

Geological and climatic influences on mountain biodiversity

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Mountains are key features of the Earth's surface and host a substantial proportion of the world's species. However, the links between the evolution and distribution of biodiversity and the formation of mountains remain poorly understood. Here, we integrate multiple datasets to assess the relationships between species richness in mountains, geology and climate at global and regional scales. Specifically, we analyse how erosion, relief, soil and climate relate to the geographical distribution of terrestrial tetrapods, which include amphibians, birds and mammals. We find that centres of species richness correlate with areas of high temperatures, annual rainfall and topographic relief, supporting previous studies. We unveil additional links between mountain-building processes and biodiversity: species richness correlates with erosion rates and heterogeneity of soil types, with a varying response across continents. These additional links are prominent but under-explored, and probably relate to the interplay between surface uplift, climate change and atmospheric circulation through time. They are also influenced by the location and orientation of mountain ranges in relation to air circulation patterns, and how species diversification, dispersal and refugia respond to climate change. A better understanding of biosphere-lithosphere interactions is needed to understand the patterns and evolution of mountain biodiversity across space and time.

Lithosphere dynamics, including exhumation, surface uplift and relief development, as well as related climate change and variability, create diverse environments in mountain regions (Box 1). Mountain building establishes topographic heterogeneity and creates new habitats where species evolve and diversify^{1,2}. It also provides nutrients to surrounding lowlands, increases sediment delivery and heterogeneity of soil types, affects local and regional climates, facilitates the establishment of immigrant species, leads to *in situ* speciation, and serves as a source of new species to neighbouring areas^{3–7}. At the same time, biome changes linked to orogeny⁸, such as formation of unique montane forest types, grasslands or alpine vegetation, feed back into climatic and tectonic processes^{9,10}. Biological and geological processes are therefore closely linked, although precise causal mechanisms remain elusive.

Recent advances in the study of Earth surface processes include stable-isotope palaeoaltimetry^{11,12} and continued growth of thermochronometric techniques that can constrain the rate and timing of mountain building and their demise¹³. These advances parallel

new methods and increasingly larger public databases that allow the estimation of how and where species are distributed¹⁴, and when and under which conditions they originated and diversified^{15–17}. Macroevolutionary, genetic and stable isotopic methods, coupled with growing datasets on species distributions, soil types, palaeoaltimetry and climate, constitute an unprecedented opportunity to explore how geological and evolutionary processes have interacted during Earth's history^{18,19}. Present-day global and regional species richness patterns (Box 2) are highly correlated with contemporary climate, especially temperature and precipitation variables, meaning that warm and wet climates generally sustain the highest species richness^{20,21}.

Species richness is also greater in heterogeneous environments, such as those comprising many soil types and varied topography^{22–24}. Correlative analysis of present-day climate and environmental heterogeneity can explain 50–70% of the variation in regional and global plant and animal species richness^{21,25}. Furthermore, strong correlations between climate and biodiversity are not only

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Box 1 | Mountain building, climate and erosion

Mountains can be defined as landforms that rise prominently above their surroundings, generally exhibiting steep slopes, a relatively confined summit area, and considerable local relief⁶³. When ruggedness is taken as a measure, mountains from all continents except Antarctica make up around one-tenth of the Earth's surface and host about one quarter of all terrestrial species³⁹. The topographic diversity of mountain systems and their shape (linear, plateau, high or low) depend on their tectonic and climatic history, position in relation to the continental interior, passive or active margin, or if they are formed by volcanism^{64,65}.

Advances in the field of thermochronology now enable geoscientists to quantify the timing and rates of erosion and exhumation—and thus estimate relief formation—around the globe⁶⁶. The movement of rock towards the Earth's surface can be measured within minerals that preserve the timing of when thermal boundaries in the upper 10 km of the crust were crossed. This and other recent techniques make it possible to quantify global long-term erosion patterns with sedimentary records of Neogene–Quaternary age^{49,66,67}. Only recently¹³ have global data on the timing and rates of erosion and relief formation become available for biodiversity researchers. Global palaeoaltimetric data, however, are still scarce for many of the important centres of biodiversity.

Macroecological studies have shown that the key features linking high biodiversity to mountains are orographically enhanced precipitation, the elevational and climatic gradient, and environmental heterogeneity^{1,20,22}. Mountains have an important effect on climate through their orographic barrier effect. As such, they interfere with global atmospheric circulation patterns, including the position of the Intertropical Convergence Zone, leading to increased precipitation on the slopes facing the charged air masses, and a rain shadow on the lee side (for example, the Andes^{68,69}). This process affects the taxonomic composition and vegetational belts along slopes, with species on the wet slopes being moist-adapted and those in the rain shadow being drought-tolerant. Furthermore, the geographic location and orientation of mountains in relation to atmospheric circulation patterns, including the position of monsoons, also influence biotic distribution⁷⁰.

The elevational (and climatic) gradient in mountains consists of a decrease in temperature and air pressure at increasing elevation^{41,71}. In the tropics, the elevational gradient is particularly strong, as first documented by Humboldt and Bonpland⁷². Taxa that are commonly known from the temperate and arctic zones sometimes occur here at high elevation. Finally, environmental heterogeneity includes all biotic (land cover, vegetation) and abiotic (climate, soil, topography) variables²⁴.

evident today^{26–28}, but have probably existed for millions of years^{29–31}. However, many important geological processes and variables have not yet been comprehensively assessed in terms of their influence on global and regional species richness³².

Quantifying long-term processes that underlie biodiversity patterns and dynamics is challenging. Such processes include species diversification and dispersal, long-term landscape evolution and climatic history^{1,18,28,33,34}. In addition, observed biodiversity–environment relationships are often scale dependent (Box 2), and are stronger for species with large geographical ranges than for small-ranged species whose distributions are more closely linked to topographic heterogeneity than to climatic factors^{35,36}. Narrowly distributed species, sometimes endemic to a single mountain or valley, are a key feature of the high diversity of mountain regions. Since most of those species are inferred to have originated in situ³⁷, they strengthen the case for mountain building in generating high biodiversity^{1,38}.

Here, we explore links among mountain biodiversity, geology and climate. Many of the world's centres of animal and plant diversity today occur in mountain systems, which show contrasting orientations and locations within the continental interior (Fig. 1a). We evaluate this apparent correlation with several geological, climatic and biological datasets, and quantify the relative importance of climate, erosion rates, topography and soil heterogeneity on species richness. We focus our analyses on amphibians, birds and mammals, whose global species distributions are comparatively well known (Fig. 1b) in contrast to those of plants, fungi, invertebrates and other organisms. These tetrapods also constitute adequate models since their temporal evolution occurred during or after the formation of many mountain systems, and experienced major climatic changes: the most recent common ancestors of amphibians, mammals and birds date back to c. 323 million years ago (Ma), 177 Ma and 111 Ma, respectively¹⁵ (www.timetree.org; accessed 13 April 2018). We find that relief, erosion rates and soil heterogeneity are strong predictors of species richness in mountains and conclude that geological processes are essential for understanding the evolution and distribution of biodiversity at global and regional scales.

Global determinants of mountain biodiversity

We compiled a global dataset at 1° resolution of the distribution of terrestrial tetrapod diversity (Fig. 1b), as well as eight predictor variables (see Table 1). These variables capture aspects of climate (precipitation, temperature and their seasonality) and geology (topographic relief, long-term erosion, current erosion potential and heterogeneity of soil types). We used these variables as predictors in statistical models to explain spatial variation in tetrapod species richness (the response variable) within and across mountain regions worldwide (see Supplementary Table 1 for details and expected biological importance of each variable). We included grid cells that contained statistically sufficient data points for the geological information and intersect with the global delimitation of mountains³⁹. We used multiple regression models to explain spatial variation in tetrapod species richness as a function of the eight predictor variables. See Methods and Supplementary Information for details on data compilation and analyses.

For climatic variables, the global analysis shows that mean annual temperature and total annual precipitation are the two most important predictors of tetrapod species richness in mountains (Fig. 2a), although there is substantial variation among individual regions (Fig. 3). Annual temperature range has a slightly less prominent but still important role. Both temperature and precipitation exert a positive effect, that is, most mountain species are found in places with high rainfall and warm temperatures (Fig. 2b, c). The relationship with species richness is linear for temperature and logarithmic for precipitation, with species richness increasing rapidly up to c. 500 mm rainfall per year, and a slower increase after c. 1,000–1,500 mm per year (Fig. 2b). These results support previous studies suggesting that temperature and precipitation (which largely determines water availability to the vegetation and their associated biota) are key factors for latitudinal and elevational gradients of species richness for terrestrial tetrapods^{21,40,41}.

Beyond climate, our analyses provide a first quantitative assessment of the relative importance of several geological factors in explaining variation in the species richness of tetrapods across the world's mountains. Topographic relief, heterogeneity of soil types

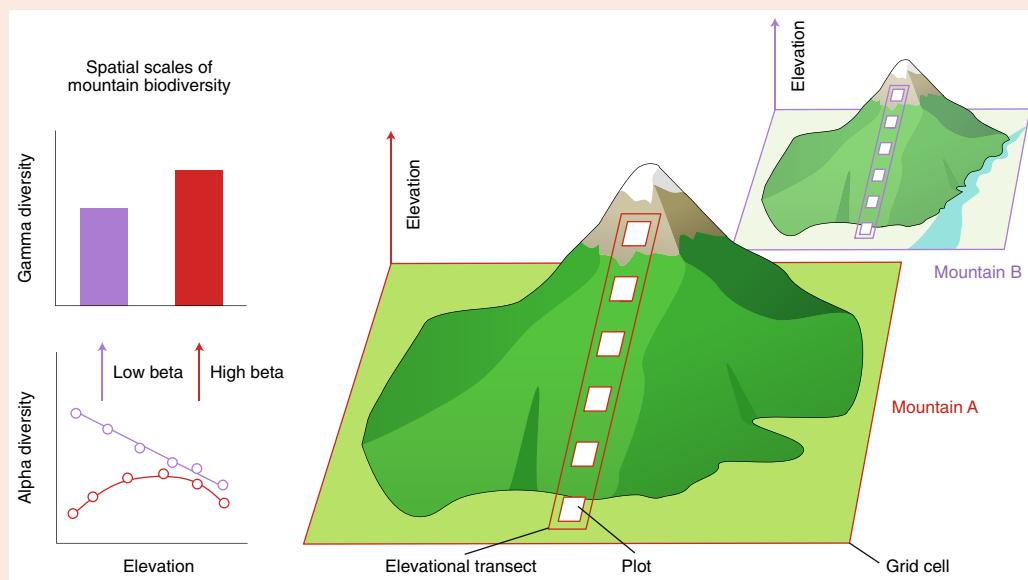
Box 2 | Mountain biodiversity

Biological diversity (biodiversity) describes the variation of life at all levels of biological organization⁷³. Among several available biodiversity measures, the most commonly used is species richness, a count of the number of species in an area. While species richness treats all species equally, other biodiversity measures such as (phylo)genetic and functional diversity⁷⁴ consider the evolutionary relatedness and the differences in morphological, physiological and phenological traits of species in a community⁷⁵. All patterns of biodiversity strongly depend on the spatial scale at which they are measured, which is particularly important for mountain regions (see Box 2 figure).

Biologists often differentiate among alpha, beta and gamma diversity⁷⁶. Alpha diversity refers to the species richness measured at small spatial scales, such as plots, transects and mountain tops. Beta diversity describes the change in species composition over space, for example, from one plot or one community to another⁷⁷. Gamma diversity is the number of species in a larger spatial unit, for example, in an entire mountain range or a grid cell (as used in this study).

Different data sources can be used to study patterns of mountain biodiversity: (1) range maps are polygons that depict the extent of occurrence of a species, usually drawn by experts for

a particular taxon (as for the mammal and amphibian distribution data used in this study). However, range maps are only available for a limited number of organisms, including tetrapods³⁸ and a few plant groups⁷⁸. Range maps usually have a continental or global extent, but they are analysed at a coarse resolution (for example, $1^\circ \times 1^\circ$ grid cells) because they tend to predict false presences at finer resolution due to variation in landscapes and habitats. (2) Species inventories, which are lists of species in a given area (for example, a national park or reserve), allow reliable comparisons of species richness, endemism and other dimensions of biodiversity among regions²⁵. Their spatial resolution (that is, area covered) varies, typically from 0.5 hectare plots to national parks (or even countries), but is typically finer than those of range maps. (3) Georeferenced species occurrences from natural history collections and observations comprise hundreds of millions of records in public databases (such as www.gbif.org, www.mol.org and www.mountainbiodiversity.org). This data source has the finest resolution (with uncertainty in the range of metres to kilometres), but is prone to uneven sampling and several sources of bias⁷⁹. Species occurrence records are the basis for species distribution models, which estimate the geographical distribution of individual species based on environmental associations⁸⁰.



The relationships among alpha, beta and gamma diversity in mountain systems. In each of the mountains depicted, an elevational transect containing six inventory plots yields six measures of alpha diversity (lower graph). When the species found among plots of the same transect vary a lot (high beta diversity; red transect), the total diversity estimated for the mountain (gamma diversity) is generally also high (upper graph).

and long-term erosion rates are statistically significant predictors in the global model (Fig. 2e). The relationships with topographic relief and number of soil types (Fig. 2f, h) are positive, probably reflecting a larger available niche space for species in environmentally heterogeneous regions²⁴. The weak negative relationship between long-term erosion rate and species richness (Fig. 2g) might suggest that excessive erosion disturbance over the long term hampers the carrying capacity of the landscape for maintaining rich ecosystems and their associated animal species, although the observed patterns may result from a complex and multi-directional interaction of processes⁴² (Box 1). These relationships demonstrate

how environmental heterogeneity, geology, climate and species richness are related and interact with each other.

Regional assessments

Around the world, mountain ranges have different geological histories, spatial configurations and orientations in relation to atmospheric circulation patterns (see Fig. 3a and Supplementary Information for a characterization of the mountain systems surveyed here). These differences determine temperature gradients, patterns of orographic precipitation, seasonality of precipitation, relief, soil types, runoff, erosion and associated sediment

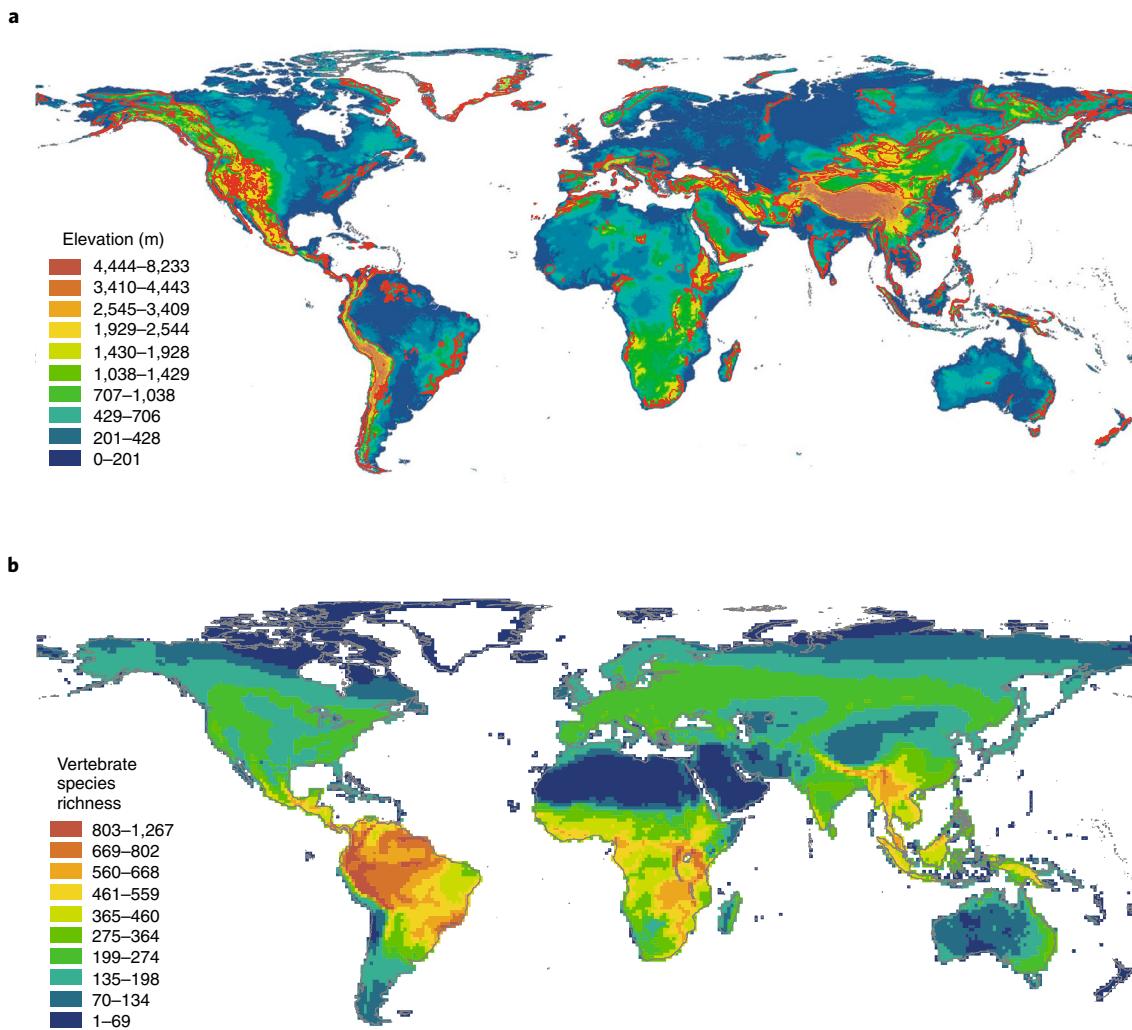


Fig. 1 | The world's mountains and patterns of biodiversity. **a**, Mountain regions (outlined in red)³⁹ plotted on a high-resolution (ca. 1 km) digital elevation model of the Earth⁶¹. The Greenland ice sheet is plotted in white. **b**, Biodiversity illustrated as the number of species of terrestrial tetrapods (amphibians, birds and mammals) present in 1° grid cells^{14,45,62}. Maps are plotted with natural-breaks classification and a World Geodetic System projection (WGS 1984).

evacuation^{43,44}. As a result, and because mountain ranges vary considerably in surface area, they occupy different geological and climatic spaces (Supplementary Figs 1–4). In addition, mountains form in different biogeographical settings, with different levels of pre-existing biodiversity and within different regional species pools⁴⁵. Hence, species may respond differently to the abiotic environment in different regions, and determinants of species richness at the global scale may therefore differ from those at regional scales. We accommodated this complexity through separate analyses of mountain regions for which statistically sufficient data for all geological and biological variables were available (Fig. 3a): the North American Cordillera, the Andes, central Europe, High Asia and Australia.

Climate. In all regional models (Fig. 3b; Supplementary Figs 5–9), climatic variables are the strongest predictors of species richness, but with varying importance and sometimes contrasting effect. Mean annual temperature and total annual precipitation are together the strongest predictors of richness for the Americas and Australia, whereas in Europe—a region with a reduced spatial gradient of annual temperature and precipi-

tation—the highest species richness occurs in cells with high monthly temperature variation and precipitation seasonality. In Asia, all climatic variables interact, but temperature range is marginally the strongest predictor, with a negative effect on species richness. This negative relationship between species richness and temperature range in High Asia probably reflects a latitudinal gradient from temperate to tropical climates (as in the Andes), whereas the positive relationship in central Europe might reflect mainly longitudinal climatic variation. Regional variation in species richness often declines with increasing precipitation seasonality, except for the Andes where a longitudinal orographic barrier is particularly strong, with a wet northeast side supporting high diversity and a dry central-western side with low diversity.

Geology. In all regions, geological variables are statistically significant predictors of species richness, and as with climate there are large regional variations (Fig. 3b; Supplementary Figs 5–9). Topographic relief (reflecting heterogeneity in local elevations) is the strongest predictor in the Americas and Australia but is replaced by current erosion potential (measured as unit stream

Table 1 | Climatic and geological predictor variables used for analysing tetrapod species richness at 1° resolution across the world's mountains

Abbreviation	Description ^a	Unit
Climate		
PREC	Annual precipitation	mm year ⁻¹
TEMP	Mean annual temperature	°C × 10
TEMP RANGE	Annual temperature range (maximum temperature of warmest month minus minimum temperature of coldest month)	°C × 10
PREC SEASON	Precipitation seasonality: coefficient of variation of monthly values	mm
Geology		
RELIEF	Topographic relief measured as mean of elevation range values (max-min) within 2.5 km radii for each 90 m resolution pixel	m
LONG EROSION	Average long-term erosion rate during the last 12 Myr calculated from low-temperature thermochronology	km Myr ⁻¹
EROSION POT	Current erosion potential calculated as USP index weighted with precipitation data	W m ⁻¹
SOIL	Number of soil types	Count

USP, unit stream power. ^aSources of data and biological importance of each variable are provided in Supplementary Table 1.

power index) in Europe and Asia (albeit with opposite direction of effects). Soil heterogeneity is the only significant variable across all regional models, being the strongest geological predictor in Europe, always exerting a positive effect on species richness (implying a higher diversity with increasing number of soil types). Long-term erosion is only regionally significant in Australia, which is also the oldest orogen analysed here.

Linking patterns to processes

Our results, combined with the current literature, support strong associations between mountains and biodiversity. But to fully understand the patterns identified here, we need to investigate how changes in the abiotic environment influence species richness through time (Fig. 4).

The formation of mountains drastically transforms previously homogenous and geologically static landscapes, often characterized by having mature soils, low erosion rates, old relict species and low speciation rates (Fig. 4a).

As land surfaces lift up due to rock uplift exceeding erosion, either through tectonic or volcanic processes, this leads to high and transient relief. Orographic rainfall may form on the windward side and create a rain shadow on the leeward side. Vegetation belts characterize elevational gradients and reflect local precipitation. Fine-scale habitat and soil heterogeneity develop, creating novel habitats and ecological niches. Range expansions and dispersals across vegetation belts often lead to local adaptations and speciation in resident lineages^{37,46}. A large surface area and wide range of available habitats facilitate the establishment of immigrant lineages from surrounding lowlands and other mountains (for example, flying birds or bats and the seeds they carry), further increasing species richness⁵. Over millions of years, these processes generally lead to a concentration of species at low to middle elevations, and a decrease in species richness towards mountain peaks⁴¹ (Fig. 4b).

When rock uplift is surpassed by erosion, mean elevation (and relief) begin to decrease, and so do species richness and the heterogeneity of the geological variables examined here. Erosion and relief formation is accelerated by global climatic fluctuations (including glacial–interglacial periods) that promote changes in glacier extent, river runoff and sediment evacuation. The formation of valleys and glaciers splits previously connected populations, which may go locally extinct or survive in refugia. The secondary contact of populations from previously isolated valleys increases with the resulting vegetation changes during interglacials⁴⁷, leading to further in situ speciation⁴⁸. Surface processes related to glaciations, especially those that characterize the Plio–Pleistocene period, may greatly reshape the overall relief^{43,49} (Fig. 4c).

Finally, rock uplift completely ceases, mountains decay and montane habitats disappear due to continued erosion. This process is similar to what happens when volcanic islands and their biota subside⁵⁰. Entire populations can also be annihilated by rapid stochastic events, such as landslides, which are particularly common during periods of deglaciation⁴⁹. Many species go extinct, in particular those that are ecological specialists or confined to particular montane habitats (Fig. 4d). Note that Fig. 4 represents a generic model and does not illustrate the temporal evolution of a single mountain or a particular region. Large regional variation exists in how mountains and their biodiversity evolve. In some cases, mountainous topography can persist for hundreds of millions of years after the end of tectonic deformation⁵¹.

Looking ahead

To further encourage the integration of geological and biological sciences, we need additional research that integrates both biotic and abiotic parameters. From biology, increased data at higher resolution on current and past species distributions and biodiversity patterns are crucial, focusing on poorly explored areas and less-studied taxonomic groups, such as invertebrates along elevational gradients in tropical mountains⁵². It is also important to understand species' characteristics (that is, ecological traits and biotic interactions) because these influence species coexistence, persistence and extinction⁵³, affect responses of species to environmental gradients, and determine their functional role in ecosystems⁵⁴. Beyond taxonomic and functional analyses, an exciting field with high potential is the study of the evolutionary history of organisms and the analysis of phylogenetic diversity⁵⁵, which will demand large and concerted sequencing efforts⁵⁶ but will enable the testing of geological hypotheses using high-resolution biological data, especially when supplemented with data from the fossil record⁵⁷.

Opportunities for the Earth sciences are equally manifold. We highlight the need for integrating Earth surface processes and tectonic studies with phylogenetic and palaeontological analyses to evaluate competing hypotheses with respect to the timing of surface uplift^{57,58}. We need Earth surface and tectonic models that address imminent biogeographical questions across spatial and temporal scales^{58,59}, including drainage reorganisation and its impact on terrestrial aquatic organisms⁶⁰. We also need to establish robust palaeoaltimetry reconstructions and accurate erosion-rate histories, extending over tens of millions of years, and taking into account topographically induced changes in the global climate system, such as changes in atmospheric circulation¹¹. These advancements will shed further light on the effects of geomorphic processes on biodiversity, including the tempo and dynamics of species adaptations to landscape changes, geographic range evolution, biotic turnovers and causes of extinctions.

In conclusion, we urge geoscientists to enhance their efforts in understanding links between biotic processes and changes in topography,

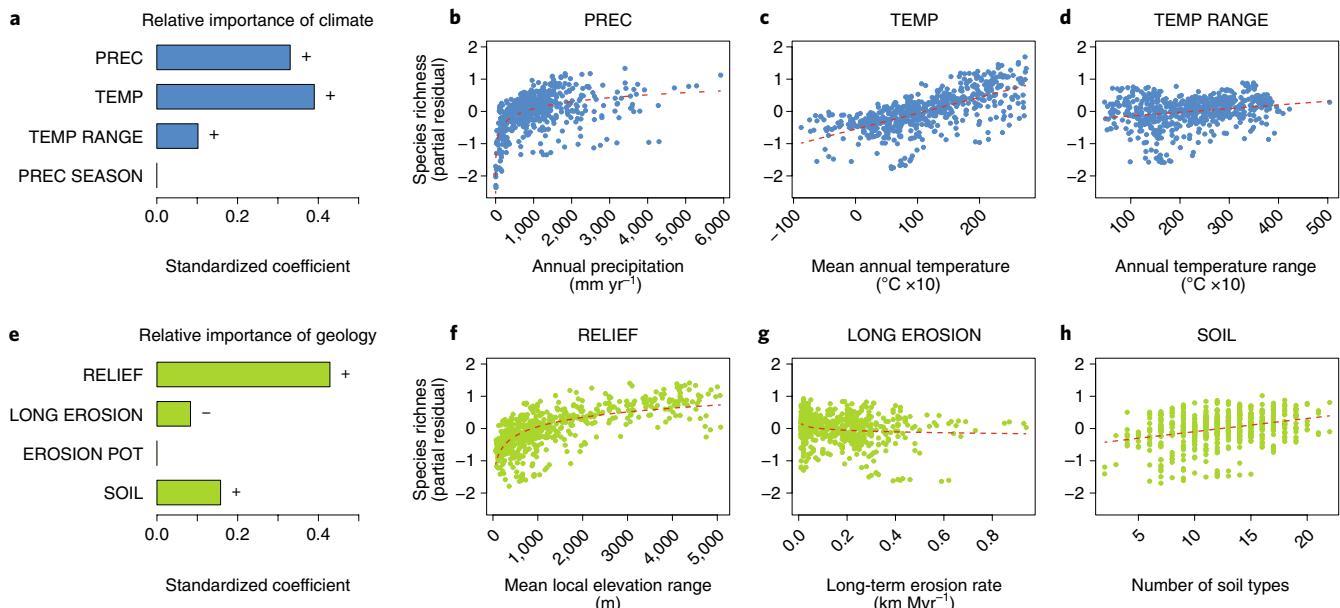


Fig. 2 | Global determinants of biodiversity across the world's mountains. **a–d**, Relationships between climatic predictor variables and species richness of tetrapods from the global multi-predictor model across 1° grid cells ($n = 585$) within mountain regions³⁹. **e–h**, Relationships between geological predictor variables and species richness of tetrapods. Relative importance plots (**a,e**) present standardized coefficients of predictor variables (the direction of effect is indicated as + or -). Partial residual plots of climatic (**b–d**) and geological (**f–h**) predictor variables represent the relationship between a response and a predictor variable when all other predictor variables in the model are statistically controlled for. See Table 1 for definitions and abbreviations of predictor variables.

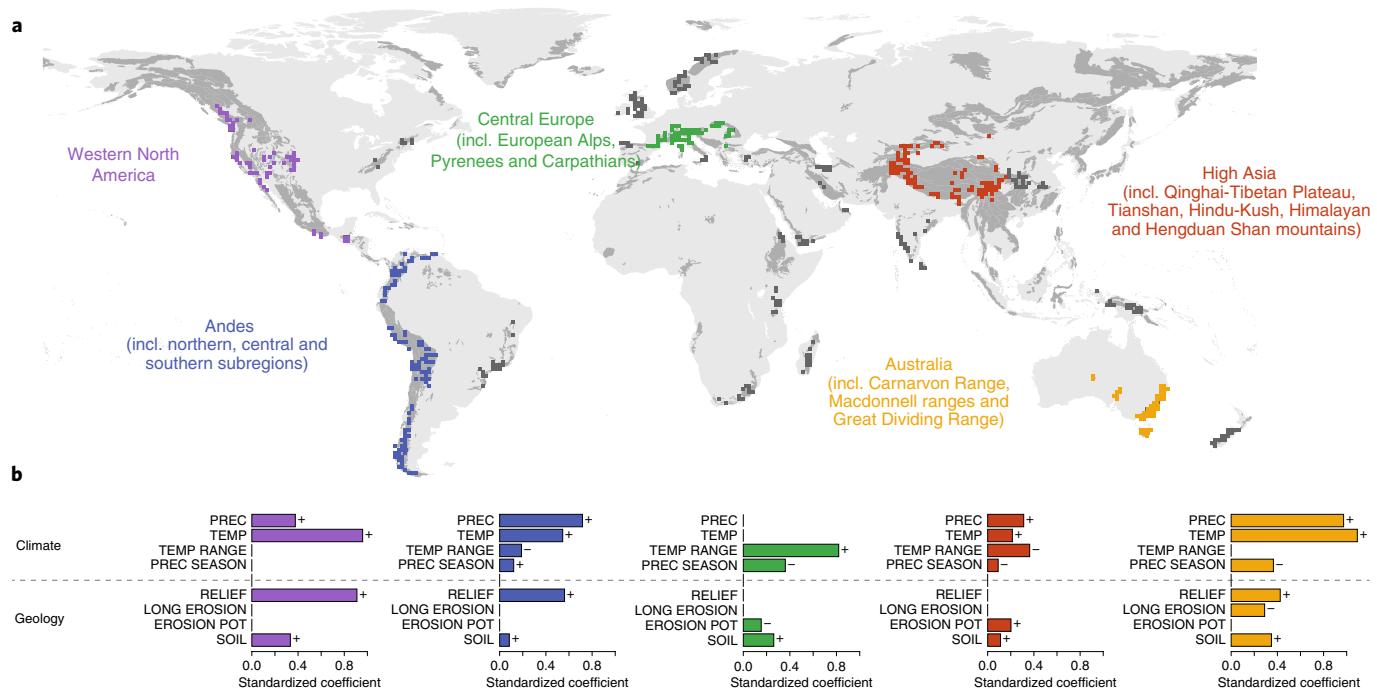


Fig. 3 | Regional determinants of mountain biodiversity. **a**, The five mountain regions with sufficient sample sizes ($n \geq 50$ grid cells at 1° resolution) representing the Northern and Southern Hemispheres, different orientations and locations of mountain ranges and different climate zones. Grid cells coloured dark grey were only included in the global analyses. **b**, Results from regional analyses illustrating the relative importance of climatic and geological variables in explaining species richness of tetrapods. The direction of effect is indicated as + or -. See Table 1 for definitions and abbreviations of predictor variables.

erosion and atmospheric circulation through time, and biologists to include Earth surface processes and palaeoaltimetry data into diversification and macroecological models. Integrating approaches and data

from biology and geosciences into a common research framework is still in its infancy, but undoubtedly opens new research avenues for understanding the distribution and evolution of life on Earth.

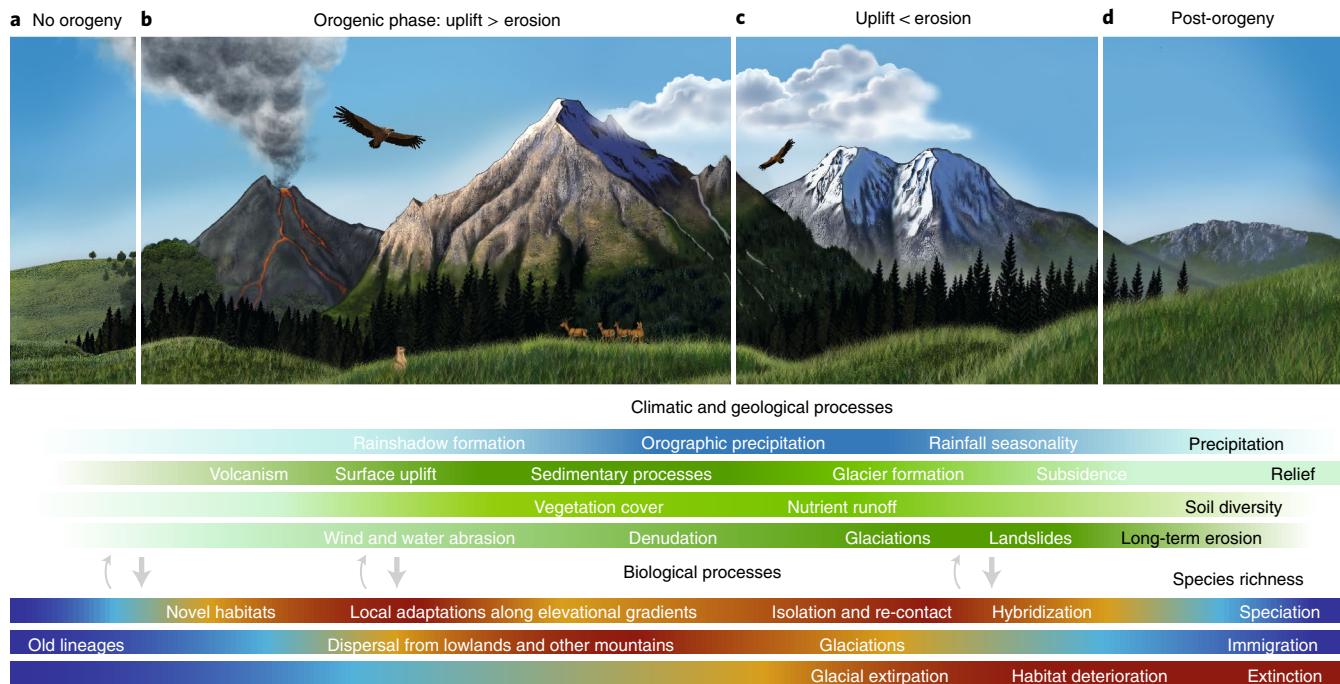


Fig. 4 | Linking the evolution of mountains and biodiversity. **a-d**, Climatic (blue bar) and geological (green bars) variables influence species richness through speciation, immigration and extinction (lower bars) through different orogenic phases. Darker/warmer and lighter/colder colours in the bars indicate high and low levels, respectively. As the arrows indicate, climatic and geological processes exert the strongest effects on species richness, but some feedback exists (such as plants colonizing bare rocks and increasing erosion, and animals affecting soils through burrowing). See section ‘Linking patterns to processes’ for a description and discussion of the different phases, and Supplementary Fig. 11 for more details. Figure courtesy of I. Voet, University of Montpellier.

Online content

Any methods, additional references, Nature Research reporting summaries, source data, statements of data availability and associated accession codes are available at <https://doi.org/10.1038/s41561-018-0236-z>.

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Author contributions

C.H., A.A. and A.M. initiated the project; A.A., C.H., W.D.K. and S.G.A.F. coordinated the work and led the writing with contributions from M.A.B, A.M., A.N.M.-R., H.K., H.P.L., C.B., J.F., S.A.F., C.R., F.H. and H.H.; C.R. provided access to the bird data; S.G.A.F, M.A.B and S.A.F compiled, cleaned and standardized all data; W.D.K. performed all analyses.

Competing interests

The authors declare no competing interests.

Additional information

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Methods

Species distribution data. All distribution data of terrestrial tetrapods were compiled at $1^\circ \times 1^\circ$ latitude-longitude grid cells⁴⁵. The global range maps of virtually all amphibians (6,086 species) and non-marine mammals (5,148 species) were based on the International Union for Conservation of Nature (IUCN) Global Assessment distributional data for native geographic ranges⁸¹. Breeding distributions for 9,650 non-pelagic species of bird were extracted from a comprehensive global distribution database for all birds⁶². Geographic ranges represent a conservative extent-of-occurrence of the breeding areas of species, based on museum specimens, published sight records, expert opinion and spatial distributions of habitats.

Predictor variables. We used a total of eight predictor variables (Table 1 and Supplementary Table 1) that we considered of potential relevance for predicting species richness of tetrapods in the world's mountains. The variables reflected climate (annual precipitation, annual temperature, temperature annual range and precipitation seasonality) and geology (topographic relief, long-term erosion rate, current erosion potential and number of different soil types). These predictor variables are described in more detail below, and an overview with data sources is provided in Supplementary Table 1.

Climate. We used the CHELSA climate dataset⁸² (version 1.2, available at <http://chelsa-climate.org/>) at 30 arc sec resolution, which includes the monthly mean temperature and precipitation patterns for the time period 1979–2013. Climate variables (PREC, TEMP, TEMP RANGE, PREC SEASON) were extracted as mean values per $1^\circ \times 1^\circ$ grid cells using the zonal statistics in the Spatial Analyst extension of ESRI ArcGIS version 10.3 (ref. ⁸³).

Topographic relief. To quantify topographic heterogeneity, we measured relief (RELIEF) as the range of elevation values (max–min) within 2.5 km radii surrounding 90 m resolution pixels of the EarthEnv-DEM90 (ref. ⁸⁴). We used the zonal statistics in the Spatial Analyst extension of ESRI ArcGIS version 10.3 (ref. ⁸³) and obtained the mean of those relief values within each $1^\circ \times 1^\circ$ grid cell.

Erosion rates. We calculated erosion rates at two different timescales. The first one reflects long-term erosion (LONG EROSION), that is, acting on geological (>1-million-year) timescales, which are defined as the average rate of erosion for a period of time >100 thousand years ago. The second variable reflects the current erosion potential (EROSION POT), which is measured on a human (1–10-year) timescale and is eventually overridden by long-term erosion.

The calculation of erosion rates is not straightforward, as it relies on particular assumptions depending on the source data, mountain location, and associated flexural and thermal parameters. Several alternative approaches and datasets have been presented, such as cosmogenic isotope-derived millennial-scale erosion rates⁸⁵, which although potentially suitable for our purposes, only cover a small subset of the data points for which we could obtain all other necessary variables (Supplementary Fig. 10). After some initial exploration, we decided to use a global compilation of thermochronometric data to estimate LONG EROSION, applying a formal inversion approach designed to interpret spatially distributed data^{13,86}. The objective of this approach is to formally invert spatially distributed thermochronometric data into maps of erosion rates back in time. This method exploits the information contained in both age-elevation profiles and multi-thermochronometric systems strategies and accounts for the conductive effects of topography on the underlying isotherms.

We assessed the influence of temporal changes of erosion rates using the dataset of Herman et al.¹³ for time intervals 0–2 Ma, 2–4 Ma, 4–6 Ma, 6–8 Ma, 8–10 Ma and 10–12 Ma. In our dataset (Fig. 3a), all long-term erosion rates for a specific time interval were highly correlated with each other and with the average long-term erosion rate (Spearman rank correlation $r > 0.90$). We therefore only present results using the average long-term erosion rate for the interval between 12 and 0 Ma (in km Myr⁻¹; LONG EROSION in Figs. 2–3, Supplementary Table 1). It is not possible to extend beyond 12 Ma without introducing a considerable degree of uncertainty¹³. This global point dataset was spatially joined to the globally distributed grid cells in ESRI ArcGIS 10.3 (ref. ⁸³) to derive the mean for those erosion values within each $1^\circ \times 1^\circ$ grid cell.

For the calculation of current erosion potential (EROSION POT), we used the unit stream power (USP) as a proxy for present-day erosion rates. In general, predictions of the intensity of erosion can be estimated using the erosion-index approach^{87,88}. The erosion index can be calculated in different ways as a function of stream power, which is the rate of potential energy expenditure by flowing water. This concept has been used extensively in studies of erosion, sediment transport, and geomorphology as a measure of the erosive power of rivers and streams^{89,90}. Stream power is commonly described as the capacity for flowing water to carry out geomorphic work⁹¹. It is a gravitational potential energy that acts as the driver for the fluvial system. This energy is converted into kinetic form through the downslope flow of water, where any energy lost due to falling must be converted into another form⁹². This transformed energy has the potential to erode channel beds or transport sediments. For our purpose, we calculated the short-term erosion rate as USP following refs ^{87,93}. We incorporated the average precipitation from

1998 to 2009 obtained by the Tropical Rainfall Measuring Mission (TRMM)^{94,95}. A Spatial Join in ESRI ArcGIS 10.3 (ref. ⁸³) was used to integrate these erosion values as a point dataset with the $1^\circ \times 1^\circ$ grid cells dataset.

We acknowledge that there are several general limitations when using cooling ages to infer erosion rates and how they vary with time. For instance, erosion rates derived from a single thermochronometer depend heavily on knowledge of the Earth's crust thermal field. In most cases, the thermal field is poorly known and a thermal model must therefore be used. This limitation can in part be circumvented by collecting samples at different elevations (in which case the slope of the relationship between age and elevation provides an estimate of the exhumation rate) or using thermochronometers with different closure temperatures. Furthermore, a thermochronometric age only provides an estimate of the erosion rate integrated over the time defined by its apparent age. Caution should therefore be taken when comparing observations made across different timescales and locations.

Soils. We obtained an estimate of soil heterogeneity (SOIL) per grid cell, calculated as the number of soil types present in each $1^\circ \times 1^\circ$ grid cell as derived from a recent global dataset of soil information⁹⁶. The data were obtained by using the FTP interface (<ftp.soilgrids.org/>) to access the 1-km global grid of soil data based on the World Reference Base (WRB) for soil resources⁹⁷. We used the variable that describes the taxonomic group of the WRB classification, version TAXGWRB_02_apr_2014. For each grid cell, the number (variety) of different soil groups was calculated using the ESRI ArcGIS Spatial Analyst tool⁸³.

Statistical analysis. *Global dataset.* A total of 585 grid cells was available for the global analysis. These grid cells intersect with the global delimitation of mountains³⁹ and contain information on all variables, that is, tetrapod species richness, climate and geology. These grid cells cover all major mountain regions of the world (Fig. 3) and show a large variation in tetrapod species richness, climate and geology (Supplementary Table 2).

Regional datasets. For the regional analyses, sample sizes (that is, number of 1° grid cells) were smaller than in the global dataset because regions represent a subset of the global pool (Fig. 3). To yield sufficient statistical power, we applied a minimum sample size of ≥ 50 grid cells, which resulted in the analysis of five regions: western North America representing the North American Cordillera ($n = 60$); the Andes, including the northern, central and southern subregions ($n = 108$); central Europe, including the European Alps, Pyrenees and Carpathians ($n = 59$); High Asia, including the Qinghai-Tibetan Plateau, Tianshan, Hindu-Kush, Himalayan and Hengduan Shan mountains ($n = 101$); and Australia, including the Carnarvon Range, Macdonnell ranges and the Great Dividing Range ($n = 50$). We implemented separate analyses similar to the global model for those five regions.

Regression models and data transformations. We built a global as well as separate regional multiple (ordinary least squares; OLS) regression models with tetrapod species richness as the response variable and the eight climatic and geological variables as predictors (Table 1). The response variable (tetrapod species richness) was log-transformed in all statistical analyses. Additionally, the predictor variables precipitation, relief, long-term erosion rate and current erosion potential were log-transformed when needed to linearize relationships with the response variable, and to improve homoscedasticity. No additional second-order polynomials were then required to account for non-linear relationships. All predictor variables were scaled to a mean of zero and variance of 1 before the analysis to make model coefficients comparable. Residuals of models approximated a normal distribution.

We used an information-theoretic model selection based on the Akaike Information Criterion (AIC)^{98,99} with separate multi-predictor models for the global and the regional datasets, respectively. Before model selection, full multi-predictor models (that is, including all eight predictor variables) were examined for multi-collinearity using Variance Inflation Factors (VIF). Predictors with high VIFs (that is, VIF ≥ 10) were removed before model selection. Partial residual plots of each predictor variable were then examined to ensure homogeneity of variance. Using the step() function in the R software (<https://www.r-project.org/>), an AIC model selection was then performed to derive a minimum adequate model^{98,99}, both globally as well as separately for each region (that is, the best model, having the smallest number of predictor variables and retaining a high explanatory power). For these minimum adequate models, we report the standardized coefficients of each predictor to compare the relative importance of predictor variables in explaining tetrapod species richness. We note that in Fig. 2, the partial residual plots are plots of $r + b_i X_i$ versus X_i , where r is the ordinary residuals from the full multiple-predictor model, b_i is the regression coefficient of the i^{th} predictor variable from the same multiple-predictor model, and X_i the i^{th} predictor variable.

Spatial autocorrelation. We tested for the presence of spatial autocorrelation in the residuals of the multi-predictor OLS models because spatial autocorrelation could affect the interpretation of regression models¹⁰⁰. We used Moran's I values (calculated with the four nearest neighbours) to quantify residual spatial autocorrelation. Because Moran's I values were significant for the OLS model

residuals (Supplementary Tables 3 and 4), we implemented spatial simultaneous autoregressive (SAR) models to account for residual spatial autocorrelation¹⁰¹. SAR models provide OLS regression with a spatial-weights matrix that accounts for spatial autocorrelation in model residuals. We used a SAR model of the error type with a row-standardization for the spatial-weights matrix¹⁰¹. We defined the neighbourhood of the spatial-weights matrix with the four nearest neighbours. For the SAR models, we quantified the explained variance of the environmental predictors (R^2_{PRED}) and the total explained variance (R^2_{FULL}) of the full SAR models (including environmental predictors and the spatial weights matrix)¹⁰¹. This was done using pseudo- R^2 values, calculated as the squared Pearson correlation between predicted and true values¹⁰¹. We present the results from the OLS models in the main text, and the results from the SAR models and the Spearman rank correlation between species richness and predictor variables in the appendix (Supplementary Tables 4–5). All statistical analyses were done in RStudio version 0.99.902 (<https://www.rstudio.com/>).

Limitations of the analyses. Besides the general limitations in terms of present-day data availability, completeness and biases mentioned above, we acknowledge that many current species distributions have been affected by long-term human activities¹⁰². Unfortunately, reliable estimates of pre-human native ranges are lacking for most species. We also acknowledge that our analyses are correlative and that causality cannot be confidently established. We emphasize that spatial patterns and analyses of species richness vary with spatial scale¹⁰³ and encourage future studies at different spatial resolutions and extents, provided that appropriate biological and geological data allow meaningful analyses.

Code availability. All code used to generate the results presented here is available in the ZENODO repository <https://doi.org/10.5281/zenodo.1341999>.

Data availability

The datasets generated and analysed during the current study are available in the ZENODO repository <https://doi.org/10.5281/zenodo.1341999>.

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