Amazonia is the primary source of Neotropical biodiversity

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The American tropics (the Neotropics) are the most species-rich realm on Earth, and for centuries, scientists have attempted to understand the origins and evolution of their biodiversity. It is now clear that different regions and taxonomic groups have responded differently to geological and climatic changes. However, we still lack a basic understanding of how Neotropical biodiversity was assembled over evolutionary timescales. Here we infer the timing and origin of the living biota in all major Neotropical regions by performing a cross-taxonomic biogeographic analysis based on 4,450 species from six major clades across the tree of life (angiosperms, birds, ferns, frogs, mammals, and squamates), and integrate >1.3 million species occurrences with large-scale phylogenies. We report an unprecedented level of biotic interchange among all Neotropical regions, totaling 4,525 dispersal events. About half of these events involved transitions between major environmental types, with a predominant directionality from forested to open biomes. For all taxonomic groups surveyed here, Amazonia is the primary source of Neotropical diversity, providing >2,800 lineages to other regions. Most of these dispersal events were to Mesoamerica (~1,500 lineages), followed by dispersals into open regions of northern South America and the Cerrado and Chaco biomes. Biotic interchange has taken place for >60 million years and generally increased toward the present. The total amount of time lineages spend in a region appears to be the strongest predictor of migration events. These results demonstrate the complex origin of tropical ecosystems and the key role of biotic interchange for the assembly of regional biotas.

biogeography | biome shift | evolution | Neotropics | phylogenetics

The Neotropical realm, spanning from Mexico to southern South America and including the West Indies (1), is one of the most species-rich regions on Earth (2, 3). This vast region comprises many different biomes and habitats such as seasonally dry forests, arid zones, high-elevation grasslands, young and old mountain systems, and extensive rainforests, such as the Atlantic Forests and Amazonia (4). Because each region and biome possesses its own species diversity and communities, it is crucial to investigate the diversification history and biotic connections of each constituent region to understand how Neotropical biodiversity was assembled (5, 6).

Consensus is emerging that Neotropical diversification results from a complex interaction of biotic and abiotic processes (2, 5), which are now being teased apart by novel analytical approaches (7). Abiotic events of biological significance include the hydrologic and topographic changes brought about by mountain uplift (4), but also by several events of global and regional climatic changes (8, 9). Biotic triggers of speciation include species interactions (10, 11) and soil adaptations (12), as well as the evolution of other organism-specific traits. Neotropical diversification has been extensive in some regions, such as Amazonia, where speciation in rainforest environments has taken place since at least the Paleocene (~58 Mya, Ma; ref. 13). Other environments, such as the high-elevation grasslands in the northern Andes, have a more recent, but still remarkable, diversification history in the last few million years (14, 15).

What remains less clear, however, is the role of biotic interchange in the standing diversity of Neotropical regions. In addition to differences in speciation and extinction rates, regional diversity is determined by the immigration of species from other regions over time. In some cases, immigrant lineages may constitute a substantial proportion of the local diversity, such as in Ecuadorian Amazonia, where ca. 20% of all tree species arrived by dispersal from other regions (16). Within the limits of a single region, dispersal events have been high in several plant genera (17, 18). In contrast, dispersal events (including successful establishment) across environmentally disparate regions are considered rare on a global scale (19).

Current evidence from the analysis of dated molecular phylogenies has shown that some Neotropical regions might be more permeable than others. South American savannas, for instance, have been colonized multiple times independently by ancestors from other regions (20, 21). Alternatively, intrinsic differences among taxonomic groups (such as dispersal ability) may allow some lineages, but not others, to colonize new regions. Although some taxa tend to maintain their ecological requirements over time, staying in their region of origin or dispersing to distant regions with the same environmental conditions (i.e., niche conservatism, refs. 19 and 22), others show frequent regional and ecological shifts

Significance

Amazonia is not only the world's most diverse rainforest but is also the region in tropical America that has contributed most to its total biodiversity. We show this by estimating and comparing the evolutionary history of a large number of animal and plant species. We find that there has been extensive interchange of evolutionary lineages among different regions and biomes, over the course of tens of millions of years. Amazonia stands out as the primary source of diversity, which can be mainly explained by the total amount of time Amazonian lineages have occupied the region. The exceedingly rich and heterogeneous diversity of the American tropics could only be achieved by high rates of dispersal events across the continent.

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(21, 23, 24). For the great majority of Neotropical regions and taxonomic groups, however, our knowledge of their biotic interchanges and dispersal histories remains surprisingly poor, with few exceptions (e.g., refs. 25 and 26). In particular, we lack an understanding of which regions served as primary sources and sinks of biodiversity, defined here as providers and receivers of lineages, respectively, rather than implying habitat quality as in population biology (27).

Understanding the dynamics of biotic interchange is challenging, as several abiotic and biotic factors are likely to be involved (28). Based on the Theory of Island Biogeography (29), there should be a positive relationship between the number of dispersal events and the area of a region, and a negative relationship with geographic isolation. Similarly, the more shared perimeter (adjacency) two regions have, the more interchange should also be expected (28). However, many Neotropical regions and biomes have changed considerably through time (9), making it crucial to also consider historical changes in a region's area and connectivity. In general, the more combined time lineages spend in a region (expressed as total branch lengths in a phylogeny), the more opportunities they should have to diversify and emigrate (30, 31). Regions with high diversity could be more difficult to enter than species-poor regions, because of competitive exclusion and niche filling (32, 33), or show the opposite pattern, based on empirical evidence from invasive species (34, 35). To date, none of these variables has been assessed as a general predictor of biotic interchange in the Neotropics.

Here we assess the evolutionary assembly of Neotropical biotas through a cross-taxonomic biogeographic analysis. Fossils can be useful for inferring biogeographic history (36), but the Neotropical fossil record is too scarce for most periods, regions, and taxonomic groups to allow robust estimates (37). We therefore take advantage of recently published, well-sampled molecular phylogenies, which hold a large but unrealized potential in revealing the evolution of tropical biotas (17, 38). We integrate these phylogenies with large species occurrence datasets, spatial information on Neotropical regions and biomes, and their evolution and connectivity through time. We address the following questions: was the amount of biotic interchange similar among Neotropical regions, or have particular regions contributed substantially more or less than others? How often were dispersal events associated with shifts between major biome types? To what extent was the direction of interchange determined by taxonomic group? Did biotic interchange among regions occur evenly through time, or were there periods of more frequent dispersal events? Which general descriptors of a region and its biota predict the amount of biotic interchange with other regions?

Results

Data Compilation and Analyses. Our vetted dataset encompassed 1,331,323 georeferenced records representing 68,329 species, derived from the integration of densely sampled molecular phylogenetic trees with a large dataset of species distributions (*SI Appendix*, Figs. S1 and S2, Table S1, and *Supporting Methods*). Our analytical pipeline identified 214 predominantly Neotropical clades including 4,450 species. These comprised 104 clades of flowering plants or angiosperms (2,114 spp; representing 46.7% of the total number of species in the utilized phylogenies), four clades of ferns (53 spp; 1.16%), 54 of birds (1,237 spp; 27.5%), 11 of frogs (155 spp; 4.13%), 13 of mammals (359 spp; 8.23%), and 28 of squamates, which comprised lizards, snakes, and worm lizards or amphisbaenians (532 spp; 12.24%). All species in all phylogenies were coded as present or absent in 10 Neotropical regions (Fig. 1): two predominantly forested/wet regions (Amazonia and Atlantic Forests), six predominantly open/dry regions, at least seasonally (Andean Grasslands, Caatinga, Cerrado and Chaco, Dry Northern South America, Dry Western South America, and Patagonian Steppe), and two regions comprising a mixture of these two major biome types (Mesoamerica and West Indies; *SI Appendix*, Figs. S3–S8 and Table S2).
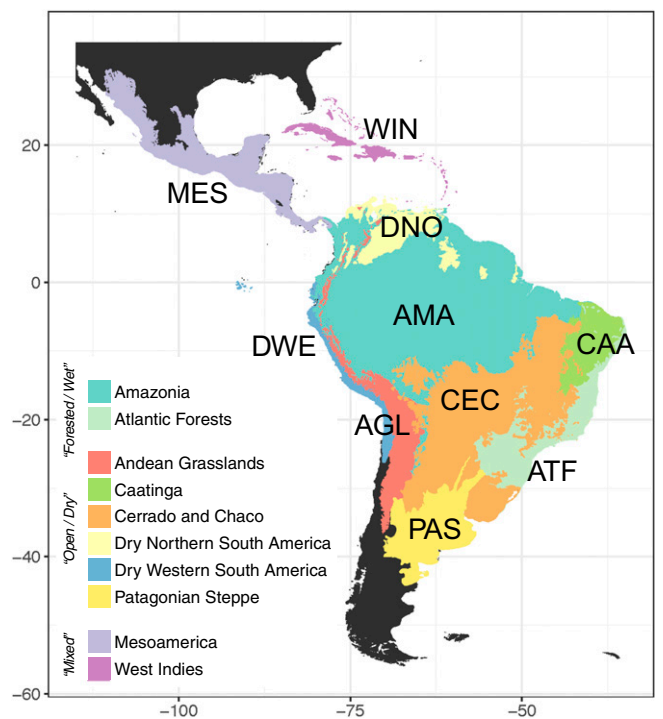

Fig. 1. Neotropical regions used in the biogeographic analyses, grouped by major biome type and plotted together with the abbreviations used for subsequent analyses. These regions are derived from the classification of terrestrial biomes and ecoregions by Olson et al. (48), but adapted to differentiate disjunct biomes and to simplify the complexity in Mesoamerica and the West Indies, which comprise both forested and open habitats.

Direction of Interchange. Our biogeographic analyses show that all regions have served as both sources and sinks of lineages (Fig. 2, Tables 1 and 2, and *SI Appendix*, Figs. S9 and S10 and Tables S4–S6). We identified a total of 4,525 dispersal events across the Neotropics, estimated under an unconstrained biogeographic model (assuming equal connectivity among regions through time), and 5,818 dispersal events inferred under a time-constrained model (reflecting the hypothesized history of existence and connectivity among regions). We focus our results and discussion on the unconstrained model, as it incurs the fewest assumptions, but we report all results in Tables 1 and 2 and the *SI Appendix*.

Amazonia was the most important source of diversity, providing 2,855 lineages (63% of all dispersal events) to other Neotropical regions. This was about 4.6 times as many as the second most important source region, Mesoamerica (615), followed by Cerrado and Chaco (455). In contrast, Mesoamerica was the most important sink, receiving the highest number of lineages (788; 17%), but it was closely followed by Dry Northern South America (771) and Cerrado and Chaco (766). Amazonia also served as a sink of diversity, but only moderately so, and ranked fifth among all regions.

An evaluation of the number of dispersal events out of Amazonia (Fig. 2 and *SI Appendix*, Tables S4–S6) revealed that about a quarter of all events were into Mesoamerica (711), closely followed by two open/dry regions: Dry Northern South America (622) and Cerrado and Chaco (517). The West Indies and the other three open/dry regions (Dry Western South America, Caatinga, Patagonian Steppe) all received fewer than 100 dispersal events each.

When considering each taxonomic group separately, Amazonia remained the primary source of lineages to other Neotropical regions (Fig. 3 and *SI Appendix*, Tables S4–S6). The second main source varied among Mesoamerica (angiosperms and birds), Cerrado and Chaco (frogs, mammals, and squamates), and Atlantic Forests (ferns).
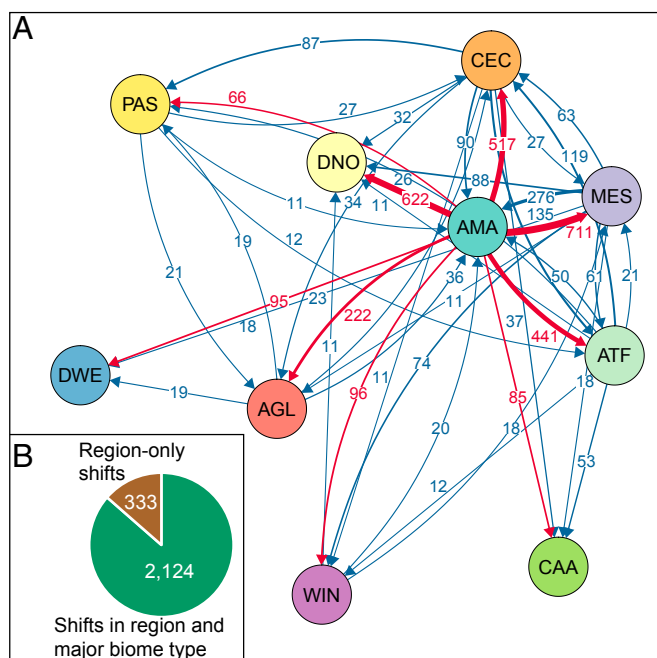
Fig. 2. (A) Biotic interchange among Neotropical regions estimated from dated molecular phylogenies, comprising 4,450 species in six taxonomic groups (angiosperms, birds, ferns, frogs, mammals, squamates). Arrows indicate the direction and number of dispersal events, with line thickness proportional to the number of events. Only connections with more than 10 events are shown (see *SI Appendix*, Tables S5 and S6 for a full list). The position of the circles in the layout reflects the biotic connection among regions, as calculated by a force-directed placement algorithm implemented in the R package qgraph (56). Dispersal events out of Amazonia are highlighted in red. The color of the circles corresponds to those in Fig. 1. AGL, Andean Grasslands; AMA, Amazonia; ATF, Atlantic Forests; CAA, Caatinga; CEC, Cerrado and Chaco; DNO, Dry Northern South America; DWE, Dry Western South America; Mes, Mesoamerica; PAS, Patagonian Steppe; WIN, West Indies. (B) Number of nonambiguous dispersal events associated with shifts in major biome types compared with shifts to other regions within the same biome type. Shifts involving Mesoamerica and the West Indies are considered ambiguous (n = 2,068; *SI Appendix*, Table S6).

A large number of dispersal events involved shifts between major biome types (forested/wet and open/dry), rather than dispersals to other regions but within the same major biome type (2,124 vs. 333 events, respectively; Fig. 1 and *SI Appendix*, Table S6). Of these, the vast majority (1,820) involved transitions from wet to dry biomes compared with shifts in the other direction (304). An almost equally large number of shifts involved mixed regions (containing both forested and open biomes) and are considered ambiguous (2,068 events).

Timing of Interchange. All regions and taxonomic groups showed fluctuations in the relative number of dispersal events through time (i.e., in proportion to the number of lineages at each time; *Materials and Methods*), rather than constant rates (Fig. 4 and *SI Appendix*, Figs. S11–S13). We found a general increase in the number of relative dispersal events toward the present, in particular during the last 10 My.

Differences in Biogeographic Models. We found a general congruence in the main results obtained under the unconstrained and the time-stratified connectivity matrices between regions. Under both models (Fig. 2, Tables 1 and 2, and *SI Appendix*, Fig. S9), Amazonia remained the most important source of dispersal events, and Mesoamerica the most important sink. A general agreement was also found for individual clades (Fig. 3 and *SI Appendix*, Fig. S10), whereas the temporal pattern of dispersal events between

regions was affected by the prespecified constraints (*SI Appendix*, Figs. S11 and S12). We encountered differences for some pairs of regions, such as a marked asymmetry in dispersal events involving Mesoamerica under the constrained model compared with a stronger balance under the unconstrained model.

Predictors of Emigration and Immigration. The total branch length in a region was the strongest predictor for immigration and emigration (Fig. 5 and *SI Appendix*, Figs. S14–S19 and Tables S7 and S8), followed by a region's current area (positively associated with emigration) and isolation (negatively associated with immigration). These were the only predictors identified as important (95% credible intervals do not contain 0) in the global model; that is, considering all regions and taxa simultaneously. For three of the four clades with enough representation to be included in our models, we found less immigration into Amazonia than expected, and for angiosperms and birds, we found higher emigration than expected.

Discussion

The Reticulate Assembly of Neotropical Biodiversity. Our results reveal unprecedented levels of biotic interchange across all major Neotropical regions and over tens of millions of years. Clearly, the interchange of lineages has been a pivotal process for the assembly of regional biotas. The importance of Amazonia as the primary source of Neotropical lineages is strongly supported across all analyses (e.g., Figs. 2 and 3).

The biotic interchange between Amazonia and Mesoamerica is remarkable, both for the high number of inferred dispersal events (711 across all lineages; *SI Appendix*, Tables S4–S6) and for the long period of interchange (Fig. 4 and *SI Appendix*, Figs. S11–S13). Once considered a continent in splendid isolation (39), these results reinforce the more recent idea that South America has instead had a long and continuous exchange of lineages with the North American continent (40). This interchange was not hindered by the relatively narrow water gaps between these continents, which disappeared during the final stages of the emergence of the Isthmus of Panama (41).

Shifts Across Major Biome Types. We detected a relatively high (47%) proportion of dispersal events associated with shifts in broadly defined biome types; that is, between open/dry (sometimes only seasonally) and more constantly forested/wet regions (Fig. 1B and *SI Appendix*, Table S6) compared with shifts across regions, but within the same biome type (7%). However, we expect that the majority of those shifts classified as ambiguous (46%) may also be region-only shifts (e.g., rainforest dwellers and mountain specialists), based on previous cross-regional studies (e.g., refs. 16–18). These results contrast with the view that biome shifts

Table 1. Regional sources of Neotropical biodiversity

Rank	Region	Unconstrained	Stratified
1	Amazonia	2,855	3,674
2	Mesoamerica	615	28
3	Cerrado and Chaco	455	860
4	Atlantic Forests	296	303
5	Andean Grasslands	105	11
6	Patagonian Steppe	81	78
7	West Indies	65	249
8	Dry Northern South America	31	396
9	Caatinga	12	85
10	Dry Western South America	10	134

The ranked values correspond to dispersal events inferred from time-calibrated molecular phylogenies estimated under an unconstrained and a time-stratified biogeographic model of region connectivity (*SI Appendix*, Tables S5 and S6).
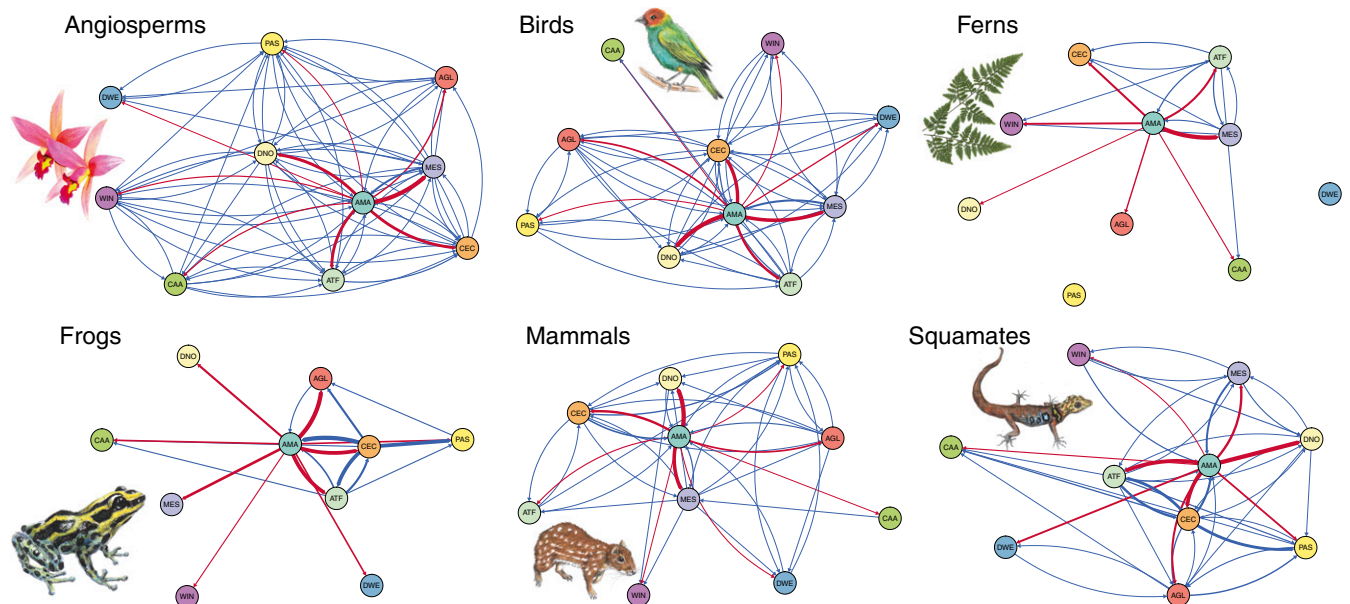
Fig. 3. Clade-specific lineage interchange among Neotropical regions, using the same color scheme and methodology as in Fig. 2. Fern image courtesy of Pixabay/Geralt. Flower image courtesy of Pixabay/821292. Animal images courtesy of Malin Laggren.

over evolutionary time are rare events, as previously demonstrated for Southern Hemisphere plant lineages (19). Among the documented shifts in biome types, most events (86%; *SI Appendix*, Table S6) involved transitions from forested/wet regions into open/dry habitats, rather than in the opposite direction, confirming a previous study on Cerrado plants (21).

We recorded a high interchange of lineages between the rainforests of lowland Amazonia and the Andean Grasslands, mostly located above 5,000 m above sea level (*SI Appendix*, Fig. S20). Although these shifts require substantial eco-physiological adaptations, our results demonstrate that they have played a major role in the assembly of Neotropical alpine ecosystems. Cross-altitudinal dispersal events had been suggested for a few taxonomic groups previously (42–44), but were not considered common. Range shifts along elevation gradients appear to be an important evolutionary process, similar to what was recently documented for Borneo (45).

The inference of a high number of shifts in major biome types could be partly masked by the large spatial scale required by our analyses. All regions and biomes comprise mosaics of different fine-scale habitats, which could have served as entrance pathways to colonizing lineages without requiring immediate adaptations. Further research is needed to assess to what extent dispersing lineages are preadapted to new environments, as opposed to developing new features in situ (28, 46).

It is notable that Amazonia provided more species to Mesoamerica, located on a landmass that has only been connected with South America for a short period of time and along a strait margin, rather than the surrounding dry regions in northern and central-east South America, with which Amazonia shares long borders and multiple transition zones. This result could primarily reflect dispersal events between the Chocó, included in Olson's (47) definition of Amazonia adopted here, and Mesoamerica. A biogeographic analysis using a different expert-based region classification, in which we adopted a more restrictive delimitation of Amazonia, suggests that most interchange indeed involves Amazonia (*SI Appendix*, Fig. S21). Our results corroborate a recent analysis of plot data for rainforest woody plants, which showed a large number of shared species between Panama and eastern Ecuador and concluded that the abundance and environmental tolerance of species were strong predictors of their ability to occupy both regions (48).

Predictors of Interchange. As expected, both the area and total branch length of a region were strongly and positively correlated with emigration (Fig. 5). It is surprising, however, that in our dispersal model including all taxa we found no positive effect of isolation or length of the perimeter on emigration. We expected a higher number of dispersal events between regions that are adjacent and broadly connected, based on theoretical expectations and empirical evidence (28).

The positive relationship between the total branch length and the number of immigration events in a region suggests that Neotropical regions are not yet saturated with species, as would have been predicted under a scenario of competitive exclusion and niche filling (32, 33). Instead, our results reflect patterns of recent invasions of nonnative plants, birds, and fishes, in which regions with the highest species richness are also those with most invasions (34, 35). The relation between species richness and
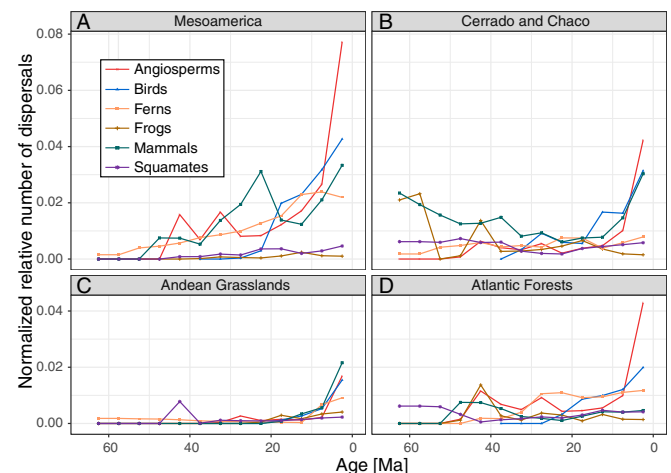

Fig. 4. Taxon-specific interchange between Amazonia and (*A*) Mesoamerica, (*B*) Cerrado and Chado, (*C*) Andean Grasslands, and (*D*) Atlantic Forests throughout the Cenozoic (older events are pruned from the figure but included in the total calculation of events). Dispersal rates are normalized in relation to the number of available lineages in each phylogeny. Age in millions of years ago (Ma).
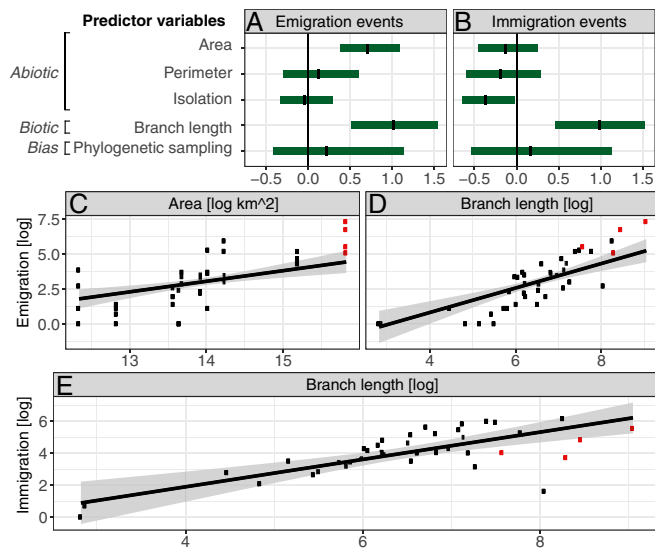
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Fig. 5. Relationship between the number of dispersal events out of a region (emigration) and into a region (immigration), and predictor variables. (*A* and *B*) Regression coefficients of a Bayesian multiple linear mixed effects model calculated based on all regions and clades. (*C–E*) Partial fit of the number of dispersal events for area and cumulative branch length, calculated for all regions and clades except ferns and frogs. The fitted lines show the posterior mean predicted values from the same model, assuming average values for all other predictors, whereas the points show the raw data. Shaded lines show 95% credible intervals. Dispersal events into or out of Amazonia are shown in red.

resilience to invasions may depend on the spatial and temporal scale considered (33, 35), and ongoing invasions are likely also related to the higher human density seen in species-rich environments (34). In addition, the high number of immigrants will, by themselves, also lead to an increase in the total branch length of a region. We also note that branch length sums were strongly correlated to the total number of occurrences in a region, meaning we cannot exclude an undetected effect of sampling biases beyond our measure of phylogenetic sampling.

Comparison Among Organisms. There was a generally high level of congruence in the directionality of dispersal events across taxa (Fig. 3), despite their biological and ecological differences. For instance, all taxa showed a substantial interchange between Amazonia and Mesoamerica, the Atlantic Forests, the Cerrado and Chaco, and the Andean Grasslands. Interchange with the West Indies and the Dry Western South America was low for all groups.

Concerning the timing of interchange with Amazonia (Fig. 4 and *SI Appendix*, Figs. S11–S13), we detected some level of taxonomic congruence (e.g., angiosperms, birds, and mammals increasing in relative dispersal rates with the Cerrado and Chaco and with Dry Northern South America in the last 20 My), but in most cases the fluctuations appear stochastic over time and across taxonomic groups. This reinforces the idea that lineages have individual evolutionary histories and biogeographic origins, and that biotas are the result of repeated interchanges followed by in situ speciation (5).

Conclusions. Our study shows that Amazonia is the primary source of Neotropical biodiversity: not only did it generate enormous in situ diversity but it also provided lineages to all other Neotropical regions, across all studied taxonomic groups, and throughout the Cenozoic. Taken together, our results demonstrate that even very dissimilar regions, in terms of environmental variables and constituent biota, do not evolve in isolation, but are highly biologically interconnected over evolutionary timescales. Biotic interchange can be largely, but not fully, predicted by simple abiotic and biotic variables. The cross-taxonomic framework applied here could be

used to investigate the evolutionary history of many other regions and biotas, to better understand the history of life on Earth.

Materials and Methods

A full description of the methodology used and known limitations of our data and methodology, such as those caused by incomplete sampling of species occurrences and molecular sequences in public databases (49, 50), are described in *SI Appendix, Supporting Methods*.

Data Compilation. We focused our analyses on the Neotropical realm as defined by Morrone (1). Within the Neotropics, we defined and delimited 10 regions, broadly corresponding to environmentally and biologically different terrestrial biomes proposed by Olson et al. (47) (Fig. 1 and *SI Appendix, Fig. S22*). We reconstructed the biogeographic history of two groups of plants (angiosperms and ferns) and four groups of vertebrates (birds, frogs, mammals, and squamates). We downloaded occurrence records for all species from the Global Biodiversity Information Facility (*SI Appendix, Supporting Methods*). We used SpeciesGeoCoder v.1.8 (51) for automated cleaning of the occurrence records. We classified each species as present or absent in each Neotropical region, using an occurrence filter of ≥5% to recognize a species as present in a region (selected to maximize inclusion while minimizing false-positives, after testing for multiple thresholds between 0% and 50%; *SI Appendix, Fig. S23*). We retrieved published large-scale time-calibrated phylogenies for all study groups (see *SI Appendix* for references), from which we extracted predominantly Neotropical clades (≥85% of the species).

Analyses. We use the terms migration and dispersal interchangeably in a biogeographic context, meaning establishment of evolutionary lineages in a new region rather than, for example, annual bird migrations. We do not attempt to differentiate between dispersal and vicariance, that is, the separation of populations by the formation of barriers, which has also contributed to shaping current diversity patterns in the Neotropics (52). We implemented the dispersal-extinction-cladogenesis model (53) in the R package BioGeoBEARS (54) to infer geographical range evolution of lineages. We developed two sets of analyses: one in which biotic connectivity among all regions was allowed at any point in time, and one in which we modeled connectivity based on paleogeographic and geological evidence (*SI Appendix, Table S3*). We identified shifts between regions in 5-My time bins. We computed the absolute number of dispersal events through time by extracting the areas and ages of all nodes from each phylogeny. The number of branches and total amount of branch lengths in any phylogeny of extant species increase with time, potentially increasing the number of dispersal events toward the present even under a constant dispersal rate (55). We therefore also calculated relative numbers of dispersal events by dividing absolute numbers by the total length of all branches within each time bin (37). We tested the dependence of the number of dispersal events estimated for each region on six predictor variables (Fig. 5; excluding one because of high correlation). We tested the covariance of the predictors using the Variance Inflation Factor and Pearson correlations. We fit two linear mixed-effects models with a random intercept, using taxon as random effect in a Bayesian framework. We excluded data from the two taxa with the fewest species sampled (ferns and frogs), as the number of dispersal events was zero for several regions in these clades, and assumed one shift for the remaining

Table 2. Sinks of Neotropical biodiversity

Rank	Region	Unconstrained	Stratified
1	Mesoamerica	788	1,756
2	Dry Northern South America	771	772
3	Cerrado and Chaco	766	806
4	Atlantic Forests	661	723
5	Amazonia	494	458
6	Andean Grasslands	298	509
7	Patagonian Steppe	210	224
8	West Indies	201	213
9	Caatinga	199	202
10	Dry Western South America	137	155

The values correspond to dispersal events inferred from time-calibrated molecular phylogenies estimated under an unconstrained and a time-stratified biogeographic model of region connectivity (*SI Appendix, Tables S5 and S6*).

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