Biogeography: Drivers of bioregionalization

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BIOGEOGRAPHY

Drivers of bioregionalization

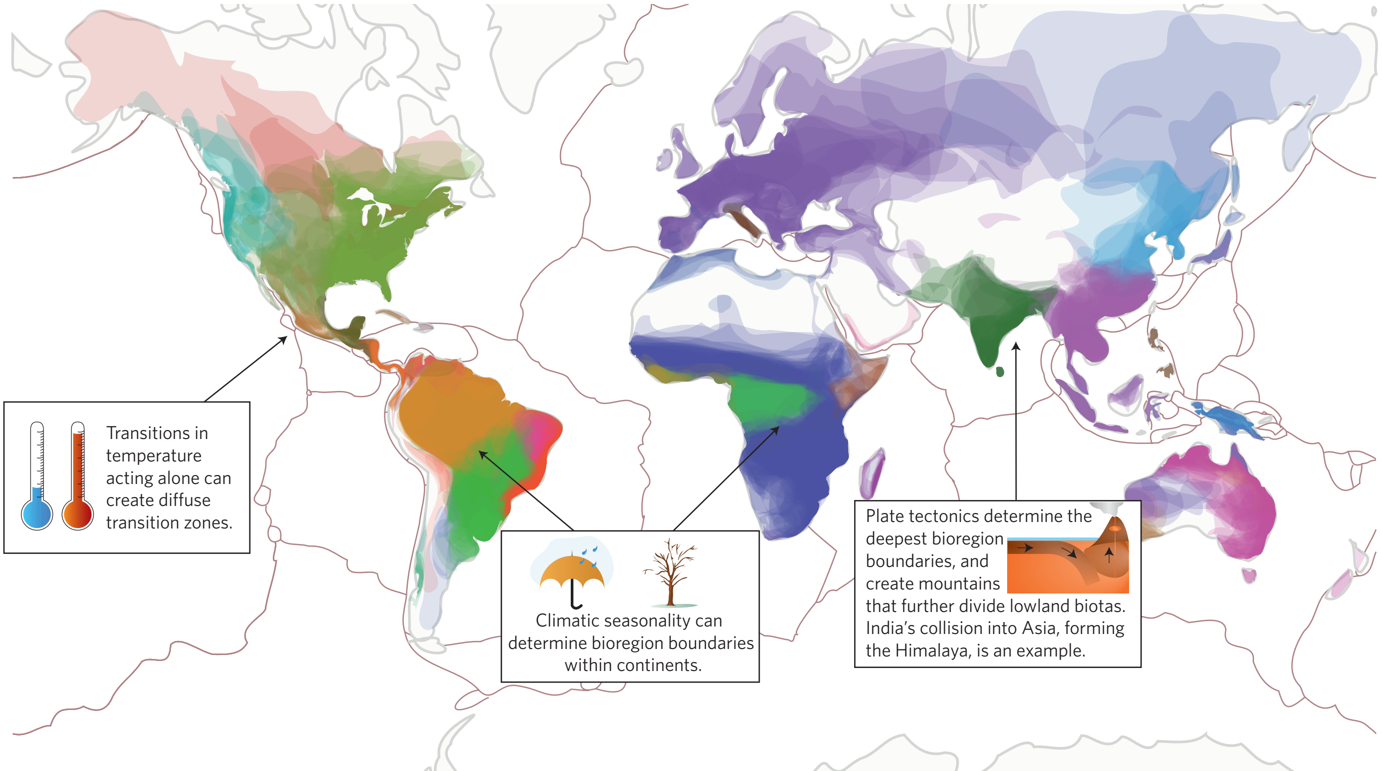
A global analysis finds that tectonics, climate and mountains have jointly shaped the evolution of the world's terrestrial biodiversity into distinct biogeographical regions.

Alexandre Antonelli

Why are there no kangaroos in Asia, no hummingbirds in Africa, and no lemurs in South America? The simplest biological questions are often the hardest to crack. Intrinsic factors are considered crucial, such as organisms' dispersal abilities. For instance, although nearly all of the approximately 2,000 species of cacti are confined to the American continent, a single bird-dispersed species (*Rhipsalis baccifera*) has naturally spread to colonize Africa and Sri Lanka. Yet, environmental conditions also play a role. Place an anaconda in Greenland, and it will certainly not thrive. Penguins, on the other hand, might be able to cope with the Arctic climate and food resources, but they may just not have been able to get there.

Naturalists have long documented major differences in the fauna and flora of different landmasses and regions, including Wallace's famous recognition of six zoogeographic regions[1]. However, explaining these differences has often relied on untested hypotheses. Through a modelling approach and spatial regression analyses based on biogeographical data from a previous study on terrestrial vertebrates[2], Ficetola *et al.*[3] present an explicit test of the main factors suggested to underlie the boundaries of the world's terrestrial bioregions (that is, more or less distinct spatial clusters of co-occurring species). But rather than focusing on intrinsic factors, the authors evaluate the role of major geological and climatic transitions, analysing the extent to which variability in these factors between neighbouring areas is most closely associated with the presence of boundaries. They also assess the determinants of bioregions at different scales — shallow, intermediate and deep — resulting from the bioregionalization analysis.

The first and most important factor determining deep biological separations is continental drift, caused by plate tectonics (Fig. 1). Even now, South America and Africa drift apart about as fast as your nails grow. This may sound slow, but wait a hundred million years and you get



Transitions in temperature acting alone can create diffuse transition zones.

Climatic seasonality can determine bioregion boundaries within continents.

Plate tectonics determine the deepest bioregion boundaries, and create mountains that further divide lowland biotas. India's collision into Asia, forming the Himalaya, is an example.

Figure 1 | Linking geology, climate and biodiversity. The map shows natural ranges of 6,069 amphibian species, coloured by the biogeographical region (bioregion) to which they belong. Plate tectonics, climatic transitions within and among continents, and mountain barriers have together contributed to the formation of bioregions across the globe. Data from https://www.iucn.org/ (amphibian ranges); ref. [9] (bioregion estimations); and ref. [12] (plate boundaries; improved by H. Ahlenius, Nordpil). Figure produced by D. Edler with advice from D. Vilhena.

the Atlantic Ocean in between, and very different bioregions on each side. Such movements have split formerly continuous populations into distinct evolutionary lineages (vicariance), and sometimes the separated landmasses also received long-distance immigrants that lost contact with their ancestors (dispersal). Different rates of speciation and extinction may further increase these differences. With time, landmasses thus develop unique bioregions, such as in Madagascar. The authors also find the pronounced relief in southern Asia to be a further example of major biogeographical transitions directly linked to plate tectonics.

Climate is identified as the second most important factor shaping biogeographical boundaries, especially for intermediate and shallow bioregions — such as those found within continents. Climatic seasonality explains the transition between rainforests and savannahs well in both Africa and South America, where differences in precipitation and temperature interact with differences in fire exposure, soil types and herbivory[3,4]. Their analysis also shows that temperature variation is crucial for explaining biogeographical transitions in the Northern Hemisphere, such as between the Neotropical and the Nearctic realms.

Finally, the authors find that mountains constitute the third most important factor, and one operating strongly at all levels of biogeographical differentiation. When mountains form, they affect biodiversity in multiple ways, fostering the diversification of unique lineages, allowing pre-adapted montane lineages to expand their range, and changing the soil and hydrology of surrounding areas[5]. But perhaps the most obvious influence is that mountains serve as barriers to lowland species. However, these barriers are semi-permeable: good dispersers, such as plants with small seeds and canopy birds, may maintain gene flow and homogenous distributions even across high mountains, while more sessile organisms may soon start developing unique bioregions.

Taken together, these results indicate that continental drift, climatic differences, and mountain chains interact to determine the boundaries of bioregions. If only one or two of these are in play, biotas can still differ but their limits will be more diffuse and ‘transition zones’ may form. Interestingly, the authors found no noticeable effect of Quaternary climatic changes on the boundaries of bioregions, further suggesting that current patterns evolved over millions of years and in connection with geological and climatic events.

It is somewhat surprising that despite a renewed interest in bioregions triggered by the increasing availability of species distribution data, so little effort has been put into understanding the processes underlying the patterns. For instance, bioregions are often described as ‘nested’ — realms comprise biomes that comprise ecoregions[6]. This structure is reminiscent of phylogenetic trees, in which major trunks (kingdoms) lead to increasingly smaller branches and leaves (families, genera, species). But contrary to phylogenies, whose branching is the result of well-understood evolutionary mechanisms, the evolution of bioregions remains an understudied and underappreciated topic in biology.

Another question to be answered is how general bioregions are. Ficetola *et al.*[3] analysed the determinants of terrestrial vertebrate bioregions, but other organisms — such as plants, fishes, microorganisms and fungi — have very different biology and evolutionary histories, and could therefore show different patterns. It would also be interesting to conduct similar studies on marine bioregions. If we want to understand the general determinants of biological organization, we should not forget less-studied organisms.

Finally, identifying bioregions and delimiting their boundaries is still far from straightforward. Although Ficetola *et al.*[3] argue that different bioregionalization methods produce consistent results, other studies have found substantial differences[7–9]; finding the ‘optimal’ number of bioregions for any dataset is still largely arbitrary, although innovative solutions from, for example, information theory are emerging[10]; and no methods are yet able to identify the robustness of particular boundaries to reflect data availability and resolution[11], in a similar way as phylogenetic trees have support values for individual clades.

The study by Ficetola *et al.*[3], although correlational, represents an important advance, brought on by their global focus and statistical approach. But perhaps most importantly, their results raise a number of new questions that will hopefully boost the community’s interest in the field of bioregionalization. ❐

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Competing interests

The author declares no competing financial interests.