceptual model of the distribution of evolutionary diversity across latitudinal and climatic gradients under two general mechanisms. (*A*) TCH—the latitudinal gradient is categorized into tropical or extratropical, and species richness is lower in extratropical regions because they comprise recently derived, evolutionarily poor (phylogenetically nested) subsets of lineages that have had less time for diversification relative to tropical lineages (i.e., lower evolutionary diversity in extratropical regions). The TCH is the prevalent mechanism addressed in studies of LDGs (e.g., ref. 2). (*B*) Extended TCH—the latitudinal gradient is categorized into four climatic domains: tropical moist, tropical dry, extratropical moist, or extratropical dry, and species richness is lower in extratropical moist, seasonally cold regions because they comprise recently derived, evolutionarily poor subsets of lineages relative to tropical assemblages. Within the tropics, species richness is lower in seasonally dry regions because they comprise recently derived, evolutionary poor subsets of lineages relative to tropical moist regions. Furthermore, extratropical dry regions, which exhibit both pronounced drought and cold temperatures, comprise recently derived, evolutionarily poor subsets of lineages relative to the other three climatic domains. Variation in evolutionary diversity differentiates regions with higher (positive values) or lower (negative) phylogenetic diversity than expected given their taxonomic diversity (e.g., species or generic richness). Thus, low values would indicate higher phylogenetic nestedness in these regions.

moist origin for most clades of extant species (3, 10, 11), under the extended TCH, we would also predict that the number of lineages able to cope with more than one stressor is even more limited. This means that assemblages in extratropical dry regions exhibiting both pronounced drought and cold temperatures will consist of yet smaller subsets of lineages relative to environments that are either tropical moist or seasonal. In these extreme environments, we thus expect the lowest evolutionary diversity of any environment.

To test the predictions of the extended TCH, we used a comprehensive dataset on the distribution of flowering plant species (angiosperms) across the Americas (18) and a time-scaled molecular phylogeny (12) for 3,847 angiosperm genera in the dataset. We then quantified species richness, phylogenetic diversity, and evolutionary diversity of plant assemblages a priori classified into one of 12 biomes (Fig. 2*A*) (19). Each assemblage represented a list of plant species contained within a 100 × 100 km grid cell, and the full extent of North and South America comprised 3,928 of these grid cells (hereafter "assemblages"). The species composition of the assemblages was derived from range maps available in BIEN (Botanical Information and Ecology Network; see *Materials and Methods* for further details). Evolutionary diversity was measured as the total phylogenetic branch length in an assemblage, standardized for the total number of genera in this assemblage, thus describing patterns of accumulated lineage diversity over evolutionary timescales—a metric we refer to as lineage diversity (LD; sensu ref. 16).

Results

Supporting the predictions from the TCH, we found that species richness of plant assemblages in the Americas consistently declines as one moves away from the equator, especially toward extratropical moist biomes (Fig. 2*B* and *SI Appendix*, Fig. S1). Phylogenetic diversity also declines away from the equator, which is expected given the tight correlation of species (Pearson's $r^2 = 0.84$; $P < 0.001$) and genus ($r^2 = 0.98$; $P < 0.001$) richness with phylogenetic diversity. Biome type explains a large proportion of species richness ($r^2 = 0.72$; $P < 0.001$) and phylogenetic diversity ($r^2 = 0.69$; $P < 0.001$). The tropical moist forest biome houses the highest species richness (45,978 species, corresponding to 68% of the total species richness in the dataset; *SI Appendix*, Table S1) and phylogenetic diversity (65,848 myrs, corresponding to 84% of total phylogenetic diversity in the time-scaled phylogeny), whereas the tundra biome houses the lowest (1,407 species, or 2%; 15,013 myrs, or 19%). Interestingly, the most diverse tropical moist forest assemblage contains higher amounts of both species richness and phylogenetic diversity than all tundra assemblages combined (*SI Appendix*, Table S1).

In contrast to recent findings (2, 20, 21), most but not all extratropical biomes are assembled from more recently derived, phylogenetically clustered subsets of tropical floras (Fig. 2 *C* and *D* and *SI Appendix*, Figs. S1 and S2). Rather, many local floras in temperate mixed forests are assembled from random draws of the angiosperm phylogeny and resemble similar patterns found in tropical moist forests (Fig. 3). This finding suggests that virtually all major angiosperm clades have representatives not just in tropical moist forest assemblages but also in temperate mixed forests. In both cases, this pattern seems to reflect accumulated LD in these biomes, with many deep phylogenetic branches relative to their taxonomic diversity (22).

The dramatically reduced LD in extratropical dry environments is consistent across North and South America—the lowest levels of LD in both hemispheres are all found in extratropical dry assemblages (Fig. 3). This result supports predictions from the extended TCH (Fig. 1*B*) and suggests that although extratropical dry environments in the Americas may have existed as long as tropical moist regions (23), angiosperms able to thrive in environments that are both seasonally cold and dry represent a more recently derived, phylogenetically clustered subset of lineages relative to all other regions. In addition, assemblages in extratropical dry biomes show the lowest values of neighbor lineage diversity (NLD) (*SI Appendix*, Figs. S1 and S3). Low values for this alternative metric of evolutionary diversity indicate that the phylogenetic branches separating close relatives in a given assemblage are relatively short, thus conforming with the results of low LD for extratropical dry biomes.

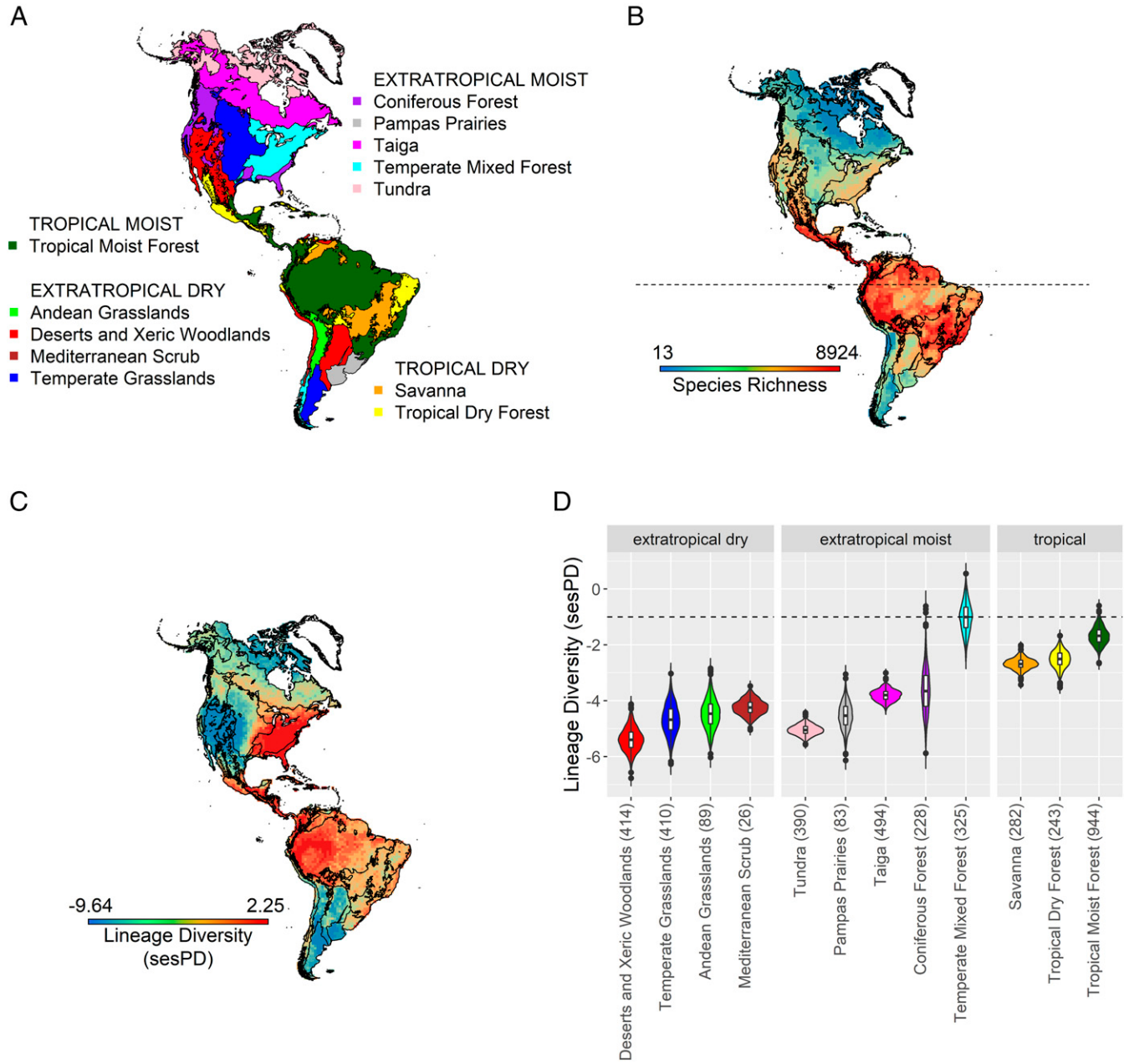

Fig. 2. Patterns of species richness (SR) and LD in angiosperm assemblages across the Americas. (*A*) Assemblages are classified into distinct biomes [following Olson et al. (19)]. (*B*) Geographical patterns of variation in SR for 3,928 angiosperm assemblages (sites). Each site is defined as the assemblage of angiosperm genera in a 100 × 100 km grid cell. Warmer colors indicate higher SR (i.e., the darkest red is assigned to the plant assemblage with SR = 8,924 species). Contours represent biome delimitations and are identical to contours in *A*. Dashed line indicates the Equator. (*C*) Geographical patterns of variation in LD for 3,928 angiosperm assemblages. LD was calculated as the total phylogenetic branch length in assemblages, standardized for genus-level richness. Warmer colors indicate higher LD (i.e., the darkest red is assigned to the plant assemblage with LD = 2.25 [sesPD]). (*D*) Distribution of LD values across biomes in the Americas, grouped by their climatic domain. Values represent 1,000 means of LD from 10 assemblages randomly selected within each biome. Colors of violin polygons are identical to *A*. Biomes are sorted by their median, and the dashed line indicates the highest median (i.e., temperate mixed forests). Values in parentheses after each biome name are the number of assemblages in that biome. Post hoc Dunn tests comparing pairwise biome means are provided in *SI Appendix*, Table S2. Refer to *SI Appendix*, Fig. S1 for a colorblind-friendly version of *B* and *C*.

Patterns of LD observed here for plant assemblages in the Americas are consistent when using a larger time-scaled molecular phylogeny (24), containing 4,566 angiosperm genera in the dataset, under different biome classifications (*SI Appendix*, Fig. S4) and after applying rarefaction methods to control for potential richness-dependence artifacts (*SI Appendix*, Fig. S2). In fact, these patterns of LD are largely congruent with the boundaries of the 12 biomes in the analyses (Fig. 2*C*), with biome type emerging as a strong predictor of LD in a generalized least-squares analysis (GLS; *pseudo-*$r^2 = 0.58$; $P < 0.001$), especially if compared to a model in which assemblages are classified as either tropical or extratropical (ΔAIC = −1,861; *pseudo-*$r^2 = 0.25$; $P < 0.001$).

Biome type remains an important predictor of LD even when variation in climatic conditions and topographic heterogeneity is statistically controlled for (ΔAIC = −1,144; *pseudo-*$r^2 = 0.21$; $P < 0.001$) and in a GLS framework that accounts for spatial autocorrelation

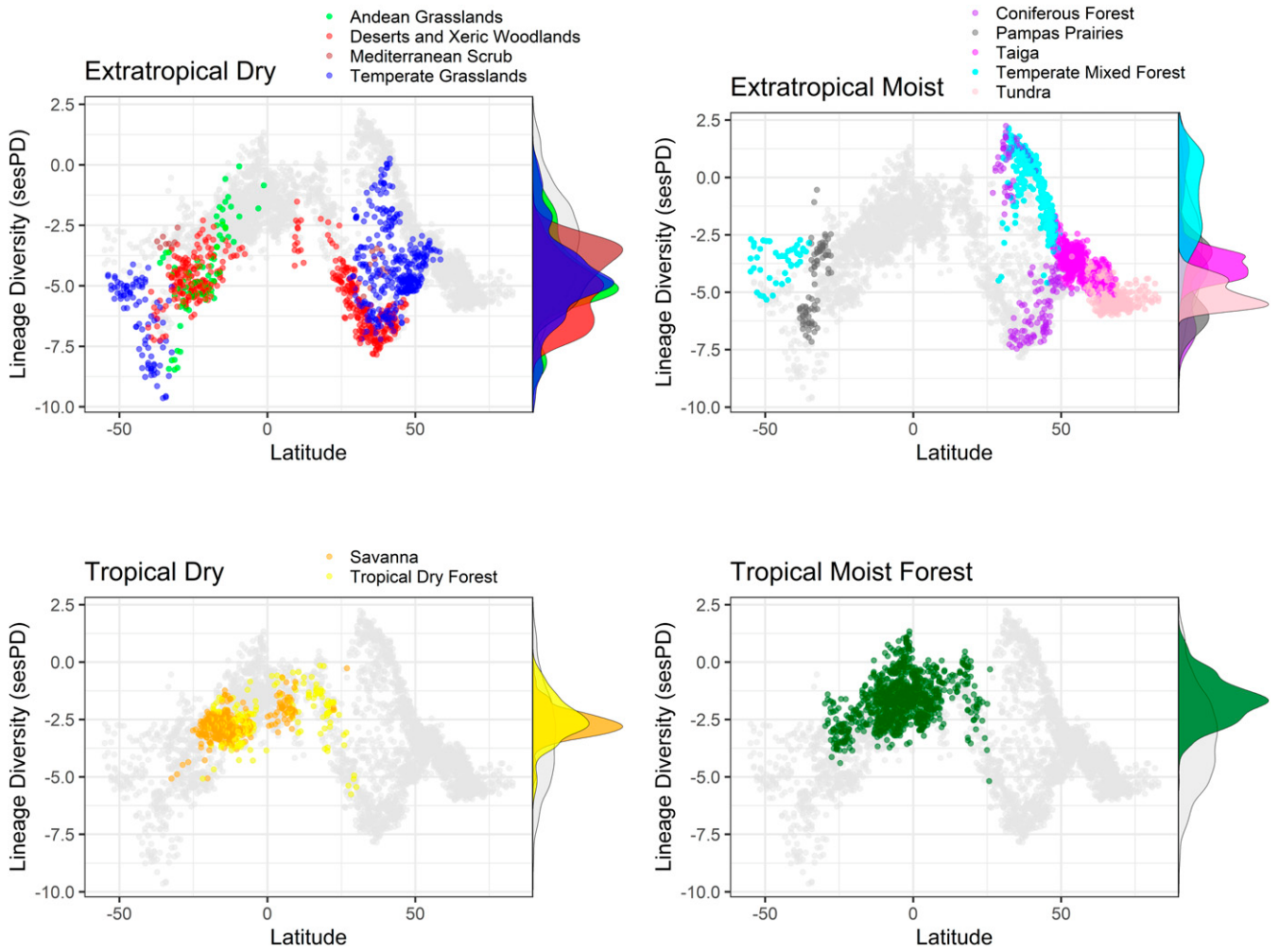

Fig. 3. Latitudinal patterns of variation in LD of angiosperm assemblages across the Americas. Each assemblage is classified into one of four climatic realms (equivalent to realms in Fig. 1*B*) and into one of 12 biomes (equivalent to biomes and colors in Fig. 2*A*). Gray circles in each plot represent assemblages from other climatic domains and are displayed as a reference. Density curves illustrate the distribution of LD across all assemblages (gray curves; for reference) and within each biome (same colors as in Fig. 2*A*). LD was calculated as the total phylogenetic branch length in assemblages, standardized for genus-level richness. Values <−1.96 or >1.96 represent assemblages that show lower or higher phylogenetic diversity than would be expected by chance, respectively. Darker shades in each color indicate overlapping circles (i.e., two or more assemblages occurring in similar latitudes have relatively high similarity in LD).

(ΔAIC = −3,062; *pseudo-*r^2 = 0.48; $P < 0.001$; *SI Appendix*, Fig. S5). These results indicate that plant assemblages within the same biome, or those found in different biomes but under similar environmental conditions (e.g., extratropical dry biomes), have similar amounts of LD, regardless of geography. This is particularly evident in deserts and xeric woodlands, as well as in temperate grasslands, where plant assemblages show the lowest amounts of LD of both hemispheres. These results are also congruent when exploring more recent phylogenetic branching (*pseudo-*r^2 = 0.37; $P < 0.001$; *SI Appendix*, Figs. S1, S3, and S5), suggesting that patterns of biome LD in the Americas are consistent across taxonomic scales.

Extratropical biomes, in general, are mainly assembled from lineages that are shared between two or more biomes. This means that plant lineages in our analyses are poor indicators for individual extratropical biomes. The few indicator (or diagnostic) lineages of extratropical biomes are clustered in clades of eudicots (Fig. 4), with an overall lack of diagnostic lineages from the other two major clades of angiosperms, namely, monocots and magnoliids. This is particularly pronounced in monocots, with entire clades (e.g., Orchidaceae) being near absent in extratropical biomes (25). The exception is temperate mixed forests, for which many magnoliids, as well as early diverging clades of monocots, are diagnostic lineages (Fig. 4). These lineages have relatively long phylogenetic branches and are often from the same clades. This is supported by the relatively high level of conservatism in the phylogenetic distribution of diagnostic lineages from temperate mixed forests and indicates that close relatives in these forests have similar values in the analysis of diagnostic lineages ($\lambda = 0.61$; $P < 0.001$; Fig. 4).

Discussion

The adaptive challenge imposed by extreme frost and high, year-round aridity led to the lowest levels of LD in plant assemblages across terrestrial biomes in the Americas. This supports a more extended view of the influential TCH [as proposed in Wiens and Donoghue (8)], whereby biomes that are radically different from the ancestral niche of angiosperms (e.g., deserts, xeric woodlands, and tundra) will have limited, phylogenetically clustered diversity relative to environments that show lower levels of deviation from this niche. The major findings from our empirical, continental-scale analysis of predictions stemming from the TCH are detailed below.

In contrast to tropical moist forests, which have representatives of virtually all angiosperm clades, both savannas and tropical dry

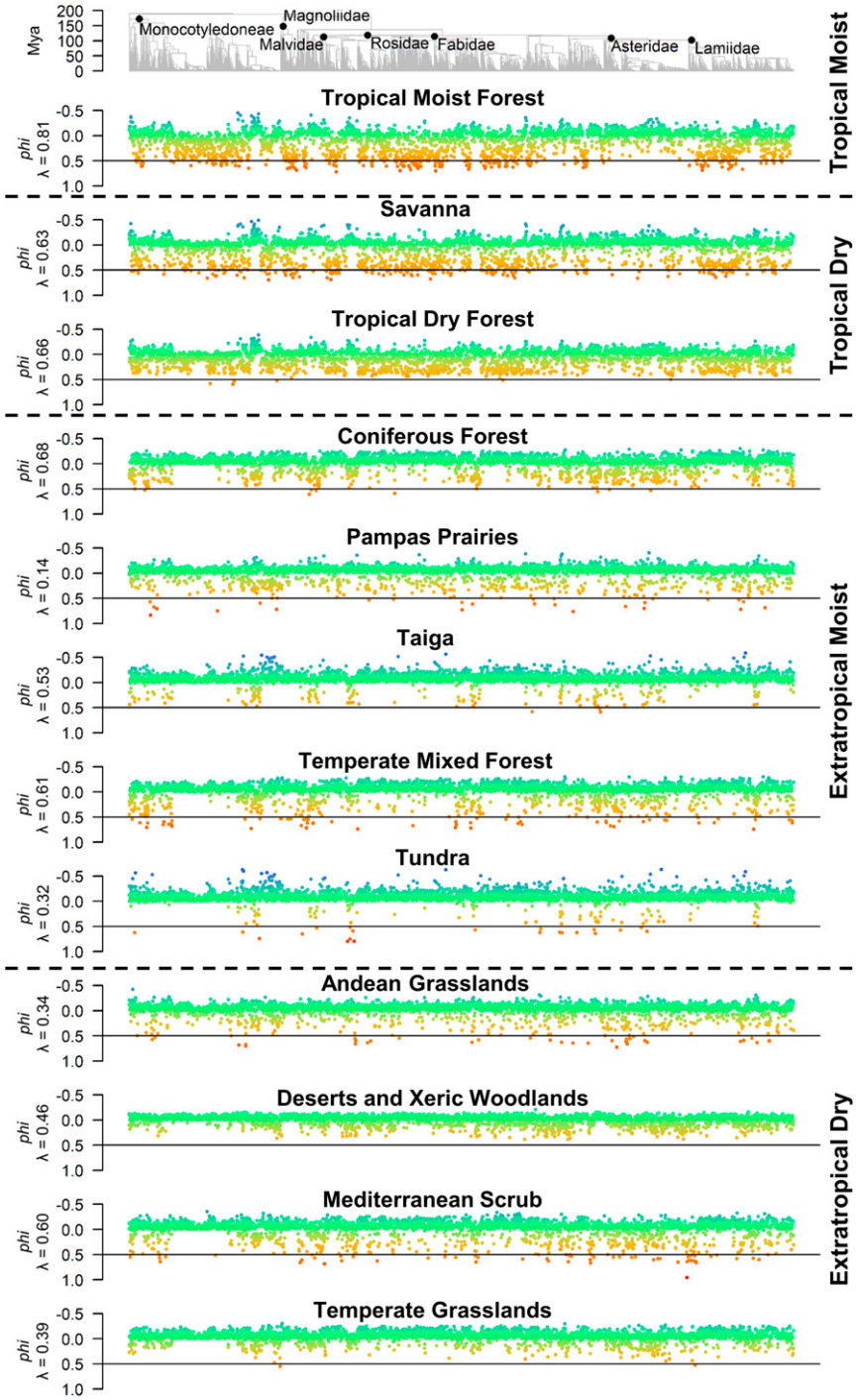

Fig. 4. Time-calibrated molecular phylogeny (12) of 3,847 angiosperm genera found in plant assemblages across the Americas. We calculated a fidelity coefficient (*phi*) for all genera in the dataset to each biome to identify diagnostic lineages (see *Materials and Methods* for further details). Colors illustrate the variation in *phi*, with warmer colors indicating higher values. The horizontal line at *phi* = 0.5 is plotted as a reference, and dots below this line represent lineages that are good indicators of a given biome (absent or near absent in other biomes). λ values at the vertical axes represent the phylogenetic signal (Pagel's lambda) of *phi* for each biome, and higher values indicate stronger phylogenetic conservatism in the distribution of diagnostic lineages.

forests are assembled from more recently derived, phylogenetically clustered subsets of angiosperm lineages, thus conforming to predictions of the extended TCH. However, considering the savannas and tropical dry forests in our analyses, the extended TCH would predict lower LD in tropical dry forests, which are found under drier conditions than savannas (16). We believe that our results showing similar LD between these two tropical dry biomes (*SI Appendix*, Table S2) are driven by the patterns of LD observed in the Cerrado of Central Brazil, which comprises the largest extension of savanna in the Americas, and represents 68% of the savanna assemblages in our dataset. Previous studies have shown evidence for a recent assembly of the Cerrado flora (c. 10 Mya) (26), with many of its plant lineages originating at 4 Mya or less. Such recent assembly is in agreement with our results, and imply

that the Cerrado savannas are mainly assembled from plant lineages with shallower phylogenetic branches relative to tropical dry forests and tropical moist forests.

Furthermore, it is striking that in contrast to savannas, tropical dry forests are mainly assembled from angiosperm lineages that are shared with two or more biomes. This runs counter to the idea of high phylogenetic conservatism in tropical dry forests (15). Although there are examples of clades that have been confined to tropical dry forests for millions of years (15), these clades seem to represent an exception. In general, plant lineages endemic to tropical dry forests (27) are from clades that also have representatives widespread in extratropical dry environments (e.g., Chaco thorn woodlands) and other tropical biomes (e.g., savannas) (28). This low degree of specificity in tropical dry forests, where plant lineages are often shared with other biomes, is supported by a recent study showing relatively low evolutionary endemism in these forests (17).

While the pattern of reduced LD in tropical dry biomes relative to tropical moist forests is consistent with predictions of the extended TCH and has been documented in recent macroecological studies (16, 20), there are two unexpected patterns that deserve careful consideration. First, the high LD in temperate mixed forests does not conform to the original formulation of the TCH, and suggests that assemblages there comprise lineages that are old and evenly distributed, or overdispersed, across the angiosperm phylogeny (29). Second, lower LD in extratropical dry assemblages suggests that these environments comprise lineages that are recently derived and phylogenetically clustered in the angiosperm phylogeny, yet we observe a higher species richness in extratropical dry assemblages than in temperate mixed forests assemblages (Fig. 2*B* and *SI Appendix*, Fig. S1 and Table S1). These paradoxical patterns are further explored below.

Lineages in temperate mixed forests are not recently derived, nor are they confined to a few angiosperm clades (Fig. 4). These results run counter to previous findings (2, 20), and such contrast may be driven by our use of assemblage-level data, in which individual plant assemblages belong to a single biome and comprise data on the whole spectrum of plant life-forms. Previous large-scale studies either spatially aggregated plant assemblages in latitudinal bands irrespective of their biome (2) or only included data on the composition of woody plant species (2, 20). Many plant clades in extratropical moist biomes may only be represented by lineages that have shifted to an herbaceous lifeform when diversifying in seasonally cold, freezing environments (12), and not including these lineages in the analyses may lead to erroneous conclusions when quantifying the amount of LD for plant assemblages in extratropical biomes. Nonetheless, a recent study that used nonaggregated data on tree assemblages from across southern South America (30) also found higher LD in extratropical moist assemblages (temperate mixed forests) relative to tropical forests (dry or moist). This suggests that aggregating assemblages from distinct biomes into spatially coarse bins (e.g., ref. 8) may have a stronger effect in LD analyses (i.e., by lowering LD values of temperate mixed forests when these are lumped with extratropical dry assemblages).

Here, we argue that comparable LD in temperate mixed forests and in tropical moist forests occurs because the phylogenetic branches separating close relatives in these temperate assemblages are considerably longer than the branches separating close relatives in tropical forest assemblages (high NLD; *SI Appendix*, Figs. S1 and S3). This pattern indicates high richness at family level but low generic richness in temperate mixed forests, possibly consistent with late-Cenozoic climate-driven extinctions in this biome (7). Conversely, while family richness is high in the tropical moist forests, there is also high richness at the genus level, which could be related to higher recent diversification in tropical moist regions relative to extratropical moist regions (thus consistent with higher Cenozoic climatic stability in the tropics) (7).

Lineages in extratropical dry environments seem to represent a recently derived subset of angiosperm lineages. Thus, relative to extratropical moist biomes, the higher species richness in extratropical dry regions despite lower LD there, seems to reflect a combination of less time for diversification and higher speciation rates. Recent radiations in extratropical dry environments, particularly in deserts and xeric woodlands, have been documented in macroevolutionary studies of animal and plant clades (31–34) and are congruent with our results showing short phylogenetic branch lengths separating lineages in extratropical dry assemblages.

There are many caveats when using large datasets in biodiversity analyses, and perhaps the most important limitations that apply to our study (and are common in macroecological studies) are the potential for lineages to be incorrectly assigned to a given biome (e.g., due to misidentifications of taxa in the field) and biomes being incorrectly delimited. Here, we minimized the effect of these potential errors statistically (e.g., randomizations and rarefactions) and believe that the overall patterns of LD described in terrestrial biomes across latitudinal gradients are real. For instance, the observed patterns of LD in tropical biomes remain largely similar across analyses even when tropical dry and moist assemblages are dramatically rarefacted to less than half of their generic diversity.

Nonetheless, we still know little about the mechanisms that created and maintained patterns of species richness and LD over deep evolutionary timescales. Here, we propose that a promising way forward would be to examine why only recently derived angiosperm lineages have colonized extratropical dry environments, which key innovations made this colonization possible, and what is the timing of their origin in the angiosperm tree of life. Answering similar questions has shed light on the mechanisms allowing plant lineages to colonize cold environments (12), but there is still more to learn about the colonization of extratropical environments that are subject to both freezing temperatures and marked drought.

Conclusions

Future studies aiming to understand the distribution of biodiversity across the full extent of latitudinal gradients should avoid the binary classification of biological assemblages into those found under tropical or extratropical climates. Using a comprehensive dataset on the distribution of plant assemblages across the Americas, we show that incorporating drought and the combined effect of seasonal cold and drought enables a better explanation of patterns of species richness and evolutionary diversity. Reduced LD in tropical dry biomes relative to many assemblages in extratropical moist biomes suggests that drought is at least as important as frost in shaping overall patterns of plant lineage diversity. It is also critical to account for drought outside of the tropics to understand observed patterns of biological diversity. In extratropical dry regions, drought combined with seasonal frost produces the lowest levels of plant evolutionary diversity observed, in sharp contrast to the pattern observed in other extratropical regions.

Furthermore, the observed pattern of higher species richness in tropical moist forests seems to be associated with the accumulation of plant lineages over deep evolutionary timescales, combined with higher recent diversification in tropical moist regions. Conversely, the evolutionary history of plant lineages in extratropical dry biomes, and particularly in deserts and xeric woodlands, might not be as deep as in extratropical moist and tropical biomes. However, their relatively high (albeit recent) diversification has led to a higher number of plant species in deserts and xeric woodlands compared to extratropical moist biomes, with these species being confined to a phylogenetically clustered subset of angiosperms clades. Nonetheless, well-resolved species-level phylogenies of clades that are both diverse and widespread across gradients of water availability (moist to dry) in both tropical and extratropical biomes (e.g., Leguminosae) are needed to provide a more accurate assessment of the role that

variable diversification rates and phylogenetic niche conservatism may play in the observed patterns of species and evolutionary diversity in these biomes.

The evolutionary rarity of drought tolerance depicted in our results indicate that an ongoing expansion of arid environments globally (35, 36) may lead to nonrandom loss of evolutionary diversity in moist biomes, either tropical or extratropical. Hence, we stress that both tropical moist forests and some extratropical moist biomes, especially temperate mixed forests, may deserve similar attention in conservation strategies predicated on protecting evolutionarily diverse regions (16, 17, 30, 37). However, the long phylogenetic branches separating close relatives in many extratropical assemblages (e.g., across eastern North America; *SI Appendix*, Figs. S1 and S3) indicate that most clades in these assemblages may be represented by fewer (if not one) plant lineages. Thus, loss of plant lineages in extratropical moist biomes is likely to entail higher loss of evolutionary diversity relative to other biomes.

Materials and Methods

Database. We used different methods to infer the geographic range of plants species in the analyses. Detailed methods of range mapping, including the workflow of species distribution modeling for species with 3+ occurrence records, is available as *SI Appendix, Supplementary Methods*. Plant occurrence records used in the range mapping were from the BIEN database (version 4; https://bien.nceas.ucsb.edu/bien/about/), which is compiled via a linked workflow that standardizes, integrates, corrects, and validates data from disparate data sources and data formats. BIEN data include herbarium collections, ecological plots, and surveys from a large variety of sources (https://bien.nceas.ucsb.edu/bien/data-contributors/all). Taxonomy is standardized using the Taxonomic Name Resolution Service (https://bien.nceas.ucsb.edu/bien/tools/tnrs/), which corrects spelling errors and updates synonyms to accepted names. Geographic validation of plant occurrences leverages the Geographic Name Resolution Service (https://bien.nceas.ucsb.edu/bien/tools/gnrs/), which flags occurrence records as erroneous if they 1) fall outside the coordinate system (e.g., longitude >180° or <−180°), 2) contain suspect coordinate values (e.g., latitude is exactly 0 or 90 or longitude is exactly 0 or 180), 3) fall in the ocean, 4) match a political division centroid, or 5) fall outside of a declared political division. Occurrence records that fall outside of a species' native range are identified using the Native Species Resolver (https://bien.nceas.ucsb.edu/bien/tools/nsr/), which uses published checklists and endemism data to determine whether the observed species is native to a given location. Observations are flagged as potentially cultivated and removed from the observation data, based on 1) keywords in the specimen locality data suggesting provenance from a farm or garden, 2) geographic proximity (≤3 km) to a botanical garden or herbarium, or 3) original observation metadata indicating a cultivated origin. Full details of the BIEN workflow can be found at https://bien.nceas.ucsb.edu/bien/tools/.

Angiosperm Diversity Maps. All range maps were produced on a 10 × 10 km Mollwide equal-area projection and subsequently aggregated to 100 × 100 km for creating diversity maps. This spatial resolution was chosen because there is growing evidence that pixels of this size include most, if not all, species whose geographic ranges they fall within (38, 39). Here, we restricted the analyses to flowering plants (angiosperms), given the lack of a robust, large-scale phylogenetic hypothesis for the early divergent spermatophyte clades (i.e., mosses, ferns, and gymnosperms). Our final species-by-site matrix comprised 67,846 angiosperm species and 3,928 sites, with each site defined as the assemblage of angiosperm species in a 100 × 100 km grid cell.

We classified all assemblages into biomes following Olson et al. (19), which represented four climatic domains (Fig. 1*B*): tropical moist (tropical moist forests), tropical dry (savannas and tropical dry forests), extratropical moist (coniferous forest, Pampas Prairies, taiga, temperate mixed forests, and tundra), and extratropical dry (Andean grasslands, deserts and xeric woodlands, mediterranean scrub, and temperate grasslands). Although this biome classification is often considered suboptimal for some biological purposes (40, 41), it provides a manageable number of categories that are appropriate for the purposes of this study. We classified biomes into climatic domains based on their mean values (across assemblages) of aridity index (42), climatic water deficit (43), minimum temperature of coldest month (44), and temperature seasonality (44). We also used the classification system of terrestrial biomes proposed in Higgins et al. (45) to assess whether the observed results are robust to alternative classifications. The biome names in Higgins et al. (45) are derived from three letters: 1) tall or short for the height of the predominant vegetation type (thus, T or S); 2) low, medium, or high for a vegetation productivity index (L, M, or H); and 3) cold, dry, both cold and dry, or nonseasonal for a growth limitation index (C, D, B, or N).

Community Phylogenetics. We used the megaphylogeny "Phytophylo" for the community phylogenetics analyses (46). Phytophylo is an update of the megaphylogeny published by Zanne et al. (12), which was generated based on seven gene regions and 39 fossil calibrations. We used a genus-level version of the Phytophylo, which comprised 3,847 angiosperm genera, and corresponded to 92% of the genera occurrences in the dataset. We used a genus-level phylogeny instead of a species-level one to avoid issues with species misidentifications, which are particularly common in the tropics (47), from which a considerable amount of our data comes.

We calculated two metrics of evolutionary diversity. NLD was computed as the mean phylogenetic distance (in million years) from each taxon to its closest relative in the assemblage, standardized for genus-level richness (i.e., sesMNTD, sensu ref. 48). We calculated LD as the total phylogenetic branch length in assemblages (49), standardized for genus-level richness (i.e., sesPD, sensu ref. 48). Because these metrics are standardized (with an expected value of 0 and an SD of 1), values < −1.96 or >1.96 represent assemblages that show lower or higher phylogenetic diversity than would be expected by chance, respectively (48), while values within this range indicate that phylogenetic diversity is no different from random expectation (i.e., assemblages are assembled from random draws of the phylogeny) (48); but refer to ref. 50 for a discussion on the skewness of null distributions in evolutionary diversity metrics). We also calculated LD using a time-scaled phylogeny for 4,566 angiosperm genera (24) in the dataset.

We tested for a potential richness-dependent artifact (51) in the observed results by calculating LD using a set of 1,000 genus-by-assemblage matrices randomly rarefacted to 1/4 of maximum generic richness (382 genera) and phylogenetic trees pruned to the genus pool in each matrix. Rarefaction ranged from no genera excluded in taiga and tundra to tropical moist forest assemblages being randomly rarefacted to an average of 41% of their generic diversity. These analyses generated 1,000 LD values for each of the 3,928 assemblages, which were used to calculate mean values per assemblage (*SI Appendix*, Fig. S2).

Because biomes in the Americas are significantly different in area (e.g., 26 Mediterranean Scrub assemblages versus 944 Tropical Moist Forest assemblages), we assessed the distribution of LD and NLD values by randomly sampling 10 assemblages within each biome, calculating the mean of these 10 values for each biome, and replicating these two steps 1,000 times. This generated 1,000 mean values of LD and NLD for each biome, which were then used to assess the distribution of both metrics within and across biomes.

We used a GLS approach to test the relationship between LD and explanatory variables: biome type climate and topographic complexity. We used climate data from Trabucco and Zomer [aridity index (42)], Chave et al. [climatic water deficit (43)], and WorldClim 2.0 [temperature of coldest month and temperature seasonality (44)] at 30–arc second (1 km^2) resolution to create a matrix containing mean values of climatic data for each 100 × 100 km grid cell (assemblage). The number of 300-m elevational belts per assemblage (range of elevation divided by 300) was calculated as a proxy of topographical complexity (5) by using the GTOPO-30 digital elevation model (52). We then performed a principal component analysis of the full matrix (3,928 assemblages, four bioclimatic variables, and one topographic variable) and selected the first two components of this analysis as environmental predictors, which accounted for 83% of the variance in the environmental matrix. Our GLS approach allowed us to account for spatial autocorrelation when testing the relative influence of biome type on LD and NLD. In preliminary analyses, we found a Spherical spatial autocorrelation structure to best fit the data, and we therefore used this structure when generating all models.

We assessed the goodness-of-fit between biodiversity metrics (e.g., species richness, evolutionary diversity) and explanatory variables (e.g., environmental variables, and biome type) through adjusted coefficients of determination and significance tests. We also used the Akaike information criterion to compare GLS models. We conducted the community phylogenetics and regression analyses and mapped the results in geographic space using graphical and statistical packages (48, 53–56) in R (57).

Analyses of Diagnostic Lineages and Phylogenetic Signal. In this study, diagnostic lineages represent those statistically associated with one or more biome types so that their presence in assemblages may be a strong indicator of the biome types themselves. We identified diagnostic lineages based on their coefficient of fidelity to a given biome (*phi*; 58). An advantage of this coefficient is that they can take negative values, which expresses the fact that a lineage tends to "avoid" a particular biome and its environmental conditions (59, 60). The significance of *phi* was obtained via Monte Carlo permutations (999). Genera with the top 10 values of *phi* are shown in *SI Appendix*, Figs. S6–S17.

We then mapped these values at terminal branches in the phylogeny to visualize their phylogenetic distribution.

We estimated the phylogenetic signal in *phi* by using Pagel's λ (61), which quantifies the amount of variance in an observed trait in relation to the expected variance under a Brownian motion model of evolution. We assessed the significance of the phylogenetic signal results by recalculating λ a thousand times on phylogenies with randomly permuted tips. We mapped *phi* across the phylogeny and conducted phylogenetic signal analyses using graphical and statistical packages (62, 63) in R (57).

Data Availability. Species range maps supporting the results are from version 4 of the BIEN database (https://bien.nceas.ucsb.edu/bien/biendata/bien-4). Time-scaled phylogenies were obtained from Qian and Jin (46) and Smith and Brown (24). Biome classifications and their polygons were obtained from Olson et al. (19) and Higgins et al. (45). Bioclimatic variables were obtained from Trabucco and Zomer (42), Chave et al. (43), and WorldClim 1.4 (44). The proxy of topographical complexity used in the analyses was obtained from the GTOPO-30 digital elevation model (52).

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