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Why mountains matter for biodiversity

Abstract

Mountains are arguably Earth's most striking features. They play a major role in determining global and regional climates, are the source of most rivers, act as cradles, barriers and bridges for species, and are crucial for the survival and sustainability of many human societies. The complexity of mountains is tightly associated with high biodiversity, but the processes underlying this association are poorly known. Solving this puzzle requires researchers to generate more primary data, and better integrate available geological and climatic data into biological models of diversity and evolution. In this perspective, we highlight emerging insights, which stress the importance of mountain building through time as a generator and reservoir of biodiversity. We also discuss recently proposed parallels between surface uplift, habitat formation and species diversification. We exemplify these links and discuss other factors, such as Quaternary climatic variations, which may have obscured some mountain-building evidence due to erosion and other processes. Biological evolution is complex and the build-up of mountains is certainly not the only explanation, but biological and geological processes are probably more intertwined than many of us realize. The overall conclusion is that geology sets the stage for speciation, where ecological interactions, adaptive and non-adaptive radiations and stochastic processes act together to increase biodiversity. Further integration of these fields may yield novel and robust insights.

1 | INTRODUCTION

Mountains matter for biodiversity. And geology and climate matter for mountains. But how do we incorporate these two non-biology topics, geology and climate, into our study of mountain biodiversity? Humboldt embraced the idea of integrative scientific studies, observing biological processes as well as the surrounding climate and geology. But in the subsequent decades and centuries scientists moved away from identifying broadly as 'naturalists' into identifying as 'biologists', 'climatologists' and 'geologists'—each field with its own practices and dogma. It became increasingly uncommon to cross disciplines. This trend persists into the present decade: an analysis of nearly 100,000 peer-reviewed papers shows that interdisciplinarity in biodiversity research has plateaued or even decreased in the last ca. 20 years

(Craven et al., 2019). Still, single-discipline studies have resulted in a deeper understanding of the processes related to the formation of mountains, their climates and their biodiversity. It is now time to harness our detailed understanding of specific taxa and focused aspects of geological and climatic processes to integrate this knowledge across disciplines, for a better understanding of mountain biodiversity.

One of the defining features of Planet Earth is plate tectonics, a process that created both the highest mountains on land and the deepest troughs in the ocean. Because of this process continents have arrived in their present arrangement. Without plate tectonics our planet would be a largely static, flat, dull surface. This mechanism is thus a cornerstone in promoting the diversification of life on Earth (Dietrich & Perron, 2006; Lammer et al., 2010; Rahbek et al., 2019; Spohn & Breuer, 2016; Stern, 2016).

Tectonic patterns are clearly visible in the global terrestrial topography, which is formed by a combination of surface uplift, relief development, weathering and erosion. This relationship is a complex and long-lasting one, which geoscientists are still working to tease apart. The reconstruction of the topographical history of the world's largest mountain ranges has brought about significant insights, mainly through the advent of stable isotope palaeoaltimetry (Chamberlain & Poage, 2000; Mulch, 2016; Mulch & Chamberlain, 2018; Rowley & Garzione, 2007; Rowley, Pierrehumbert, & Currie, 2001). Available data indicate that some mountain systems, such as the Southern Alps in New Zealand and parts of the Andes in South America (Garzione et al., 2008; Mulch, 2016) and the Himalaya in Asia (see overview in Spicer, 2017), have uplifted quickly and relatively recently (in the past 15 Ma). Still other mountain systems show clear evidence for an older topography (e.g. European Alps; Campani, Mulch, Kempf, Schlunegger, & Mancktelow, 2012; North American Cordillera, Tibet; Chamberlain et al., 2012; Rowley & Currie, 2006).

The interaction between climate and mountains produces highly intricate environmental heterogeneity that ultimately leads to high species diversity (Figure 1; Körner, 2004). In this context the orientation of mountain ranges also plays a role, along with the topography (Elsen & Tingley, 2015). Mountain systems such as the Himalaya and Andes are positioned perpendicularly to atmospheric circulation patterns, creating complex climatic and biological patterns (Barthlott, Lauer, & Placke, 1996; Barthlott, Rafiqpoor, Kier, &

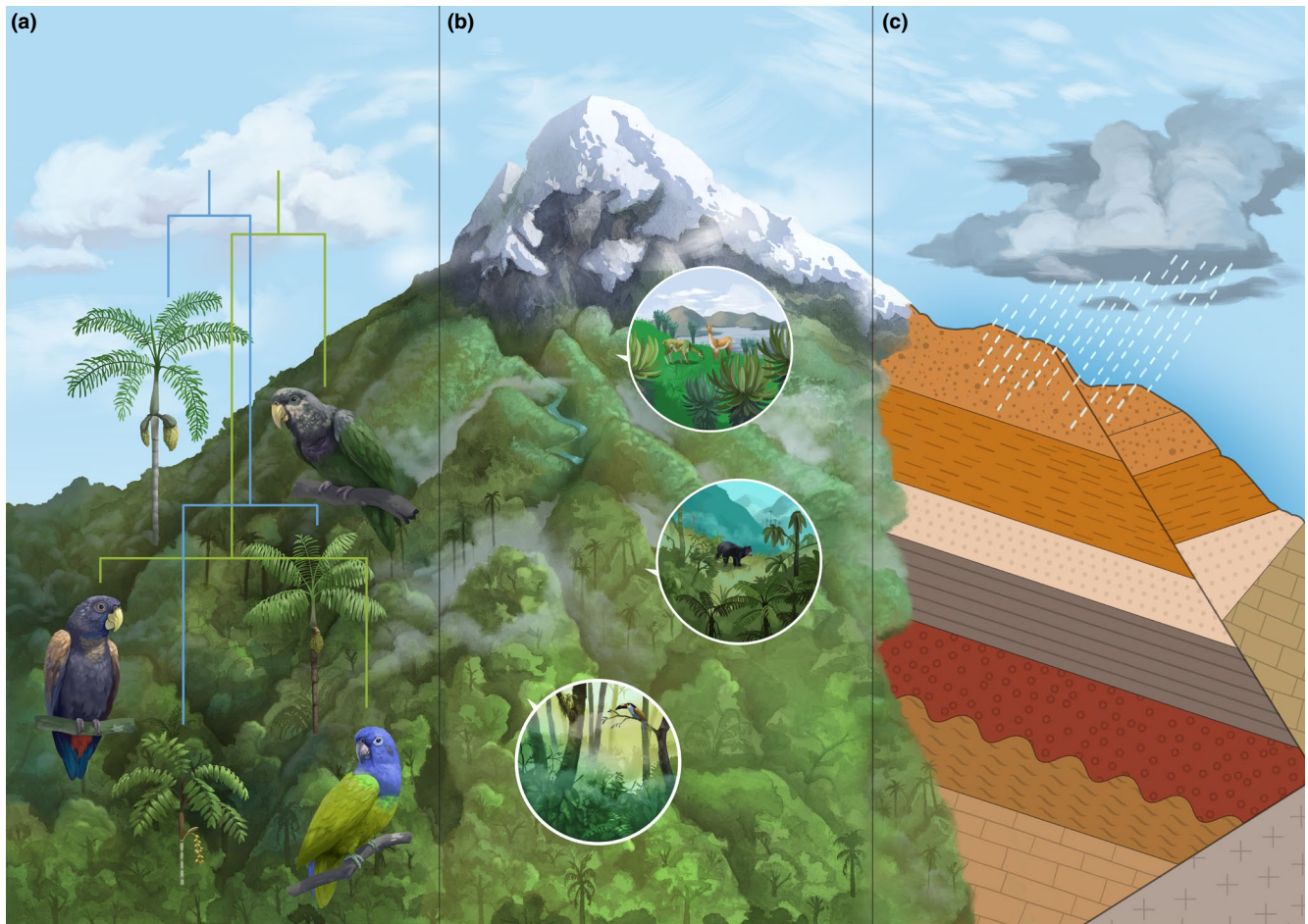


FIGURE 1 Schematic cross section of an imaginary tropical mountain. The drawing indicates (a) the biodiversity, including the phylogenetic relationships among species illustrating speciation through allopatry (for the parrots, which often have non-overlapping ranges) and edaphic adaptations (for the palms, often confined to particular soil types such as clay or sand). (b) The 'visible' biological and geological aspects of the mountain, including vegetational zonation, eroded landscapes and rocky outcrops, which often contribute to diversification and adaptive radiations by increasing biome shifts and promoting biotic interactions. And (c) the 'hidden' geological and climatic diversity and processes, including orogenic rain, weathering, soil formation, sedimentation, unconformities, a fold and thrust belt and fault lines. Illustration by Juan Felipe Martínez [Colour figure can be viewed at wileyonlinelibrary.com]

Kreft, 2005). While mountain building can change climate (Raymo & Ruddiman, 1992), climate can also influence mountain topography through, for example chemical weathering (Gabet, 2007) and post-glacial rebound (Thorson, 2000).

To unlock the mechanisms linking tectonics, climate and their relation to the evolution and distribution of biodiversity, we need to integrate our knowledge about the components in this process (Antonelli, Kissling, et al., 2018; Hoorn, Perrigo, & Antonelli, 2018). In the edited book *Mountains, Climate and Biodiversity* Hoorn et al. (2018) explore these components and their connections, and present case studies from selected mountain ranges around the world. Strong relationships among these three factors emerge consistently. Here we outline some of the aspects of these interdisciplinary findings that we consider most relevant for biogeographers, and reflect on their relevance to the future of interdisciplinary research on mountain biodiversity.

2 | WHY ARE THERE SO MANY SPECIES ON MOUNTAINS?

In evolutionary terms, speciation can be described through simple mechanisms, such as natural selection and genetic drift. On mountaintops especially, gene-flow and reproductive isolation play key roles, whereas mechanisms such as hybridization and polyploidization can also lead to speciation. In spatial terms, speciation may be allopatric, peripatric, parapatric or sympatric. Mountains play a role in promoting the isolation of populations, but the emergence of mountains is not the only way by which species diverge, and probably not the predominant one. We argue that the role mountains play in influencing biodiversity is multi-faceted, far-reaching and often indirect. Below we discuss some of the ways that mountains are involved in generating biodiversity.



2.1 | Mountains as cradles

Mountains can be safely called cradles of diversity. Most notably, there are many documented cases of adaptive radiation at high elevations. This occurs when species diversifications associated with the evolution of a particular morphological, physiological or behavioural trait allow the species to better exploit montane niches in 'island-like' environments (Hughes & Atchison, 2015). For instance Givnish et al. (2009) showed how an early shift of fruit type from dry capsules (wind-dispersed) to fleshy berries (bird-dispersed) facilitated Hawaiian lobelioids (Campanulaceae) to colonize new forest habitats in the islands' montane landscapes, leading to rapid speciation in the group. In the same plant family, the complex interactions among surface uplift, pollinator shifts, geography and morphology were linked to explain the massive pulse of diversification among Andean taxa (Hughes, 2016; Lagomarsino, Condamine, Antonelli, Mulch, & Davis, 2016). Likewise, in Neotropical *Phlegmariurus* (Lycopodiaceae) uplift and range expansion were positively correlated with diversification rates (Testo, Sessa, & Barrington, 2019). In the diverse plant family Ericaceae, multiple mountain radiations have been documented that closely follow the formation of novel mountain habitats (Schwery et al., 2015). Surface uplift is also associated with the diversification of several plant taxa in the Hengduan Mountains (Xing & Ree, 2017). In addition to adaptive radiations, non-adaptive processes (such as geographical isolation) probably play an important role in generating mountain biodiversity (Rundell & Price, 2009).

The diversity generated on a mountain does not only remain there. Several biogeographical studies have shown that mountain-derived lineages can colonize other regions, sometimes very far apart, as well as neighbouring lowlands. This has been suggested from several mountain systems, including the Andes (Antonelli, Nylander, Persson, & Sanmartín, 2009; Santos et al., 2009), Mt. Kinabalu on Borneo (Merckx et al., 2015) and across the African continent (Gehrke & Linder, 2009). Mountains are therefore engines of diversity for entire biotic realms (Antonelli & Sanmartín, 2011; Antonelli, Zizka, et al., 2018; Gentry, 1982; Rahbek et al., 2019).

One question that remains is when, or whether, mountains can become saturated with diversity. In the Himalaya, it has been suggested that the diversification rate of songbirds slowed as ecological niches were filled (Price et al., 2014). One potential explanation is that highland habitats usually have a drastically smaller total area than lowland habitats, although this is not always the case (Elsen & Tingley, 2015). Globally, species richness of birds and plants appears to be lowest at the highest elevations (Kessler, Herzog, Fjeldså, & Bach, 2001; McCain, 2009; Quintero & Jetz, 2018).

2.2 | Mountains as bridges and barriers

For many biogeographers, mountains are regarded for their role as barriers or bridges of species dispersal. Which of these roles mountains play depends on the ecological and physiological requirements of the species, as well as their dispersal ability.

The role of mountains as bridges (corridors) is clear from the widespread distribution of Northern Hemisphere taxa in Southern Hemisphere mountains, such as the European-centred plant genera *Carex* and *Ranunculus*, as well as the genus *Alchemilla* in Africa (Gehrke & Linder, 2009), and from Southern Hemisphere taxa that spread northwards following montane habitats, such as *Gunnera* (Bacon et al., 2018). Interestingly, these taxa are more adapted to a certain environment—temperate—rather than to mountains per se. Thus, they often occur at low elevations in high latitudes, and at high elevations in low latitudes, tracking their optimal conditions (Bacon et al., 2018).

Mountains acting as barriers can be seen in Amazonian freshwater fishes, where the separation of populations is congruent with the uplift of the Eastern Cordillera (Andes) (Lundberg et al., 1998). However, not all lowland species are genetically restricted by elevation barriers. Even in the Andes, forest-dwelling lowland orchids have been able to disperse between high-altitude localities multiple times over the course of their evolution, probably due to the numerous and tiny seeds they produce (Pérez-Escobar, Chomicki, Condamine, Karremans, et al., 2017).

2.3 | Mountains as reservoirs

Mountains have the potential to act as refugia for biodiversity through time. This is especially true during periods of rapid climate change, because species need to move shorter distances along a mountain gradient to find their optimal niches, as compared to lowlands (Chen, Hill, Ohlemüller, Roy, & Thomas, 2011; Sandel et al., 2011). However, mountain taxa located on islands may be susceptible to different risks. Island flora and fauna have fewer possibilities for survival when catastrophic events do occur, despite habitat heterogeneity (Taylor & Kumar, 2016; Whittaker, 1995). Islands may also serve as refugia during periods of climatic change, as in the case of conifers in New Caledonia, which originally derived from the Australian mainland (Condamine, Leslie, & Antonelli, 2017). Likewise, during ice ages local populations may persist on nunataks (exposed peaks otherwise surrounded by a glacier or snow), recolonizing downhill when the surrounding environment subsequently warms (Flantua & Hooghiemstra, 2018; Flantua et al., 2014; Flantua, O'Dea, Onstein, Giraldo, & Hooghiemstra, 2019; Parducci et al., 2012).

In the Anthropocene, mountains may play an even more important role as biodiversity reservoirs. In many regions, there is disproportionate protection of montane areas relative to lowlands (Rouget, Richardson, & Cowling, 2003). Alas, this is less due to the recognition of mountains as important centres of diversity, and rather to the historical difficulties in using steep slopes for timber extraction, agriculture or urbanization. The biodiversity of these same areas has been disproportionately spared from human influence for many of the same reasons (Sandel & Svenning, 2013). Other non-biological reasons for mountain protection include scenic qualities and their role in water provision (Hamilton & McMillan, 2004). As the human population continues to increase worldwide,

it seems given that the protection of mountains and their biodiversity will be more important than ever in order to preserve these functions that are beneficial to humans, as well as their biodiversity (Wilson, 2016).

3 | EMERGING METHODOLOGIES

3.1 | Relating mountain uplift to species diversification

A long-standing hurdle in biogeography has been the correlative nature of analyses. Is congruence in time and space sufficient to derive causation? Probably not. Instead, we need explicit statistical frameworks for inferring and testing biogeographical processes, while incorporating the complexity of natural processes. After all, mountain building happens concurrently with environmental, climatic and biotic pressure changes.

One possible solution is the use of mechanistic models, which simulate biological processes. These allow researchers to test how well variables such as species richness, diversification and dispersal can be explained by simple parameters, such as habitat changes (Connolly, Hughes, & Bellwood, 2017; Descombes et al., 2018). However, the assumptions in those models are often simplistic and may not necessarily demonstrate causality (McGill & Potochnik, 2018). When robust models are developed, they allow the comparison between simulated and empirical biodiversity patterns and the identification of regions containing fewer or more species than expected (Rangel et al., 2018).

An approach that can build on these mechanistic models is to fit them to empirical data and estimate the influence of particular variables on biogeographical processes, for example using maximum likelihood (Condamine, Rolland, & Morlon, 2013) and Bayesian (Silvestro & Schnitzler, 2018) frameworks. The application of such methods shows that for several montane Andean plant taxa, surface uplift is associated with increased speciation (Pérez-Escobar, Chomicki, Condamine, de Vos, et al., 2017), but that this effect is strengthened by several biotic and abiotic variables such as pollination type, temperature changes and fruit type (Lagomarsino et al., 2016). However, the effect of surface uplift is probably taxon dependent. For Andean hummingbirds, for instance, surface uplift is still correlated with speciation rates, but has a negative effect—meaning that as mountains rose, speciation decreased (Condamine, Antonelli, Lagomarsino, Hoorn, & Liow, 2018).

The evolution of freshwater fishes in New Zealand further illustrates the close relationship between mountain building and biotic evolution (Craw, Upton, BurrIDGE, Wallis, & Waters, 2015). In this geologically active region, environmental and ecological elements can often act as confounding factors. However, numerical modelling shows a relationship between tectonic zones and drainage patterns. A clear correlation between landscape evolution and fish diversification is apparent, with uplift leading to the separation of fish populations in the rivers.

3.2 | Measuring the timing of mountain formation

Do evolutionary processes coincide with mountains uplift? When considering that uplift is counteracted by erosion (Antonelli, Kissling, et al., 2018; Molnar, 2018), mountains typically rise at about 1 mm/year (Graham, Parra, Mora, & Higuera, 2018), with extreme rates reported for Timor (c. 5 mm/year; Nguyen, Duffy, Shulmeister, & Quigley, 2013). But even though these rates sound slow from a human perspective, on a geological scale these processes can have a major impact on mountain taxa. Determining when and how fast mountains rise is therefore of crucial importance for testing evolutionary hypotheses.

Several methodologies can be used to understand mountain uplift through time. Unfortunately, these may seem complex and inaccessible to biogeographers. We have summarized many of the major methodologies in use today in Table 1. Understanding the terminology, area of use and applications of these methods may provide a starting point for biogeographers interested in employing this valuable information in their own work.

There are various ways to reconstruct the geological history of an area. The most suitable method for a study is dependent on the timescale in question, as well as the topographical information needed. Mountain uplift can indirectly be quantified through thermochronology, which consists of measuring the exhumation and cooling age of rocks. Although this methodology provides an age framework to mountain building (Reiners & Brandon, 2006) it does not give a palaeoaltitudinal range. In this sense, stable isotope-, botanical- and biomarker-based palaeoaltimetry are perhaps among the most valuable techniques in the geologist's toolbox (Table 1). They can be used to reconstruct past elevations and thus to trace the evolution of both mountains and taxa over time. The results of these analyses can be directly applied to historical biogeographical studies in mountain regions (Lagomarsino et al., 2016; Mulch, 2016; Rohrmann et al., 2016; Spicer, 2017).

In addition to palaeoaltimetry, new methods in quantifying denudation histories (the removal of the top layer of Earth's surface by both biotic and abiotic processes) also contribute to our understanding of the genesis of mountain ranges. Cosmogenic radionuclide analysis (Table 1), in combination with thermochronology and palaeoaltimetry, has vastly improved models on global mountain building. In these models, Quaternary climate change—after or parallel to mountain building—was responsible for large changes in relief and denudation, followed by intense biological diversification (Antonelli, Kissling, et al., 2018). Examples of this are young mountain systems such as the Andes, the Himalaya and the Hengduan Mountains (Favre et al., 2015; Madriñán, Cortés, & Richardson, 2013; Spicer, 2017; Su et al., 2019; Xing & Ree, 2017).

With this toolbox (Table 1), we have the possibility for a much better (albeit spatially biased) understanding of when high surfaces were established around the world's mountain systems. These methods can be readily integrated into biogeographical studies to improve models of biodiversity over time.

**TABLE 1** A toolbox of geological methodologies for biogeographers. Terminology of key concepts, their applications and key references to inspire researchers where to search if they require exhumation and palaeoaltitude data to inform biogeographical models

Method name	Variables provided	Age range	Selected references
Thermochronology: used to infer the timing and rates of geological processes. Relevance in biogeography: Identification of which regions have been geologically active, and when			
Low-Temperature Thermochronology	Rate and timing of exhumation; time-temperature paths that can be linked to the exhumation history, i.e. erosion	100–1,000 My	Bernet, Torres Acosta, and Bermúdez (2018); Reiners and Brandon (2006)
⁴ He/ ³ He–Helium Thermochronometry	Rate and timing of exhumation		Shuster and Farley (2004)
Optically stimulated luminescence (OSL) Thermochronometry	Rate and timing of exhumation	<500 Ky (perhaps up to 1,000 Ky)	Herman, Rhodes, Braun, and Heiniger (2010); King, Herman, Lambert, Valla, and Guralnik (2016)
Cosmogenic nuclides	Past erosion rates, timing & relief formation (also relevant for soil formation and climatic models)	<15 My for ¹⁰ Be; <30 My ²⁶ Al; <100 My ²¹ Ne (erosion rate dependent)	Bernet et al. (2018)
Palaeoaltimetry: used to infer palaeoaltitudes, dates and rate. Relevance in biogeography: Provides metrics for analyses of correlates of diversification and diversity patterns			
Stable isotope-based palaeoaltimetry (D, O)	Precipitation gradient		Mulch and Chamberlain (2018)
Clumped isotope thermometer	Past temperatures and palaeoaltitude in areas of high precipitation		Mulch and Chamberlain (2018)
Volcanic deposits-vesicular lavas	Palaeoaltitudes and palaeoatmospheric pressure		Sahagian and Maus (1994); Sahagian, Proussevitch, and Carlson (2002)
Hydrogen isotope palaeoaltimetry-biomarkers	Climate reconstruction & palaeoaltitudes		Mulch and Chamberlain (2018)
Palaeobotany, fossil leaves, Climate Leaf Analysis Multivariate Program (CLAMP)	Climate reconstruction & palaeoaltitudes	<150 My	Spicer (2018)
Palaeobotany, fossil leaves, stomatal density	Palaeoaltitudes	<150 My	Spicer (2018)
Palynology, sporomorph chemistry	Palaeoaltitudes, atmospheric changes, Ozone (O ₃) variations	c. 440 My	Spicer (2018)
Palynology, sporomorph nearest living relatives, Coexistence Approach (CA)	Climate reconstruction & palaeoaltitudes	Mesozoic-Cenozoic	Spicer (2018)
Palaeontological ecometrics	Climate and ecosystem reconstruction, precipitation		Polly et al. (2011)
Dynamic Topography: Provides information on changes in earth topography. Relevance in biogeography: Habitat evolution in mountains, freshwater biogeography in lowlands			Eakin and Lithgow-Bertelloni (2018)
Isostasy: Indicates uplift due to isostatic rebound after glaciations (Quaternary). Relevance in biogeography: Glacial-interglacial dynamics of diversification and secondary contact			Molnar (2018)

4 | CHALLENGES AND PROSPECTS

4.1 | Data

The study of biogeographical patterns and processes is probably more sensitive to the lack of data in mountain systems than in lowlands. This is because of the relatively large geographical and environmental heterogeneity of mountains. In areas of high relief, even small distances may confer dramatic changes in rainfall patterns, soil types and vegetation. Unfortunately, the spatial units in many biogeographical and macroecological studies—usually 1 degree,

which is equivalent to ca. 110 × 110 km at the Equator—may blur important signals in the underlying biodiversity data in mountains (Zizka & Antonelli, 2018). Reliable climatic data are equally crucial for biogeographical research, but suffer from similar problems in terms of resolution and observations. Popular sources of climatic data such as WorldClim (Fick & Hijmans, 2017) are based on the interpolation of relatively few weather stations, despite their global reach. There is also a major shortage of biologically relevant geological data, such as rates of surface uplift, bedrock age and erosion rates that extend beyond 12 Ma (Herman et al., 2013). Palaeoclimatic data can also be problematic as it often depends

largely on marine oxygen isotope records, which are not always an ideal proxy for terrestrial systems, although several alternatives to this are available (Abels & Ziegler, 2018). Palaeontological data are a promising source of information for reconstructing climatic variable and ecosystem metrics back in time as well (Polly et al., 2011), but the incompleteness of the fossil record and sampling biases continue to pose a major barrier for such methods to be widely employed (Benton, 2015).

Several initiatives are now attempting to address these issues. These include the increased recording of species, for instance through the use of monitored citizen science projects (Silvertown et al., 2015). This work complements—but does not replace—the collection of vouchered specimens (Rocha et al., 2014). Similarly, the use of remote sensing techniques (Véga, Renaud, Durrieu, & Bouvier, 2016) and global circulation models (Karger et al., 2017) are producing increasingly reliable, high-resolution climatic data, but still require proper ground truthing. Whenever suitable, biogeographical analyses may consider the use of variable grid sizes depending on data availability, or 'adaptive resolution' (Edler, Guedes, Zizka, Rosvall, & Antonelli, 2017).

To fill up key data gaps in the most efficient way, transdisciplinary synergy is crucial. This is particularly important during the early phases of project design, when decisions are made on which methodologies to use to address a particular question, which parameters to measure, and where to sample.

4.2 | Method overview

In general, we call for an increased appreciation and collaboration among empiricists and theoreticians. We need suitable methods to address exciting and complex biological questions, and new methods and theories need empirical applications for further validation and refinement.

In molecular phylogenetics, one challenge is to fully incorporate the information contained in genomic data for estimating when and where different lineages originated. The bottleneck at this point is often not to produce such data, but rather how to analyse matrices of hundreds or thousands of loci for as many species or populations under realistic phylogenetic models (Bravo et al., 2018). Advances in this area should considerably reduce the uncertainties in biogeographical analyses (such as divergence times and geographical range evolution), allowing a better investigation into the links between diversification and mountain formation.

Likewise, in geology, one of the main challenges is to incorporate the feedback mechanisms of plants onto soils, and surface processes into geomorphological models. To address this, an evolutionary geomorphological model in which vegetation dynamics forms the key mechanism in altering the earth surface has been proposed (Corenblit et al., 2011; Corenblit & Steiger, 2009). Plant roots and areal structures significantly modify the earth surface: the oldest record of this was observed in the Emsian, early Devonian, c. 393–408 Ma (Elick, Driese, & Mora, 1998). The effect of this over geological time is still to be unravelled. However, geologists have

asserted that the impact of the rise of plants on the planet relates to a significant rise in the volume of terrestrial mudrock, which is one of the most common sediment types on Earth, important in ocean chemistry and for its influence on climate (McMahon & Davies, 2018). In addition to plants, fish also modify Earth's surface, by (re)shaping the geomorphology of drainage basins (DeVries, 2012; Fremier, Yanites, & Yager, 2018). This suggests that biological processes play a major role in geomorphology that is insufficiently quantified.

4.3 | Mountains and mountain diversity—chicken or egg?

There is little question that mountains host a substantial proportion of the world's terrestrial species (Spehn, Rudmann-Maurer, & Körner, 2011). What is more debated, however, is what came first. Some of the research discussed above points to a simultaneous development of mountain landscapes with their inherent species. Under this scenario, mountain diversity could either be the result of in situ diversification following dispersal and range expansions from other areas (e.g. Antonelli, 2015; Huang, Meijers, Eyres, Mulch, & Fritz, 2019; Merckx et al., 2015) or, possibly, reflect the uplift of whole communities from the lowlands, which become subsequently adapted to the montane conditions (Heads, 2019; Hoorn et al., 2019).

Other studies, however, do not show a similar link—suggesting instead that the generation of mountain diversity is disconnected from uplift. For instance Smith et al. (2014) analysed a large amount of DNA sequence data from 28 Amazonian bird species, concluding that their population divergence largely post-dated the formation of major geographical features like the Andes and major Amazonian rivers. Similarly, Renner (2016) reviewed over a hundred papers suggesting a link between species diversification and the uplift of the Tibetan Plateau, concluding that many studies have referred to over-simplistic, or largely dismissed, geological scenarios. In most cases, diversification took place millions of years after mountain systems had been formed (but see also Mosbrugger, Favre, Muellner-Riehl, Päckert, & Mulch, 2018; Muellner-Riehl, 2019).

4.4 | Are we blinded by the ice ages?

Recent studies conclude that most montane radiations are relatively recent, many of them dating back to the Pleistocene (e.g. Hughes & Atchison, 2015; Madriñán et al., 2013). But we would like to postulate another possibility: that some mountains could have been biologically diverse already deep in the past, only to have their diversity largely decimated by the onset of ice ages at around 2.7 Ma. Given that Earth was essentially warm for tens of millions of years throughout the Cenozoic, we expect that many warm-adapted taxa would have suffered considerably from the onset of glaciations. If so, the lineages surviving such a 'cooling bottleneck' could have become more likely to withstand subsequent climatic fluctuations.



The biological importance of the putative first glaciation has been poorly studied, but may have been large, based on our fragmentary evidence from molecular phylogenies and the fossil record (Bacon et al., 2016; Silva, Antonelli, Lendel, Moraes, & Manfrin, 2018). We therefore propose that this is a plausible scenario that could have led to the recency of many extant mountain lineages, a hypothesis that should be further investigated and tested.

5 | CONCLUSIONS

In the spirit of the early naturalists, we need to integrate the studies of geology, earth sciences and biology, in particular biogeography, in order to untangle the complex history of life on Earth. This can potentially help us to improve future predictions. To achieve this, we must look beyond our own snake traps and Petri dishes to the overarching patterns. This requires cross-disciplinary collaboration that is not presently fostered by the divisive structure of many research institutions and funding programmes. Already from undergraduate studies, aspiring geologists and biologists struggle to understand each other's fields without access to appropriate-level reference texts. 'Mountains, Climate and Biodiversity' (Hoorn et al., 2018) was one contribution aimed to address this, and we hope that further studies will follow this integrative theme. Several initiatives are now in place that will support efforts such as these. For example the German Centre for Integrative Biodiversity Research's synthesis centre (sDiv) has open calls for researchers to bring together diverse teams to work on far-reaching questions (Winter, Hahn, Their-Lange, & Wirth, 2016). This opens the door for individual researchers to propose projects that incorporate the knowledge-bases of colleagues in various fields, in order to address big questions from new angles and ultimately find answers that no single discipline could have produced.

Looking forward, researchers should be encouraged to increase collaborations across disciplines, and endeavour to understand the basics in both methodology and terminology in disciplines outside our own. We argue that by tackling a question from different angles and incorporating interdisciplinary lines of research in joint research projects—from project design, to field work, analyses and interpretation of results—we can move research on mountain biodiversity forward with larger steps and higher impact than we have yet seen.

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DATA AVAILABILITY STATEMENT

Data sharing is not applicable to this article as no new data were created or analysed in this study.

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BIOSKETCHES

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