

REVIEW

Building mountain biodiversity: Geological and evolutionary processes

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Mountain regions are unusually biodiverse, with rich aggregations of small-ranged species that form centers of endemism. Mountains play an array of roles for Earth's biodiversity and affect neighboring lowlands through biotic interchange, changes in regional climate, and nutrient runoff. The high biodiversity of certain mountains reflects the interplay of multiple evolutionary mechanisms: enhanced speciation rates with distinct opportunities for coexistence and persistence of lineages, shaped by long-term climatic changes interacting with topographically dynamic landscapes. High diversity in most tropical mountains is tightly linked to bedrock geology—notably, areas comprising mafic and ultramafic lithologies, rock types rich in magnesium and poor in phosphate that present special requirements for plant physiology. Mountain biodiversity bears the signature of deep-time evolutionary and ecological processes, a history well worth preserving.

Mountains are topographically complex regions formed by the interplay of tectonic and volcanic processes. They are intrinsically unstable systems, undergoing substantial changes in response to tectonic, erosional, and climatic processes over geologically short time scales. The interaction of mountain substrates, life forms, and climate systems—at a range of spatial scales—establishes diverse and distinct montane environments (1–4). These environments are transient, and their ongoing changes drive the splitting and subsequent isolation of species ranges, evolutionary adaptation to changing conditions, and consequently, population differentiation. These biological processes create a shifting balance between speciation and extinction, in which mountains may act as “cradles” (areas of especially rapid species origination), “museums” (areas of especially long-term persistence of species), and “graves” (areas with especially high rates of extinction) for biodiversity (1, 5). The high levels of richness and endemism of species on most mountains thus reflect enhanced speciation, coexistence, and persistence of evolutionary lineages with distinct evolutionary trajectories.

Mountain regions, especially in the tropics, are home to aggregations of small-ranged species (6) that form highly diverse centers of endemism. These aggregations cannot be predicted from underlying global patterns of species richness (7) or by models that are based purely on contemporary ecological conditions (3). One possible explanation is that statistical models have not adequately captured the high spatial heterogeneity of ecological and environmental variables characteristic of mountains (3). However, current mountain diversity may also bear the signatures of deep-time evolutionary and ecological processes, driven by changing climate over topographically complex landscapes and by biotic interchange with neighboring areas (1, 5, 8). The fluctuating dynamics of mountain speciation, evolutionary adaptation, dispersal, persistence, and extinction may ultimately explain diversity patterns across entire continents.

Geological dynamics are increasingly recognized as a key driver of these evolutionary processes, influencing the buildup (and sometimes decline) of mountain diversity (1, 2, 4). The fossil record allows robust analyses of how species diversification in mountain landscapes has been affected by the break-up and merging of lithospheric plates, in the context of plate tectonic processes (9, 10), and by changes in global temperature (11). Linking biogeographical dynamics to detailed reconstructions of mountain formation has become increasingly feasible through such analyses (10). Here, we discuss how evolutionary processes associated with climate history, orogenic processes, and the geological composition of mountain regions shape large-scale geographical patterns of species diversity.

Key roles of mountains for biodiversity

Over long periods of time, topographic, geological, and geophysical conditions modify the rates

and properties of four key processes that determine the distribution and diversity of life on Earth: speciation, dispersal, persistence, and extinction (Table 1). The emergence of the Andes, for example, influenced plant diversification and evolution in South America in at least four different ways: (i) by creating a region of novel, high-elevation habitats for species; (ii) as a dispersal barrier to lowland organisms, splitting populations east and west of the mountain range, as well as internally in valleys and peaks; (iii) as a north-south corridor for species dispersal; and (iv) as a modifier of environmental, hydrological, and mineralogical conditions in the rest of the continent, through montane effects on the climate system and as a source of mineral components released by continued erosion and weathering (12, 13).

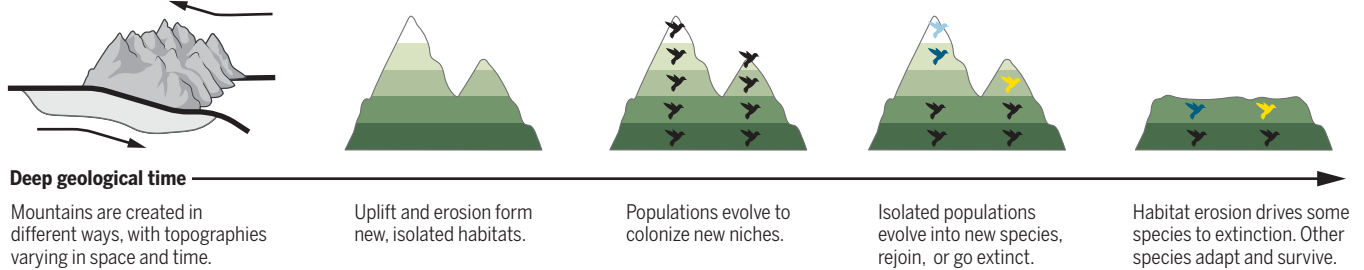
The impact of mountain regions on biodiversity extends far beyond their topographical limits, often affecting entire continental biotas. For example, although the Andes region is in itself the most biodiverse region on Earth, Andean orogeny is also considered a key driver for the buildup of biodiversity across all of South America (13). Over roughly the past 10 million years, Andean orogeny has changed the regional topography repeatedly, forcing the Amazon drainage basin to change its course. These changes altered gene flow across the Amazonian lowlands, affecting both terrestrial and aquatic biogeography (14). Mountain regions may also play a role as sources of new evolutionary lineages that later colonize lowland regions. Phylogenetic and biogeographical reconstructions reveal an Andean origin for many Amazonian species, including plants (12), amphibians (15), and tanagers (16).

The influence of specific mountain ranges on the biodiversity of broader regions and entire continents depends on their geographical location, spatial orientation, local biotic context, and history (2). Thus, the European Alps, oriented east-west, have been recognized as refugia for cold-adapted species but provide insufficient habitat connectivity to enable the persistence of many late-Neogene lineages in Northwestern Europe through the Pleistocene (17). By contrast, the north-south-oriented Rocky Mountains have facilitated latitudinal range adjustments, providing dispersal corridors during fluctuating climates and boosting the persistence of North American Neogene populations and species through Pleistocene glacial-interglacial climate cycles (18). These processes are often cited to explain why the tree flora of Western Europe is so depauperate in comparison with the tree flora of North America (18).

The influence of mountains likely differs among taxonomic groups. Speciation in plants, for example, often reflects adaptations to particular soil geochemistry and mineralogy (19). In birds, speciation may be more susceptible to the breakup of species ranges that follow narrow elevational habitat bands. These include shifts in the tree line and the cloud forest belt (20) and the fragmentation of geographic ranges by major rivers (21). For invertebrates, many speciation events are

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A Orogeny—Creating new species over millions of years



B Dynamic changes in connectivity—Speciation driven by mountain climate cycling

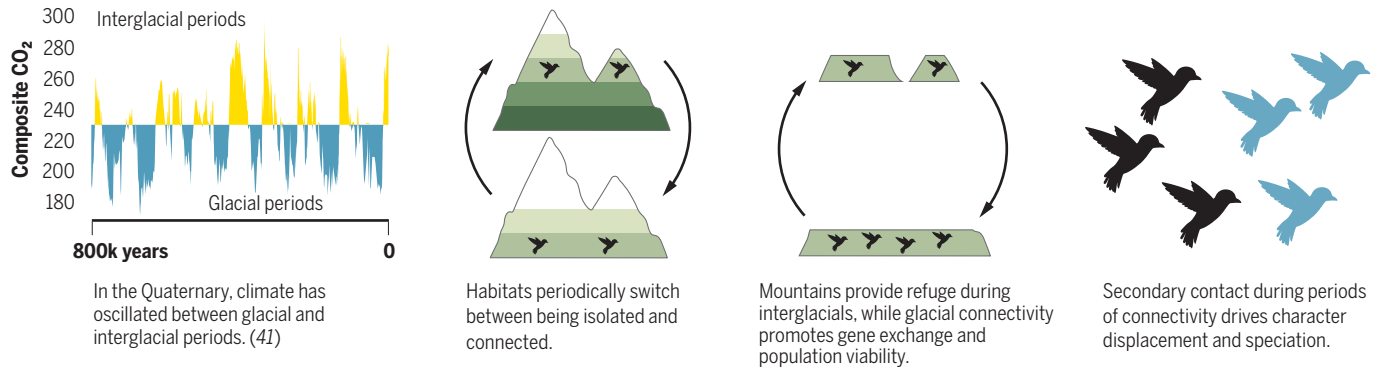


Fig. 1. Schematic view of two temporal scales of buildup of mountain diversity. (A) Mountain ranges are tectonically dynamic over millions of years, leading to isolated changing environments and the long-term adaptation of species colonizing these new habitats. (B) Climatic dynamics in the Quaternary, induced by Milankovitch orbital cycles, caused habitats and climatic zones to move up and down mountain slopes, repeatedly, on the scale of tens of thousands to hundreds of thousands of years. These movements led to rapid, repeated dynamics of range splitting and secondary contact, stimulating diversification. [Graph at left is based on publicly available data (41).]

likely to follow plant specialization linked to the production of specific metabolites.

Evolutionary processes in mountains

Mountains are hotbeds of speciation, influenced by geological and climatic dynamics over deep time. Mountains can form during both compression and stretching of the lithosphere. Orogeny—mountain building—typically includes tectonic stacking of lithosphere domains of diverse age, origin, and composition, including upducted ocean floor, emplacement of intrusive magmatic bodies, and building of surface volcanic structures. Mountains are thus lithologically and topographically heterogeneous regions. Evolutionary radiations of species are often associated with phases of active uplift, suggesting that orogenic processes play a role in driving diversification (Fig. 1A) (14, 22, 23), principally through the recurrent formation, connectivity, and disappearance of habitats within mountain ranges (Fig. 1A) (24). Orogenic dynamics, including surface uplift and formation of intermontane basins and subsequent erosion, create shifts in hydrological catchments, river flows, and nutrient fluxes. These processes change soil composition and nutrient levels, driving adaptation of plants and their associated biota in new habitat types. Mountain formation also affects local climate,

creating zones of rain shadow or persistent mist, with a strong filtering effect on species communities (2).

During the past ~2.6 million years, the climatic cyclicity of the Quaternary has impelled dynamic shifts in habitat connectivity that stimulated speciation in certain groups (Fig. 1B) (25). These changes are linked to the Milankovitch eccentricity cycle, with a periodicity of around 100,000 years, possibly amplified by the ~41,000-year obliquity cycle, and are further thought to instigate cyclic, climate-driven habitat changes that drive temporally rapid “species pumps” (10, 25, 26). Vegetation belts moved upslope during warm and wet interglacials, leading to the fragmentation of populations and genetic divergence. As temperatures dropped again in glacial episodes, vegetation belts moved downslope, forcing secondary contact of populations, leading to founder effects, disruptive selection, and character displacement, thus creating the conditions classically associated with allopatric speciation. In a process-based simulation model of range dynamics in South America, Rangel *et al.* recently found support for these predictions, with the Andes acting as an episodic species pump (Fig. 1B) (5).

At large spatial and temporal scales, these processes can yield very different distributions of species, some that descended from ancient,

isolated lineages and some that originated from recent radiations. The relative contribution of these two groups to mountain diversity varies greatly among mountain regions [compare Fig. 2 with (3), figure 3]. Badgley *et al.* defined specific, testable predictions from three (nonexclusive) models for the occurrence of radiations in topographically complex landscapes: (i) Active tectonic dynamics drive speciation, (ii) speciation is constantly elevated in the habitat mosaic of topographically complex areas, and (iii) climate-driven immigration stimulates speciation (4). In an empirical study of North American rodents, Badgley and colleagues found some support for the first and third scenarios (4). In a recent global analysis, Antonelli *et al.* also found a substantial effect of mountain relief on species diversity, although with relatively weak effects of erosion and erosive potential, which are otherwise formative influences within geologically dynamic landscapes (2).

Mountains—Cradles, museums, or graves of diversity?

Stebbins (27) famously asked whether species diversity in the tropics is so high because the tropics are cradles (areas of especially rapid species origination) or museums (areas of especially long-term persistence of species). Other

metaphors have since been added (Table 1), including the notion of graves to describe geographical areas with especially high rates of extinction. Identification of graves from contemporary distribution data or fossils remains elusive. However, their existence, location, and timing have been predicted with process-based simulation models (28) of geographical range dynamics through time, driven by simulated paleoclimates (5).

For the most diverse tropical mountains, it appears that the answer to Stebbins's question is that mountains are both cradles and museums (Fig. 2C) (29). To exemplify, the Andes not

only are home to several recently diversified species clusters with high phylogenetic relatedness but also host many old, relictual lineages aggregated in centers of endemism (30). The combination of both cradle and museum effects appears crucial to the emergence of the Andes as the most diverse region on Earth (3).

Whereas the Andes have high numbers of both early divergent and recently derived species, the mountain regions of Southeast Asia are primarily occupied by species that are recently derived (Fig. 2). A plausible explanation for these regionally distinct patterns is that tropical mountain ranges with very high peaks and more rugged

terrain, such as the Andes and Southeast Asia, are home to a high-elevation biota characterized by a small number of lineages adapted to colder environments. These few lineages may become regionally very species-rich as a product of rapid, local diversification (31). In the Andes, this process may have occurred more repeatedly than in Southeast Asia. By contrast, the Afrotropical regions and the Atlantic Rainforest mountain region of South America both show a greater predominance of early divergent species.

In a simulation of temporal range dynamics of the South American biota, cradles derived from Andean founders (each simulation began with one initial "seed" species) were found to be concentrated along the Andean slopes, whereas graves tended to be at lower elevations in the upper Amazon Basin (5). By contrast, biotas derived from Atlantic Forest founders had a much higher spatial coincidence of cradles and graves. These results align with the view that topographic complexity and elevational climate gradients promote range fragmentation and act as cradles, while at the same time acting as museums by providing climatic refugia from extinction (5, 26, 32). The simulations also revealed that the spatial positions of cradles, museums, and graves can be dynamic, changing shape, size, and intensity over time and in response to Quaternary climate cycles (5). These temporal and spatial dynamics imply that inferring cradles or museums on the basis of the current distributions of extant young and old lineages may be misleading.

Geological heterogeneity and biodiversity

The potential importance of mountain geology, including the mineralogical composition of substrates, has been highlighted in recent work (1, 2, 4). Mountain substrates generally differ substantially from those of surrounding lowland basins, which are frequently dominated by eroded materials derived from the mountains and deposited in valleys and plains. Mineral composition and nutrient levels in the soil affect plant physiology, vegetation composition, primary productivity, and consequently, species diversity. In addition, mountain regions with a high level of geological heterogeneity are likely to support higher levels of species spatial turnover and local endemic forms, particularly among plants. However, empirical studies that establish a relationship between diversity of edaphic conditions and plant species diversity are scarce, and little is known about how edaphic heterogeneity affects diversity at higher trophic levels.

In a recent global analysis, which also confirmed the classic correlation of species diversity with topographic relief and climate (3, 33, 34), Antonelli and co-workers found correlations of species richness of mammals, birds, and amphibians with both long-term and short-term erosion rates and a measure of soil diversity (2). Although the association was generally weaker than the correlation of richness with climatic variables, soil heterogeneity was consistently a significant predictor of richness across multiple

Table 1. Proposed biogeographical roles of mountains, the key processes involved, their underlying mechanisms, and examples of outstanding research questions.

Role of mountains	Process	Mechanism	Exemplar questions
Cradles	Speciation and diversification	Fragmentation of species ranges, with potential for local adaptation of populations	What drives adaptive diversification in mountains, and how important is nonadaptive speciation?
Innovation hubs	Adaptive radiation	Adaptive response of isolated populations in a heterogeneous environment to local selection	Do higher environmental ultraviolet levels directly affect mutation rates? Do localized, distinctive soils generate speciation cascades?
Elevators	Dispersal (passive)	Passive movement of species and their substrates from lowlands caused by surface uplift	How can we differentiate between passively uplifted species and those actively dispersed?
Corridors	Dispersal (enhanced)	Continuous linkage of similar highland habitats	What are the relative contributions of local recruitment versus long-distance dispersal to high-elevation biotas?
Barriers	Dispersal (blocked)	Vicariance of lowland species, preventing further gene exchange	How can we test this hypothesis, given uncertainties in paleoclimatic models, molecular data, and geological reconstructions?
Reservoirs	Maintenance	Persistence of species during climate change by tracking their climate niche through elevational range shifts	How do species persist on mountains with limited possibility for elevational migration or discordant shifts in temperature and precipitation?
Refugia	Maintenance	Mountains acting as sources to restock lowlands after episodes of climate-driven extinction	How representative is the Last Glacial Maximum for the role of mountains as refugia in the context of previous glaciations?
Museums	Maintenance	Collapse of once-larger ranges, leaving remnant populations in favorable mountain microclimates	How important is climatic and topographic complexity for the persistence of lineages?
Sinks	Extinction	Local extirpation due to patchy habitat availability	How does the role of sinks vary with latitude?
Graves	Extinction	The failure of species to disperse to suitable climates or adapt, under changing conditions	How important will mountaintop extinctions be, compared with human-induced landscape changes?

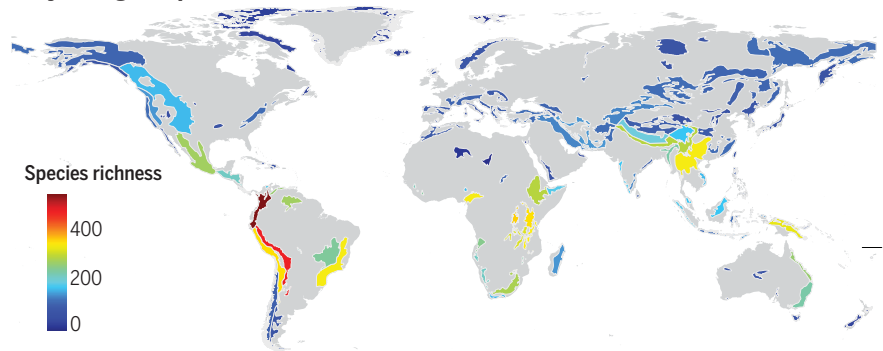
biogeographical regions of the world. Antonelli and co-workers suggested that soil heterogeneity underlies fine-scale habitat turnover, creating new habitats and ecological opportunities, increasing local and regional species richness. In Fig. 3, we further explore the relationship between species diversity and bedrock heterogeneity, as measured by the number of major categories of bedrock that are represented within each mountain region.

Geological heterogeneity, simplified in this way, does not explain much of the variation in total species richness and fails to account for the high richness of small-ranged species that is characteristic of mountains at low latitudes [compare Fig. 3A with (3), figure 3]. This disconnect may imply that the way rock classes translate into ecologically relevant soil properties is substantially more complex than captured by our simple classification. An ecologically relevant special case is the presence or absence of mafic and ultramafic rocks (Fig. 3C). Soils originating from ultramafic rocks have a well-described effect on plant adaptations and diversity. Their unusual geochemistry, with high magnesium content and low availability of phosphorus (35), demands specific adaptations and slows growth rates for plants. The vegetation of serpentine soils, which form on ultramafic bedrock, is highly specialized and generally woody, with high levels of phenols and lignin in leaves, driving secondary effects on the cycling of nutrients in the decomposition of leaf litter. Serpentine soils pose strong selective filters for plants, excluding many groups but fostering radiations of clades that tolerate these soils (36). Ultimately, habitat heterogeneity, patchiness, and specialized dietary adaptations of herbivores may impel speciation cascades in these habitats across all major groups of organisms, including vertebrates.

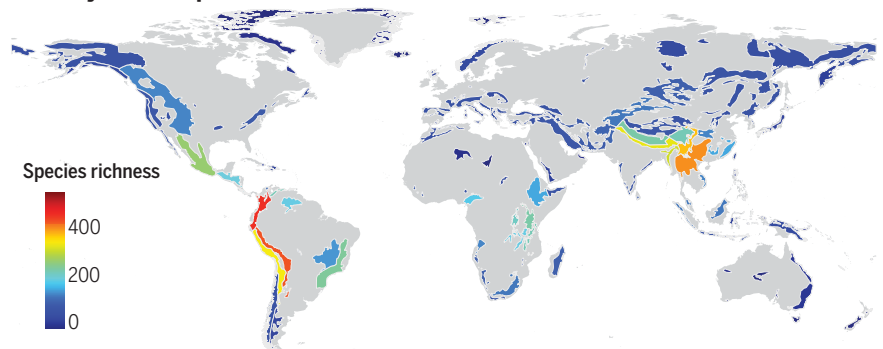
Mapping the global occurrence of larger, contiguous mafic and ultramafic rock domains in mountain regions (Fig. 3B) reveals that all hyperdiverse mountain regions are rich in such rocks. Intercalated mafic and ultramafic rock domains often form part of ophiolites, slivers of oceanic lithosphere upducted and emplaced within continental orogens during plate collision. Emplacement of ophiolites is thus an integral part of the orogenic processes that form cordilleran mountain chains. Ultramafic and mafic rock, mostly associated with ophiolites, underlie >5% of the dark red area in Fig. 3B.

Almost all the most biologically diverse mountain regions have three features in common: high rock diversity, presence of upducted oceanic lithosphere, and a geographical location in the humid tropics (Fig. 3C). By contrast, mountains with low rock diversity and without ultramafic components, even in the mesic tropics, tend to be relatively species-poor. Mountain regions without oceanic lithosphere components show little relationship between biodiversity and rock diversity, regardless of climatic zone. Understanding the geochemical contrast between continental and oceanic lithosphere components may thus be key to understanding how bedrock geology

A Early divergent species



B Recently derived species



C Overlap

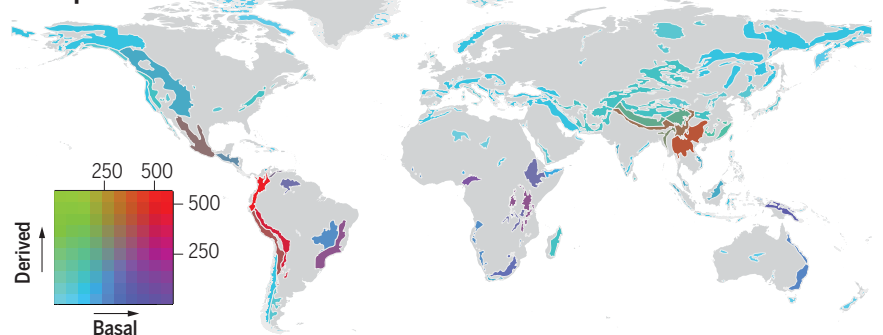


Fig. 2. Global richness pattern of early divergent and recently derived species in mountain regions.

(A) The number of early divergent birds, mammals, and amphibians, defined as the 25% of species that are separated from the crown node of their class in the molecular phylogeny by the smallest, ranked node distance. (B) The number of recently derived species among the 25% with the largest, ranked root distance from the crown node. (C) The overlap of early divergent and recently derived species reveals which mountain regions represent museums (purple), cradles (green), or both (red). Light blue areas have low richness of both groups. Distribution and phylogeny data are from Holt *et al.* (42), and mountain regions are as defined in Rahbek *et al.* (3). The classification into early divergent or recently derived was done independently for each class, and values for all three classes were added to give the depicted total.

might influence the production and maintenance of species richness.

The high turnover of distinct habitat patches created on geologically heterogeneous surfaces, even within the same local climate, might contribute substantially to the process of population-splitting and differentiation that characterizes mountain speciation dynamics. Plant characteristics on soils derived from emplaced ultramafic rocks may also pose challenges for herbivorous

animals. Soil geochemistry affects plant metabolism and may increase the production of secondary metabolites, with plants on these soils investing heavily in chemical and physical defenses against herbivores. Such adaptive challenges facing the plant-dependent fauna may stimulate a higher rate of adaptive divergence among consumers during phases of population isolation and thus precipitate locally extremely high rates of diversification, as seen in nectarivores

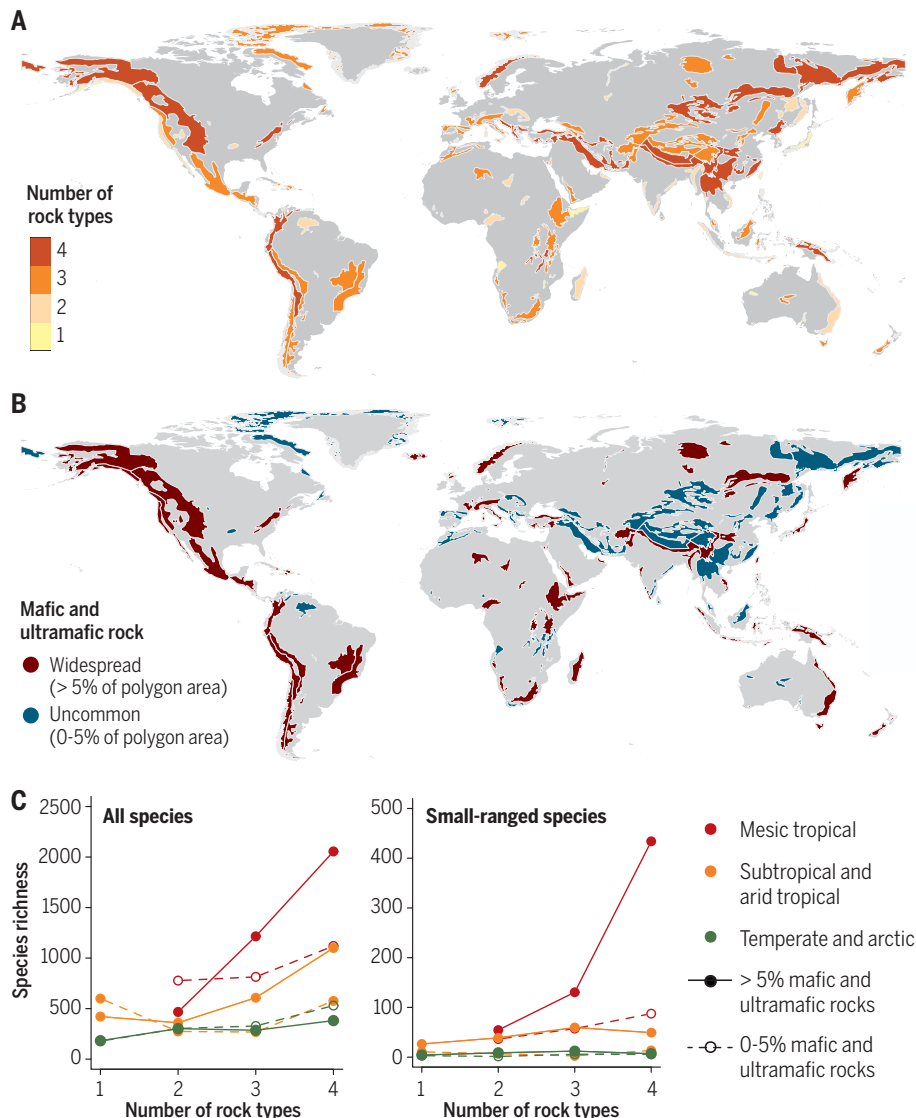


Fig. 3. Mountain geology and vertebrate diversity. (A) Geological diversity, quantified by categorizing rocks on the basis of mineral composition and depositional setting, and counting the number of categories occupying at least 5% of the area of each mountain region. Categories are (i) siliciclastic and (ii) carbonate sedimentary rocks, (iii) metamorphic rocks, and (iv) felsic and (v) mafic igneous rocks. The map shows counts, not categories. (B) The occurrence of mafic and ultramafic rocks, most commonly derived from upducted oceanic lithosphere in mountain regions. Soils formed on these rocks have distinct geochemical properties that require specialized plant metabolism. (C) Richness of all species and of the 25% of species with the smallest ranges, for mountain regions, as a function of geological diversity, climate band, and the widespread occurrence of mafic and ultramafic rocks. Points show the mean value for each category. The richest mountain regions of the world are geologically diverse mountains in the tropics with ultramafic rocks. Mountain regions follow Rahbek *et al.* (3), and the geological data were compiled from sources at <http://onegeology.com>.

(such as hummingbirds) and frugivores (such as New World sparrows and tanagers).

Concluding perspective

The idea that geology and biology are intertwined runs as a consistent undertone in von Humboldt's *Cosmos*, expressed as his “unity of nature” (37). Later, in 1880, Wallace inferred the recurrence of glaciations in Earth's history from the distribution of related animal species

on islands in the Indo-Pacific (38). Although much research has been stimulated by these early works, the lack of data and robust analytical frameworks has long hampered efforts to fully incorporate biological and geological processes into rigorous statistical models for mountain species diversity and evolution (2).

New methods in geomorphology—including stable isotope altimetry, thermochronology, and advances in digital multispectral imaging (39)—

are paving the way for accurate reconstructions of geological dynamics, thus creating a strong foundation for testing evolutionary theories on the origin and maintenance of mountain diversity over time. Combined with genomic sequencing, these approaches may allow inference of the timing, and perhaps even the location (by using environmental ancient DNA), of changes in effective population sizes and genetic bottlenecks. The next generation of geologically and evolutionarily explicit models may, in this way, radically change our understanding of biotic evolution and resolve the historically contentious debate over the extent to which ecological and evolutionary processes, historical contingency, or simply stochasticity and time shape the diversity and distribution of life on Earth.

The idea that heterogeneity in geological substrate properties may directly affect evolution is still based primarily on circumstantial evidence, supported by statistical patterns with weak or mixed correlations with diversity (as in Fig. 3) (1, 2, 4). Quantifying the specific geological variables that are biologically relevant and distinguishing topographic from geochemical effects remain open challenges for establishing causality. Alternative, process-based explanations should be sought in the interactions between individual mountain regions and other components of the Earth system, especially the atmosphere and the oceans. An emerging conjecture is that mountains are hubs of innovation to such a degree that Earth's biodiversity would have been completely different in the absence of high mountain regions. For example, do mountains in the tropics provide exceptional environmental conditions that encourage fixation of mutations and drive localized adaptive change in plants, in turn driving speciation cascades (the speciation of one group leading to speciation in other groups)? Flenley suggested that the higher ultraviolet B levels on tropical mountain peaks might directly affect DNA, causing a high rate of mutation and leading to evolutionary innovation (40). According to this hypothesis, climatic warm periods that drive species upslope, such as interglacials, should be followed by increased levels of speciation.

A growing consensus holds that models that explicitly incorporate geological and ecological dynamics must take as their starting point the holistic view that all of these processes, acting at different temporal and spatial scales, shape contemporary patterns of biodiversity. The looming challenge is to incorporate these insights within a unified model that generates predictions that can be tested with independent data.

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