

Amazonia is the primary source of Neotropical biodiversity

Alexandre Antonelli^{a,b,c,d,1,2}, Alexander Zizka^{a,b,1}, Fernanda Antunes Carvalho^{b,e,1}, Ruud Scharn^{a,b,f}, Christine D. Bacon^{a,b}, Daniele Silvestro^{a,b,g}, and Fabien L. Condamine^{b,h}

^aGothenburg Global Biodiversity Centre, SE-405 30 Gothenburg, Sweden; ^bDepartment of Biological and Environmental Sciences, University of Gothenburg, SE-405 30 Gothenburg, Sweden; ^cGothenburg Botanical Garden, SE-41319 Gothenburg, Sweden; ^dDepartment of Organismic and Evolutionary Biology, Harvard University, Cambridge, MA 02138; ^eDepartment of Botany and Zoology, Federal University of Rio Grande do Norte, Natal, RN 59078-970, Brazil; ^fDepartment of Earth Sciences, University of Gothenburg, SE-405 30 Gothenburg, Sweden; ^gDepartment of Computational Biology, University of Lausanne, 1015 Lausanne, Switzerland; and ^hCNRS, ISEM, University of Montpellier, 34095 Montpellier, France

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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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¹A.A., A.Z., and F.A.C. contributed equally to this work.

²To whom correspondence should be addressed. Email: alexandre.antonelli@bioenv.gu.se.

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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).



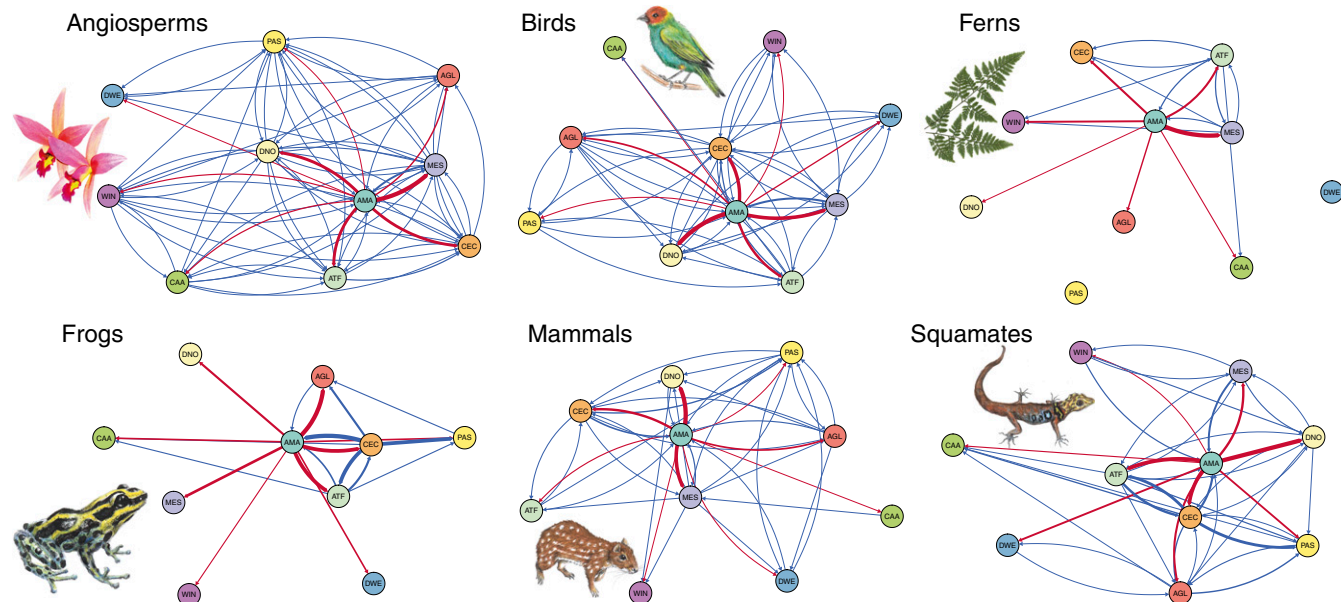
Fig. 1. Neotropical regions used in the biogeographic analyses, grouped by major biome type and plotted together with the abbreviations used for subsequent analyses. These regions are derived from the classification of terrestrial biomes and ecoregions by Olson et al. (48), but adapted to differentiate 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).



three cases with no observed shifts to enable logarithmic transformation. We log-transformed predictors and responses and used a gamma prior with shape 1 and scale 0.5 for the hyper parameters of the random intercepts per taxon.

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